Self-domestication and Language Evolution

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Declaration

I hereby declare that this thesis is of my own composition, and that it contains no material previously submitted for the award of any other degree. The work reported in this thesis has been executed by myself, except where due acknowledgement is made in the text.

James Geoffrey Thomas

Dedication

To Barbara Scholz, much missed, who was wonderfully critical of my work and wonderfully uncritical of me.

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I thank my supervisors, Simon Kirby, Richard Shillcock and Barbara Scholz, for many years of sustained guidance, support and encouragement.

I would also like to thank all the members of the Language Evolution and Computation Research Unit, past and present, for providing a continuously supportive and stimulating intellectual environment. I have learned much from many of you, both in formal talks and casual conversations.

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Finally, none of this would have been possible, from undergraduate onwards, without the continuous support of my parents. It is not only the shoulders of giants on which we stand.

Abstract

This thesis addresses a major problem facing any attempt to account for language structure through a cultural mechanism: The processes required by such a mechanism are only possible if we assume the existence of a range of preconditions. These preconditions are not trivial, and themselves require an explanation. In this thesis I address the nature and origin of these preconditions.

I approach this topic in three stages. In the first stage, I pull-apart the functioning of one prominent cultural account of language evolution—the Iterated Learning Model—to identify the preconditions it assumes. These preconditions cluster into two main groups. The first concerns the *traditional transmission* of the communication system. The second relates to the emergence of particular skills of *social cognition* that make learned symbols and language-like communication a possibility.

In the second stage, I turn to comparative evidence, looking for evolutionary analogies that might shed light on the emergence of these preconditions. Two case studies—the Bengalese finch and the domestic dog—are considered in detail, both of which show aspects of one of the preconditions emerging in the context of *domestication*. In each case I examine what it is about the domestication process that led to this outcome.

In the final stage, I consider whether this same context might explain the emergence of these preconditions in humans. The claim that humans are a self-domesticated species has a long history, and is increasingly invoked in contemporary discussions of language evolution. However, it is often unclear exactly what this claim entails. I present a synthesis and critique of a range of empirical and theoretical perspectives on self-domestication. I conclude that human self-domestication is a coherent concept, and that there are several plausible accounts of how it might have occurred. The realisation that humans are a self-domesticated species can, therefore, provide some insight into how a cultural account of language structure might be possible at all.

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Introduction

Self-domestication and Language Evolution

This thesis is motivated by the conviction that two old ideas, both now enjoying something of a renaissance, have much to say to each other. The first of these ideas is that *language is the product of an evolutionary process*. The second is that *humans are a self-domesticated species*. The link to be explored between them concerns how the behavioural, cognitive and temperamental outcomes of self-domestication might have formed the preconditions for the emergence of structured language through a cultural process.

In making this link, the thesis informally divides into three sections. The first section focuses on one particular cultural account of language evolution, the Iterated Learning Model (ILM). This section aims to get really clear about how the ILM functions, both internally and in a wider evolutionary context. The purpose of this exercise is to make clear what it is that the ILM has to assume in order to work at all, what you might call its necessary *preconditions*. The second section presents a detailed exploration of two comparative case studies, which suggest that those preconditions might emerge in the evolutionary context of domestication. Finally, the third explores the idea that humans might be a self-domesticated species, thereby opening up the possibility that domestication might also account for the emergence of those preconditions in humans.

In this introduction, however, I want to say something briefly about each of the two ideas themselves. In the case of language evolution, I will attempt to situate this thesis in the wider context both of language itself—as the phenomenon requiring evolutionary explanation—and of other approaches to language evolution. I will then address the question of why *cultural* accounts of language evolution, such as work in the ILM, are particularly in need of the kind of approach adopted in this thesis. In the case of self-domestication, I focus on the lack of clarity surrounding the concept, together with how it might relate to the evolution of language.

I – Language evolution

It has been suggested that the evolution of language might be amongst the hardest problems in science (Christiansen & Kirby, 2003). Initially, this may seem somewhat hyperbolic. However, regardless of what one thinks of this suggestion, its twin rhetorical motivations are clear[1]. The first concerns the diversity of questions—and therefore disciplinary perspectives—that are inevitably drawn-in when thinking about language evolution (for a flavour of just how wide the disciplinary net needs to be cast see MacWhinney, 2005 and the contributions to Christiansen & Kirby, 2003). The second motivation concerns the nature of language itself, as revealed by work in linguistics (e.g. Jackendoff, 2002; O'Grady et al., 1997). The nature, that is, of the *language phenotype*—in all its phonological, syntactic, semantic and pragmatic complexity—that stands in need of evolutionary explanation in the first place. No single work can ever hope to address everything that falls under the rubric of 'language evolution'. It will be useful, therefore, to say something about the scope of the present thesis.

i. The scope of the thesis

As noted above, the focus of this thesis is on one particular account of the emergence of language structure, the ILM, and how the effects of domestication might account for its necessary preconditions. I present a lengthy discussion of the ILM in chapter one. For now, however, it will be sufficient to say that work in the ILM explores how aspects of language structure can be seen to emerge as a result of language itself adapting to the circumstances of its transmission. This kind of approach has been successfully applied to a range of linguistic phenomenon. These include the emergence of compositionality (Kirby, 2002; Brighton et al., 2005; Kirby et al., 2008); regularity and irregularity (Kirby, 2002); recursive syntax (Kirby, 2002); subjacency (Christiansen et al., 2002); the emergence of arbitrary signals (Theisen et

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[1] Indeed, it is in just this kind of rhetorical spirit that I take the original suggestion to have been made.

al., 2010) and discrete phonological units (Oudeyer, 2005, 2006); and even duality of patterning (Roberts & Galantucci, 2012).

This is by no means an insignificant list of linguistic phenomena. However, we should not be misled into thinking that this even begins to cover the full scope of the complexity of the language phenotype. Indeed, this can be seen even if we restrict ourselves solely to aspects of language structure. For example, the iterated learning approach currently has no compelling account of the emergence of the contentive-functional split (Kirby, 2013). The spilt, that is, between contentful or *open-class* words—such as 'dog', 'run' and 'green'—the meaning of which can stand independently of more complex, sentence-like constructions; and functional or *closed-class* words—such as 'the', 'to' and 'if'—the meaning of which is tightly bound to the grammatical role they play in those complex constructions (Lyons, 1995).

Many of the intricacies of syntax[2] are also not directly addressed by this approach. For example, it provides no account of the rule-like nature of *movement* in language, such as in the formation of questions. Work in iterated learning currently offers us, therefore, no explanation as to why forming the question in (2) is grammatical, but the question in (4) is not:

(1) John likes Sally
(2) Who$_i$ does John like t_i?

(3) John is unhappy when Sally hits Molly
(4) *Who$_i$ is John unhappy when Sally hits t_i?

Finally, although the iterated approach does address some aspects of phonology, it provides no real account of the hierarchical nature of phonological structure above the level of the individual segment. This includes the division of syllables into *onset*

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[2] See Bickerton (2003) and (2007) for a forceful presentation of how many of these intricacies are often overlooked in discussions of language evolution, especially by non-linguists. In addition, Pinker and Jackendoff (2005) present a useful, evolutionarily oriented, overview of the major classes of syntactic phenomena.

and *rhyme* (with the latter further subdivided into a *nucleus* and a *coda*) but also the grouping of syllables into metrical patterns, and the relationships between the two levels, such as syllables with heavy rhymes 'wanting' to be associated with heavy metrical stress (Jackendoff, 2003)[3].

Moving beyond purely structural considerations, an even larger range of questions can be discerned, reflective of the deeply interdisciplinary nature of language evolution research, about which work in the ILM has little to say. Some of these are physical in nature; for example, the necessary changes to the brain (e.g. Deacon, 1997) and to the structure of the vocal tract (e.g. Lieberman, 1968; Fitch, 2002). Others are related to aspects of cognition, such as the nature of reference and meaning in language (Jackendoff, 2002) and its evolution (Hurford, 2007). Others still, concern the social environment in which a language-like system might likely evolve (e.g. Dunbar, 1995).

ii. Approaches to language evolution

The complexity evident in the language phenotype has lead, quite naturally, to a wide variety of perspectives not only on how language might have evolved but also on how best to characterise language itself. The differences between these perspectives can be seen, at least in part, as a reflection of the different aspects of the language phenotype upon which they have been mainly focused. In this section I will briefly discuss some of these perspectives, as part of the necessary background for a more specific comparison of cultural and biological approaches to language evolution.

One particularly prominent view, primarily associated with the work of Noam Chomsky (e.g. 1968, 1988, 2005), characterises language in extremely abstract terms. The details of this conception have varied over the years. In earlier forms, this view emphasised the role of a Universal Grammar: a set of grammatical *principles* underlying all languages, whose *parameters*—the specifics of a particular

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[3] It should be noted that much of this analysis also applies to sign languages.

language—were set during developmental experience (e.g. Chomsky, 1968). In more recent revisions, the emphasis has shifted to the role played by a small number of computational routines, such as Merge (e.g. Chomsky, 2005). What has remained constant, however, is the close identification of 'language' with the complex, generative, rule-like regularities of *syntax*, with other features, including various motor, cognitive and articulatory capabilities, regarded as somewhat peripheral (see Hauser et al., 2002 for a wider discussion).

While evolutionary considerations have never been central to Chomsky's own work, many others have approached the topic of language evolution with a similarly abstract and syntactic conceptualisation of language. For some, the complex, seemingly arbitrary, rule-like systems of syntax totally defy any attempt at an adaptive evolutionary explanation (e.g. Piattelli-Palmarini, 1989). How, for example, might subjacency possibly be *adaptive* for our primate ancestors? How, in other words, might arbitrary structural rules have any impact on differential reproductive success? This is the view of much of the emerging field of biolinguistics (Di Sciullo & Boeckx, 2011), in which the origins of syntax are sought not in adaptive evolution, but in its emergence from the fundamental regularities of physics and mathematics (e.g. Uriagereka, 1998)[4]. Others, however, have taken the Chomskyian abstract-syntactic conception of language and attempted to construct an adaptive account of its emergence (e.g. Pinker & Bloom, 1990; Pinker, 2003). On this position, then, the rule-like regularities of Universal Grammar are encoded in the genome, and have been gradually accumulated over evolutionary time as part of a much wider complex adaptation for communication (Pinker & Jackendoff, 2005)[5].

The close identification of language with *rule-like syntax* central to the approaches discussed above is not, however, universally accepted. Some, for example, have argued that the key innovation in language is not syntactic structure but the crossing of a 'symbolic threshold[6]' (e.g. Deacon, 1997), and that many aspects of syntactic

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[4] See chapter one, section **1.4.5.2**, for further discussion of this perspective.

[5] See chapter one, section **1.2.2**, for further discussion.

[6] That is, the emergence of a system based on symbolic relationships between sign and signified, rather than indexical or iconic relationships, in the sense of Peirce (1931-1958).

structure actually fall out of the ‘semiotic constraints’ embodied in such a symbolic system (Deacon, 2003a). Others have focused on the cognitive dimension of language, particularly those capacities of social cognition that stand as prerequisites both for its evolutionary emergence (Tomasello, 1999, 2008) and its acquisition during development (Tomasello, 2003). From this perspective, then, the key innovation is not the structural or semantic properties of language itself, but the cognitive skills that allow us to utilise such a system for communicative purposes. Others still have taken a comparative approach, in which they attempt to break language down into a suite of component traits and look for parallels of those components in other species (e.g. Fitch, 2005, 2010). From this perspective, there is little reason to assume a single, unified adaptive account for all aspects of the language phenotype; rather, each component of the wider language faculty may have had very different origins.

One feature of language not emphasised by any of the perspectives discussed so far, but which is at the core of the ILM approach, is the fact that it is *culturally transmitted*. In recent years, a large body of work has emerged that places the fact of cultural transmission at the heart of understanding many aspects of the language phenotype (Kirby, 1999; Kirby & Hurford, 2002; Galantucci, 2005; Kirby et al., 2008; Swarup & Gasser, 2009; Theisen et al., 2010; Garrod et al., 2010; Fay et al., 2010; Scott-Phillips & Kirby, 2010; Roberts & Gallantuci, 2012; Verhoef et al., 2014). On this view, which includes all the work discussed above under the ILM, many aspects of the language phenotype can be related to facts about the way language is transmitted between generations of language users.

iii. Cultural and biological accounts

One dimension on which approaches to the evolution of language differ—a dimension that is of central importance to the present thesis—concerns the contrast between those explanations that point primarily to *biological* evolution (e.g. Pinker & Bloom, 1990), and those explanations that focus on *cultural* evolution (e.g. Kirby et al., 2008). The question of what primarily distinguishes these two kinds of accounts is interesting in itself[7]. As a first approximation, however, biological accounts posit that aspects of language structure are encoded in the genome, whereas cultural accounts suggest that structure emerges as a result of language itself adapting to the circumstances of its transmission. The general position adopted in this thesis is that cultural accounts have much to recommend them. However, biological accounts do have one significant advantage over their cultural rivals: the genetic mechanism they posit is, in evolutionary terms, *a given*. All known life is underpinned by genetic inheritance. If the mechanism responsible for delivering structured language consists solely in the encoding of that structure itself in the genome, then we face no further task in terms of accounting for the mechanism itself.

Cultural accounts, on the other hand, suggest that structure emerges as a result of a particular kind of iterated transmission, in which a communication system is not just learned but learned *from others*. This mechanism is *not* a given. Indeed the *very possibility* of this mechanism itself requires explanation. In the absence of such an explanation, cultural accounts fail to offer a complete alternative to biological accounts. Instead, they jump in 'half way through', assuming the possibility of a mechanism that itself needs explanation, and proceeding from there. Present cultural models of language evolution assume, in other words, the existence of certain preconditions. Once these preconditions are in place, the process of transmission can deliver structured language as described in the models. However, cultural accounts cannot constitute a full alternative to biological accounts until they are paired with an explanation of how such preconditions themselves are possible. Those working within this framework are clearly aware of this problem (e.g. Smith & Kirby, 2008), but it still needs to be addressed in a more systematic way.

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[7] For example, should they be distinguished by *whether* they invoke natural selection, or by their appeal to different *mechanisms* whereby natural selection influences the emergence of structured language? I will return to this question towards the end of chapter one.

II – Self-domestication

If domestication is to play an explanatory role in the human case, it is necessary to get clear about what 'self-domestication' might mean. However, this clarity is often absent in many discussions that invoke the concept of self-domestication. For example, consider the following quotation, from (Deacon, 2009: 750):

> We are in many ways a self-domesticated species. Would it be too humbling to see ourselves as a somewhat genetically degenerate, neurologically dedifferentiated ape?

Despite suggesting that humans are a self-domesticated species, Deacon provides no clear account of what this claim might mean. This is problematic for two major reasons. Firstly, one could be forgiven for thinking that the notion of *self*-domestication is inherently nonsensical. After all, doesn't domestication definitionally require a domesticat*or*? Isn't it, in other words, something done *by* one species *to* another species? If so, who is 'doing it' to humans? The question here, then, is whether the concept of self-domestication is one that can be talked about with any coherence at all.

Secondly, even if we assume that self-domestication is a coherent concept, we are still left with the question of *how* such a process could possibility have occurred. Domestication is often seen as the outcome of artificial selection and selective breeding. Yet who or what has been selectively breeding human beings? One possibility, is that humans have been practising something akin to selective breeding on themselves. Another is that domestication is a much more complicated and multi-faceted process than its equation with selective breeding would have us believe. We need also, then, to get clear about what 'domestication' itself means and how it works.

In the quotation above, Deacon likens domestication to a form of 'degeneracy'. As we shall see, there is much to recommend this view, with many of the typical outcomes of domestication reflecting the breakdown of previously adaptive structures and behaviours under conditions of relaxed selection. However, it will also become apparent that this only forms a partial account of how domestication functions.

Consider, also, the following quotation from Hare and Tomasello (2005: 443):

> ...one might seriously entertain the hypothesis that an important first step in the evolution of modern human societies was a kind of self-domestication (selection on systems controlling emotional reactivity) in which a human-like temperament was selected...

Again, while Hare and Tomasello talk about 'self-domestication' in general terms, they don't address in any detail the question of *how* this could possibly have occurred. Where Deacon related it to degeneracy, Hare and Tomasello seem to relate domestication to changes in systems governing emotional reactivity. This, too, is a view that has much to recommend it, as we shall see, particularly in chapter three. However, once again, there is reason to think that selection on emotional reactivity is also an insufficient characterisation of domestication, at least when considered in isolation.

One further question that arises in connection with both the quotations above, concerns the degree to which 'self-domestication' should be understood literally or figuratively. Should it be seen as a metaphor, as a concept that is useful tool for *thinking* about human evolution? Or, should it be seen much more literally, as a *description* of human evolution? In other words, are there merely some useful parallels to be drawn, or does it make sense to say that humans are *actually domesticated* in much the same way as cows, pigs, and dogs? At the very least, it would be useful to have some criteria by which this decision could be made.

III – Self-domestication and language evolution

Despite their lack of clarity about how it might occur, both Deacon (2009) and Hare and Tomasello (2005) explicitly link their discussion of self-domestication to the evolution of language. For Deacon, the key link concerns the breakdown—the *degeneration*—of previously constraining communicative biases. Deacon argues that the emergence of a complex, *learned* system of communication like language first requires the breakdown of biases that had previously prevented learning from having an influence on the communication system. For Hare and Tomasello, the key link is between selection on temperament and the emergence of a range of skills of social cognition. These cognitive skills, largely centred on the capacity and motivation to engage in co-operative, joint-attentional activities, are seen as vital because linguistic communication is itself just such an activity, involving the recognition of communicative intent and the inference of meaning against the backdrop of mutually shared knowledge (see chapter one **1.4.3** and **1.4.5**).

Each of these perspectives captures something important. It is clear, for example, that language is learned. It is also clear that linguistic communication is a process of co-operative inference. What is less clear, however, is how these two perspectives might link to the emergence of *language itself*. How they might link, that is, to the emergence of the highly structured system of signal-meaning associations which constitute language. The aim of this thesis is to explore the possibility that the ILM provides just such a link. Or, to re-frame the point more clearly, that the two consequences of self-domestication identified by the authors quoted above—an increased role for learning and the emergence of key socio-cognitive skills—together form the preconditions for a structured language to emerge via the process described by the ILM.

IV – Chapter plan

In **chapter one** I present a critical examination of the ILM, in an attempt to get clear about how it functions to produce a structured language. Based on this examination, I then consider the preconditions it would require to function in that manner. Two preconditions are identified: the importance of *traditional transmission* and the *sensitivity to communicative intent*.

In **chapter two** I present a detailed account of how the first of these preconditions—an increased role for traditional transmission—appeared in the Bengalese finch following domestication.

In **chapter three** I discuss the emergence of the second precondition—a sensitivity to communicative intent—in the domestic dog. In both cases I examine what it is about domestication that brought about these specific preconditions.

In **chapter four** I consider the general *coherence* of the claim that humans are a self-domesticated species. This involves an examination of the evolutionary processes and typical outcomes associated with domestication, together with a review of the concept of domestication itself.

In **chapter five** I try to make the concept of self-domestication more *concrete.* This involves the critical examination of three different accounts of how self-domestication might actually have occurred.

Finally, in **chapter six** I provide a summary and discussion of the argument as a whole, together with an exploration of some possible wider implications, some potential criticisms, and some ideas for future work.

Chapter 1

The Iterated Learning Model and its Preconditions

The overall aim of this thesis is to explore the possibility that the preconditions for a cultural account of language structure may have emerged in the context of self-domestication. In order to do this, however, it is first necessary to get a clear understanding of what those preconditions might be. In this first chapter, I present a detailed examination of one prominent cultural account of language structure, the Iterated Learning Model (ILM). This examination will have two main aims. The first is to explore how the ILM account of language structure works. This will require a clear understanding of the internal dynamics of the iterated cultural process itself. The second is to pinpoint the preconditions required for it to work in that manner. This will require situating the cultural process as a whole in a much wider evolutionary context. In order to fulfil these aims, however, it will be useful first to situate the ILM against the backdrop of some issues to which it can be seen as a response.

1.1 – Formalism, functionalism and the ILM

Historically, the question of language structure has been approached from two major perspectives, which, broadly speaking, can be labelled as *formalism* and *functionalism* (Newmeyer, 1991; Hawkins, 1988; Jackendoff, 2002). The formalist approach, most closely associated with the work of Noam Chomsky (e.g. 1968, 1988), views linguistic structure as reflecting a set of autonomous syntactic primitives, collectively referred to as Universal Grammar (UG) (Newmeyer, 1991). From this perspective, language has the structure it does because language learners come to the task of language acquisition with this set of primitives. In contrast, functionalist approaches relate language structure to language use. Functionalists view language structure as a reflection both of its communicative function and the processing, memory and general cognitive constraints of language users (Hawkins, 1990, 1999).

As we shall see, the ILM can be seen as a species of functionalism. Nevertheless, it is clearly distinguished from previous functionalist perspectives in terms of stressing the explanatory importance of *cultural transmission* in accounting for linguistic structure (e.g. Kirby, 1999; Kirby & Hurford, 2002). Central to this approach is the concept of iterated learning, which has been described as:

> ...a process in which an individual acquires a behaviour by observing a similar behaviour in another individual who acquired it in the same way
> (Kirby et al., 2008: 10681).

The ILM is an attempt to model this process. In particular, to examine how the nature of individual learners interacts with the circumstances of cultural transmission, and the population-level results of that interaction. As noted in the introduction, work within the ILM paradigm has examined a range of different linguistic phenomena. However, the property of language that has been most thoroughly explored using the ILM is *compositionality* (e.g. Kirby, 2002; Kirby et al., 2008). A language can be described as compositional when:

> ...the meaning of a signal is a function of the meaning of its parts and the way in which they are combined
> (Brighton et al., 2005: 222).

I shall discuss the nature of compositional structure and the ILM account of how such structure might have emerged in greater detail below. For now, however, it should be noted that the ILM can be seen as something of a reaction to a problematic aspect of many previous functionalist (and indeed formalist) accounts of language structure, the problem of linkage.

1.2 – Biological accounts and the linkage problem

1.2.1 – The linkage problem

One of the early motivations behind work on the ILM was the insight that the existing explanations of language structure, formalist and functionalist alike, both shared a common defect, which has been described as the *problem of linkage* (Kirby, 1999). Various discussions of the linkage problem have seemingly emphasised different factors, with some focusing on the link between form and function (e.g. Kirby, 1999) and others on the explanatory link between data sets (e.g. Kirby et al., 2004). This difference in emphasis reflects the fact that the problem actually occurs in *two* forms, which we might call the *special* and the *general* problems of linkage, respectively.

The *special* problem of linkage concerns the close fit shown by some language universals between their *form* and their *function*—that they *appear to be designed* with particular functions in mind, in ways that are adaptive for the language user (Kirby, 1999). More broadly, Hurford (2002) has argued that many aspects of language—from phonology to syntax—exhibit complex properties that make them well suited to the function of communication. In addressing this problem, formalist and functionalist approaches reveal complementary weaknesses. The formalist approach has an account of *how* universals emerge—as a reflection of the shared set of syntactic primitives—but fails to provide any account of *why* any such universal should so neatly dovetail with function. The functionalist approach, by contrast, explicitly relates language universals to function, but fails to explain how—fails to provide a *mechanism*—whereby a functional constraint might come to be embodied in a linguistic universal (Kirby, 1999).

The *general* problem of linkage concerns the question of how one set of data can serve as explanatory for another: put simply, is it sufficient to explain data set *A* by pointing to data set *B*? In its functionalist form this involves pointing to the context of use, processing constraints and other factors and citing them as explanatory of linguistic structure. In its formalist guise it involves pointing to the autonomous syntactic primitives and citing those as explanatory of linguistic structure. As Kirby et al. (2004) observe, however, both approaches do exactly the same thing: point to some feature of individuals—whether that be facts about processing and use or an autonomous Universal Grammar—and then declare that feature to be an explanation for an aspect of language structure. This is problematic because facts about language structure are abstract generalisations over data; whereas facts about processing constraints or innate autonomous syntax concern aspects of individual psychology. Neither the functionalist nor formalist approach provides a mechanism connecting these two data sets.

It should be clear, then, that the special problem is a subset of the general problem. To solve the general problem we only need to find a mechanism which relates facts about *A* (aspects of individual cognition) to facts about *B* (language structure). To solve the special problem we also need to show *why* this particular mechanism should produce language structure (*B*) that was *adaptive* from the perspective of language users (*A*). These two tasks, while related, are distinct. To be successful, therefore, explanations of linguistic structure need to address *both* forms of the linkage problem. I shall return to this point repeatedly below.

1.2.2 – Natural selection and the linkage problem

The issues raised by both forms of the linkage problem are not restricted to linguistics. Similar questions are also important in evolutionary biology. In biological terms, the special problem concerns how to explain the emergence of *adaptive complexity*—the close fit of form to function, or the appearance of design—

in many of the structural and behavioural traits of organisms. The accepted explanation for this in biology is *natural selection*. The general problem, in contrast, concerns how we might account for the presently observed pattern of relationships between organisms (data set *A*) and the environment (data set *B*). Natural selection is part of the explanation here, too, but any full account of this pattern needs to factor in other processes like genetic drift, and historical contingencies such as mass extinction events (Gould, 1996, 2002; Jablonski, 2005).

It is perhaps not surprising, then, that some might be tempted to draw on the resources of evolutionary biology in order to address the linkage problems in linguistics. Or, more precisely, that some might identify those linkage problems as the *same*. The now classic statement of this view was put forward by Pinker and Bloom (1990), who attempted to bring together the formalist account of autonomous syntax with the synthetic theory of evolution. Looked at from the perspective of the two linkage problems, Pinker and Bloom's proposal is not entirely successful, but its pattern of success and failure will be instructive when we come to discuss the ILM.

Pinker and Bloom argued that language, too, exhibits adaptive complexity, the appearance of design. They then went on to observe that only three explanations for the appearance of design have ever been proposed: (i) an extremely unlikely chance event; (ii) the existence of an actual designer; and (iii) the process of natural selection. Leaving the first two options to the gambler and the theologian, respectively, Pinker and Bloom concluded that the adaptive complexity of language was good evidence that it was the product of natural selection.

In addition, however, Pinker and Bloom also identified the evolutionary *function* that they believed this adaptive complexity to be fulfilling. Language, they argued, represents a cognitive adaptation for *communication*, in particular the communication of propositional utterances through a serial channel. In identifying this function, Pinker and Bloom tacitly adopted the *code model* of linguistic communication. As we shall see (**1.4.5.3**), taking this of this view of communication has serious consequences for our thinking about language evolution. For now, however, it is enough to note that in identifying code-like communication as the relevant evolutionary function, Pinker and Bloom also had to adopt a particular view about *what* was being selected. This view is well illustrated by the following quotation:

> Every *detail of grammatical competence* that we wish to ascribe to selection must have conferred a reproductive advantage on its speakers, and this advantage must be large enough to have become fixed in the ancestral population (Pinker & Bloom, 1990: 721, my emphasis).

As this quotation makes clear, Pinker and Bloom were arguing that the *specifics* of language structure—the "detail[s] of grammatical competence"—must themselves be under selection. This follows from the adoption of the code model, because code-like communication is heavily dependent on all involved sharing the same set of encodings (Origgi & Sperber, 2000; **1.4.5.3**), making it natural to assume that an evolved system of coded communication would require selection to act on the production and maintenance of the code itself.

Pinker and Bloom's argument, then, can be summarised in the following three points:

(1) Language exhibits adaptive complexity, the appearance of design in order to fulfil some function. Therefore language structure is the result of natural selection, the only natural process able to account for that appearance of design.

(2) The function in question is the "communication of propositional structures over a serial channel" (p. 712).

(3) The *specific details* of language structure have themselves been under selection and are encoded in the genome.

In point (1) they identify the *fact* of adaptive complexity, and thus invoke natural selection. In point (2) they pinpoint the exact function that complexity is adapted to perform, propositional communication over a serial channel. Finally, in point (3) they identify *what* was under selection: variation encoding the specific details of language structure. There are, then, multiple ways in which Pinker and Bloom might be wrong.

Regarding point (1), they might be wrong that language exhibits adaptive complexity at all, although this would seem a hard argument to make. Alternatively, they might be right about that adaptive complexity, but wrong to invoke natural selection in order to explain it. To argue in this vein would require proposing an alternative to natural selection as a solution for the special problem of linkage. Regarding point (2), they might have incorrectly identified the relevant function. This misidentification might be total, such that communication was not the relevant function at all (e.g. Bickerton, 1990). Such claims are, however, unconvincing on a number of grounds (Hurford, 2002, 2007). Alternatively, they might be correct in pointing to communication, but wrong to characterise that communication in terms of the serial transfer of propositional utterances (Sperber, 1990; Scott-Phillips, 2010). Finally, as point (3) follows closely from point (2), if they were found to have misidentified the function, they would likely be wrong regarding what was being selected.

So how does Pinker and Bloom's proposal fare as a solution to the two linkage problems? Regarding the special problem they do rather well. By linking the formalist syntactic primitives to the theory of evolution by natural selection, they provided a principled explanation of why formalist syntactic primitives should exhibit the appearance of design. Regarding the general problem, Pinker and Bloom's position essentially represents a denial of its existence. For them, language is a cognitive trait underpinned by a genetically encoded UG. The languages we see in the world are merely a reflection of this evolutionary adaptation for communication. Although they do not say so explicitly, Pinker and Bloom's argument entails the assumption of an *isomorphism* between the properties of individuals (UG) and the pattern of languages we see in the world.

On Pinker and Bloom's own terms, this position is entirely coherent: if language is a biologically evolved trait of the type they suggest, then this isomorphism is what we should expect. However, this position has two further implications. The first is that it should be possible to 'read off' the properties of language(s) from the properties of individuals. The second is that there should be a large range of strong universals across the world's languages, as the UG which they reflect is an adaptation shared by the whole human species. Both these implications can be increasingly seen as problematic. The direct link between cognition and language has been called into question by recent work showing that cultural transmission—which is uncontroversially how languages are passed on—can have a strong mediating influence on the resulting language structure (Smith & Kirby, 2008; Smith, 2010). In addition, the very existence of the kind of universals that would be expected under Pinker and Bloom's analysis is being called into question (e.g. Evans & Levinson, 2009; Dunn et al., 2011). As a result, Pinker and Bloom's assumption of isomorphism, and thus denial of the general problem of linkage, has become increasingly difficult to accept.

It is useful to note that what works about Pinker and Bloom's proposal derives from their point (1): by appealing to natural selection they are able to provide a principled account of why form and function should match, thus solving the special problem. By contrast, what doesn't work derives from their points (2) and (3): the emerging picture of what language *is* appears inconsistent with it being the kind of adaptation envisaged by Pinker and Bloom.

In sections **1.3** and **1.4** I will undertake detailed examination of the ILM and its necessary preconditions. One outcome of that discussion will be to totally reject Pinker and Bloom's point (3): the specific details of language structure do not need to be encoded in the genome because they emerge as a result of language adapting to the circumstances of its transmission. It will also be argued that in point (2) they mischaracterised the nature of linguistic communication, and therefore misidentified the relevant evolutionary function of language. Point (1), however, will emerge supported: natural selection does indeed play an important role in accounting for language structure, although not at all in the way Pinker and Bloom envisaged. In short, while they were right to invoke natural selection, they mischaracterised the function of language to which it related, and as a result were wrong about *what* was being selected.

Before turning to the ILM, however, it will help us to consider one more background issue, which will serve a vital role in getting clear where Pinker and Bloom went wrong.

1.2.3 – Extra-biological regularities in evolution

One important characteristic of Pinker and Bloom's point (3) is its focus on natural selection acting to encode the *specific details* of a trait—language structure—into the genome. There is no reason, however, to assume that natural selection must always operate in this way. This is particularly true where evolution is able to exploit the extra-biological regularities of other systems, such as the laws of physics or mathematics (Kauffman, 1993; Goodwin, 1994; Stewart, 1998). Consider the following example. Stewart (1998) describes the embryological development of the frog, which exploits physical regularities relating to symmetry and shape. Briefly, by the *blastula* stage the developing embryo is a symmetrical, spherical mass of about one thousand cells. During the next stage of development—stomach formation or *gastrulation*—one area of the surface collapses in on itself, and breaks the symmetry of the thus-far symmetrical embryo. What Stewart highlights, however, is that the *manner* in which this symmetry breaks need not be genetically encoded, because it is the same way that the symmetry of all spherical objects—ping pong balls as well as frog embryos—tends to break when subjected to certain pressures. Frog embryological development simply exploits this pre-existing regularity.

It is worth comparing Stewart's account with one cast in the mould of Pinker and Bloom's view of language. This alternative would first cite the adaptive complexity of the symmetry breaking as evidence that it arose through natural selection. It would then go on to argue that the *specific details* of how the symmetry breaks must itself be encoded in the genome. It should be clear that this second point need not necessarily follow from the first. In other words, even with something as delicate and vital as early embryological development there is not necessarily a warrant to assume that every feature of the process is encoded in the genome. Crucially, however, this does *not* imply that natural selection has nothing to do with the process of symmetry breaking. The manner in which the symmetry breaks need not be genetically encoded, because it arises from a system of extra-biological regularities; but it *is* the result of natural selection, because what has been selected is the *capacity to exploit those regularities*.

This last point is well illustrated by the mechanics of human bipedal locomotion. The raising of the leg in the up-step requires a system of muscular and neural control that has clearly been honed by natural selection. In contrast, the down-step simply exploits the extra-biological regularity of gravity (McGeer, 1990). Indeed, once the forward motion of walking has been established the interplay between two physical factors—the potential energy of gravity and the kinetic energy of forward motion—results in less additional energy being required for each successive step (Capaday, 2002). Bipedal locomotion exploits, therefore, a range of extra-biological regularities. However, the gravity-exploiting down-step is as much a product of natural selection as the bodily-powered up-step, because selection has put in place a system capable of exploiting this gravitational regularity.

Frog embryology, bipedal locomotion and language structure are clearly very different cases, but the insights from the first two might well illuminate the third. In particular, and to anticipate somewhat the later discussion, if the ILM were to be seen as describing and exploring a system of extra-biological, *informational* regularities—potentially exploitable by natural selection—then this might provide grounds for questioning Pinker and Bloom's point (3). Rather than acting directly on the specifics of language structure, natural selection could instead have put in place the capacity to exploit those informational regularities.

1.3 – Cultural accounts and the linkage problem

The last section examined the strengths and weaknesses of one prominent biological account of language structure, particularly as regards its success in addressing the two problems of linkage. In this section I will ask much the same questions of the ILM approach to language structure, with a view to getting clear about how this particular cultural account actually works. We can then begin to ask what kind of preconditions might be required for an account of this kind to be possible in the first place.

To really uncover how the ILM operates, it is necessary to ask the following two questions, each of which represents one of the two linkage problems cast in terms specifically for the ILM.

1. **What are the processes and pressures involved in the ILM account of language structure?**

This first question requires an examination of how the ILM works internally. In particular, it requires an account of how the balance between various pressures on the language can cause structure to emerge through an iterated cultural process. This question is a form of the general problem of linkage, because it concerns the details of the mechanism linking facts about learners (data set *A*) to facts about languages (data set *B*). Many discussions of the ILM (e.g. Kirby et al., 2008), concerned as they are with the internal details of the cultural system, remain firmly focused on this first question. For the purposes of this thesis, however, the answer to this question, whatever it might be, immediately raises a second one.

2. **Why does the ILM involve *those* particular processes and pressures and not other ones?**

This question concerns the *origin* of the pressures identified in answer to the first question. If language structure is the result of language itself adapting to certain pressures, then we are owed an account of why it is *those* pressures in particular to which language has to adapt. This is particularly pressing if the outcome of the process is also adaptive from the perspective of language users. As such, this represents a particular instance of the special problem of linkage. If the mechanism linking *A* and *B* also produces an outcome that is *adaptive* for *A*, what is it about that mechanism that explains this, and how did it get there?

In the following sections, these two questions will be addressed through a critical comparison of two instantiations of the ILM, one computational and one experimental.

1.3.1 – Iterated learning I: simulations

Most of the early work in the iterated learning paradigm took the form of computational work with simulated agents (e.g. Kirby, 1999; Kirby & Hurford, 2002). The main focus was to tease apart the subtle relationships between the circumstances of cultural transmission, the biases of individual learners, and a range of other factors that might influence the resulting linguistic structure. This work had two major findings, both of which are well illustrated by Brighton et al., (2005), on which the rest of this section is primarily based.

The first finding concerns the importance of a *transmission bottleneck*, in which each individual learner is only exposed to a subset of the possible utterances in a language. This mirrors the situation in natural languages, in which a system capable of expressing an infinite number of meanings has to be acquired on the basis of a finite number of utterances. The importance of the bottleneck lies in the pressure it generates on the learner to be able to generalise from the subset of utterances to which they are exposed to the full set of all possible utterances. The following simple examples illustrate the nature of compositional structure and show why that structure is such a good solution to the pressure to generalise.

{1, 1}, *DeeLoo*; {1, 2}, *DeeMoo*; {2, 1}, *DooLoo*; {2, 2}, *DooMoo*

The simple language above is fully compositional, and consists of meanings (*1* and *2*) and signals (*Dee*, *Doo*, *Loo* and *Moo*). Notice how an initial *1* is always associated with the signal *Dee*, while a final *2* is always associated with signal *Moo*, etc. The meaning of the signal *DeeMoo* is, then, a function of the meaning of the signal *Dee* (initial 1) and the meaning of the signal *Moo* (final 2). Given this pattern, a language learner does not need to be explicitly exposed to the signal for *{1, 2}*, *DeeMoo*, in order to realise that it should begin with *Dee* and end with *Moo*, as this could be generalised from an exposure to the signals for *{1, 1}* ***Dee****Loo* and *{2, 2}* *Doo****Moo***. It is this property of generalisability that makes compositional languages such an effective solution to the problem of the bottleneck.

In contrast, this second simple language is holistic:

{1, 1}, *FooTaa*; {1, 2}, *BeeZuu*; {2, 1}, *HooPaa*; {2, 2}, *ViiDaa*

Each meaning is represented by its own unique signal. The structure of those signals bears no relation to the structure of the meanings with which they are associated: for example, it is clearly impossible to generalise in any way at all from the signal for {1, 1} to the signal for {1, 2}, even though both meanings have a *1* in the initial position. To learn this holistic language it would be necessary to be exposed to every single item.

The first finding, then, is that once there is a bottleneck on transmission, any language which cannot be successfully reconstructed from a subset will simply not be transmitted. In other words, what changes in these simulations is not the agents' genomes—perhaps by encoding an ever more compositional language as the simulation proceeds—but the *language itself*. The language becomes structured, therefore, simply as a result of responding to this pressure to pass through the transmission bottleneck, thereby turning the Chomskyian notion of the 'poverty of the stimulus' on its head (Zuidema, 2003). This first pressure can be described variously as a pressure to be *generalisable* (from the subset to the whole), a pressure to be *compressible* (with the structure of the whole describable by a subset) or the pressure to be *learnable* (such that the whole can be acquired simply by acquiring the subset).

Of course, this kind of generalisability is only an advantage for compositional languages if language learners are actually capable of generalising. This point leads neatly into the second finding of the computational ILM studies, which relates to the kinds of biases required of individual learners in order for compositionality to emerge. The biases explored by Brighton et al. are a subset of those examined by Smith (2002; 2004), with regard to agents' ability to learn, maintain or construct an 'optimal' (by which Smith means unambiguous) communication system. However, the simulations reported in Brighton et al. extend this work to explore the interaction between these learning biases and the presence of a bottleneck on transmission.

The first bias relates to a preference for componential analysis over atomistic analysis, without which the agents are incapable of generalisation at all. However, as Brighton et al. show, the emergence of compositional structure also depends on two further biases. The first of these is a bias against many-to-one mappings of signals to meanings, without which even a perfectly compositional system is always at risk from being corrupted through the introduction of noise (Brighton et al., 2005). The second is a bias against one-to-many mappings between signals and meanings.

Agents without this bias are actually unable to learn a system of signal-meaning mappings in the first place (Smith, 2002; 2004). The cumulative effect of these three biases is a bias in favour of *one-to-one mappings*.

These biases constitute the second pressure in the system. They play an extremely important role, because it is the interplay of the bottleneck and the biases that produces a language with a high degree of *communicative accuracy*[8] (Brighton et al., 2005). In other words, the resulting language is not only compressible, and therefore easy to learn, but is also highly *expressive*, allowing the unambiguous communication of its associated meanings. What makes this particularly interesting is that there is no communicative dimension to these simulations and no selection for communicatively successful agents. In other words, by adapting in ways that benefited *itself*—that enabled its continuing transmission—the language also changed, quite inadvertently, in such a way that also benefited *language users*, by becoming structured in a way that facilitated communication. For Brighton et al. (2005: 202, my emphasis), this suggests a fairly radical interpretation:

> ...our explanation for linguistic structure also offers an explanation for linguistic function —the model results presented here suggest that the prerequisites for compositionality also deliver communicative function as a side-effect, *without the necessity for any explicit pressure for communication*.

To understand the alternative account provided by Brighton et al., it is necessary to review the answers they provide to the two questions posed above, and thereby to the two linkage problems outlined in section **1.2.1**. In terms of the first question, concerning the processes and pressures in the ILM, Brighton et al.'s findings suggests that the major dynamic at work is between the pressure to become *compressible*—in order to be successfully transmitted through a bottleneck—and the pressure to be unambiguous, or *expressive*, which arises as a consequence of the agents having a bias for one-to-one mappings. Compositionality emerges as a result of language

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[8] As defined in terms of the probability, over all encounters, of a signal produced by one agent being interpreted by a second agent in the way intended by the first.

having to adapt to these two pressures in order to be successfully transmitted. The interplay between these two pressures begins, then, to supply the details of a mechanism linking facts about individuals (data set *A*) to facts about language (data set *B*). In doing so, it provides a clear answer to the general problem of linkage, something Pinker and Bloom conspicuously failed to do.

The picture becomes more complicated, however, when we begin to consider the second question, concerning the origin of these pressures. Why it is that the language finds itself having to adapt to *these* pressures rather than other ones? The first step in answering this question is to note that there is one very important difference between the two pressures. The pressure to be compressible is actually a kind of *informational regularity.* General models of cultural transmission (e.g. Brighton, 2003; Brighton et al., 2005) suggest that this pressure will, if unchecked by any other pressures, result in culturally transmitted systems becoming increasingly simplified and compressed. As a result, and this will be of great importance later, *cultural transmission is an inherently structure-producing process*. The pressure for compressibility is, then, *inherent* to the process of cultural transmission[9]. As such, the fact that culturally transmitted languages face a pressure to compress needs no further explanation.

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[9] There are two possible ways in which this claim might be read. The first, emphasised here and in this thesis more generally, focuses on the role of a bottleneck, and thereby on the cognitive and temporal limitations of learners. Languages that fail to adapt to those limitations, by becoming more structured and thus easier to learn, simply do not get passed on. The second focuses on the finding that repeated instances of transmission can serve to amplify the effects of weak biases (Smith & Kirby, 2008; Reali & Griffiths, 2009). In this view, each learner comes to the language-learning task with a weak bias in favour of structure. The cumulative effect of repeated transmission between multiple generations of weakly biased learners, is that the language becomes much more structured than might be expected from the strength of the bias of any given learner. There are two reasons why the choice between these options is not crucial in the present context. Firstly, in any real case *both* these factors are likely in operation. There are, as far as we know, no omniscient learners, so for large systems such as language all learners likely face some kind of bottleneck. Furthermore, some kind of structure-assuming bias is likely necessary for learners to be able to make *any* kind of inductive inferences at all (Mitchell, 1980). Such biases simply represent the condition of being an inductively capable learner. Secondly, even if the two options could be entirely divorced, the role played by cultural transmission is essentially the same in each. In both cases it serves to amplify the effects of some aspect of individual learners—whether that be their cognitive limitations, or biases that are required simply to function *as learners*—such that the learned material becomes progressively more structured over time. It is for this reason that cultural transmission can be described as inherently structure-creating.

In contrast, the pressure to be expressive is not inherent to cultural transmission, it is *contingent*, and therefore stands in much greater need of explanation. To account for the expressivity pressure, we need to identify a factor external to the cultural system that can 'check' its inherent tendency to compress (Kirby, 2012). In this case, that factor is the pre-existing learning biases of the agents. Here, then, is Brighton et al.'s answer to the special problem of linkage. Their mechanism produces languages that are adaptive for *language users* because, in addition to the need to compress, transmitted languages also find themselves having to adapt to a set of pre-existing biases, favouring one-to-one mappings. The language still takes on a simpler, more compressible structure, as would be expected given cultural transmission, but it does so in such a way so as to remain unambiguous and thus, as a side-effect, adaptive for communicating agents.

For Brighton et al., then, the special problem of linkage is solved through a fortuitous side-effect of some pre-existing cognitive bias. To some, this will seem less satisfying than the answer provided by Pinker and Bloom. The power of natural selection as an answer to the special problem of linkage lies in its providing a principled account not only of *how* such form-function matches might occur but also why we should *expect* them to occur. This latter component is missing from the account just discussed. Nevertheless, the modelling work suggests that this account is plausible: the bottlenecked transmission of a system of signal-meaning pairs, in a population already biased, for whatever reason, towards one-to-one mappings, *could* produce a compositional, communicatively adaptive language. In terms of accounting for the origin of the pressure for expressivity, this might be termed the *pre-existing bias explanation*.

Of course, this invocation of a pre-existing bias has lead some to wonder where the bias itself might have originated. One suggestion, put forward by Smith (2004), was that the presumption in favour of a one-to-one mapping between meanings and signals originates in aspects of theory of mind, and in particular the understanding of communicative acts that it allows. In exploring this idea, Smith observes that:

> Armed with such an understanding, children should expect language to exhibit a one-to-one mapping between meanings and signals, and this indeed appears to be their initial expectation. In other words, the human vocabulary acquisition bias may not have evolved specifically and exclusively for the acquisition of communicatively functional vocabulary, but rather be *a consequence of a more general cognitive capacity which evolved due to a raft of benefits it provided, including perhaps communication*.
> (p. 141, my emphasis)

As we shall see, Smith may well have been on to something quite significant here. It will not, however, be possible to appreciate the true significance of Smith's observation until later in the chapter.

1.3.2 – Iterated learning II: experiments

Computational simulations provide an extremely flexible way to examine all the different combinations of learner biases and transmission bottlenecks, and as such have made a valuable contribution to the development of the ILM. However, there remains one major concern about the validity of such work:

> ...skepticism remains as to how well computational models of learning match the abilities and biases of real humans.
> (Kirby et al., 2008: 10681)

Confronting this challenge directly, Kirby et al. outline a framework for implementing the ILM with human participants rather than simulated agents. The results of this work represent an important confirmation, extension and clarification of the previous computational studies. Most revealing, however, are the differences between the two sets of findings. To get a clear picture of how the ILM explanation for compositionality actually works—and thus to be in a position to pinpoint its necessary preconditions—it is important to reconcile the computational and experimental results.

Kirby et al. implemented a transmission-chain design in which the input for each link of the chain consisted of the output of the last link, thereby implementing the central logic of the modelling work. The input of each link (participant) consisted of a 3x3x3 meaning-space of *shape* (square, circle, triangle), *movement* (straight line, zig-zag, circular motion) and *colour* (grey, blue, red), and an (initially random) set of signals distributed across that meaning space. So, for example, a red square moving in a straight line might be represented by the string *kihemiwi*, with each of the other 27 possible combinations of meaning being represented by a similarly random string of syllables.

The procedure for each participant was divided into two sections, a training phase and a testing phase. In the training phase, the language (the set of 27 picture-syllable string pairs) was split into roughly equal sets of *seen* and *unseen* items, with the participant only being trained on the *seen* set. In the testing phase, participants were presented with a picture and asked to produce the syllable string for that shape; crucially, participants were tested on pictures from both the *seen* and *unseen* sets. For the first participant this procedure was carried out with the original, randomly generated set of strings paired with the meanings. However, subsequent participants were trained using the final output of the previous participant's testing phase.

It should be clear, then, that this procedure closely mirrors that used with simulated agents. The first participant is asked to learn a random language, but there is a bottleneck on transmission (as implemented through training being restricted to the *seen* set). As a result, when that participant is tested on the *unseen* items, they are required to *generalise* from the subset of the *seen* items to the language as a whole. As the language moves along the transmission chain, therefore, the extent to which the input language of participant *n+1* resembles the input language of participant *n* will depend in large part on how easy it was for participant *n* to generalise from the subset of the language to which he or she was exposed (the *seen* set) to the rest of the language (the *unseen* set). In other words, for a language to survive it has to adapt to pass through the bottleneck.

Kirby et al.'s first experiment was conducted exactly as described above, and thus implemented the logic of Brighton et al.'s computational study in human participants. Intriguingly, however, the results showed both similarities and differences with those of the simulations. As in the simulations, the language adapted to cope with the pressures it found in its environment; however, the form of this adaptation was different. Whereas in the computational study the language had adapted by becoming compositional, in the experimental study the language adapted by becoming *systematically underspecified*. In other words, one signal came to stand for many different meanings. For example, the signal *tuge* might come to refer to all shapes, of whatever colour, moving in a straight line; whereas, *poi* might come to refer to all shapes, of all colours, moving in a circle.

The first point to note here, is that, much like in the simulations, iterated cultural transmission resulted in a more structured language[10]. This confirms the finding that the very fact of cultural transmission has structure-creating powers. The second point, however, is that this structure *was not compositional*. This is intriguing, especially given that this first experiment should have included all the necessary ingredients to replicate completely the findings of the simulations. There was an iterated process of cultural transmission; a bottleneck on that transmission, such that learners in each generation were not exposed to the entire system; and a group of human participants, whose biases were supposedly approximated by those of the simulated agents. Given all this, why did this first experiment have a different outcome than the earlier simulations?

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[10] It might seem misleading, especially in the context of language, to describe a systematically underspecified system—the limiting case of which is a system with only a single signal that was mapped to every meaning—as being 'structured'. This is clearly not what is usually meant by 'structure' in relation to language. However, *relative to a random system*, a systematically underspecified system—much like a compositional system—is far more constrained, ordered and predictable. In both cases, it is this increased order and predictability—something which I think reasonable to term 'structure'—that allows these systems to pass through the bottleneck.

One possible answer is that the language was simply faced with a different set of pressures to those it had faced in the simulations. This experiment included a bottleneck, and thus the pressure to be compressible was definitely in operation. This leaves the pressure for expressivity. The simulations showed that such a pressure could, quite plausibly, follow from pre-existing biases. What had yet to be demonstrated was that those biases would have that effect in humans. The results of this first experiment might be taken to suggest that those biases—the reality of which are well attested more generally (e.g. Markman & Wachtel, 1988; Mazzocco, 1997) —were not, in fact, capable of accounting for the expressivity pressure. This is particularly significant given Smith's proposal that the biases originated in theory of mind, as this was certainly a capacity shared by all the participants. More importantly, where might this leave our account of the expressivity pressure?

Kirby et al.'s second experiment was largely the same as their first except that they added a filter for *homonymy*. In other words, before passing one participant's output as the input for the next participant, they filtered the *seen* set such that if any string was assigned to more than one meaning then all but one of those meanings was removed from the training data. The results of this second experiment once again confirmed the importance of adaptation by the language itself, however this time, with the homonymy filter preventing the language from adapting through systematic underspecification, that adaptation took a compositional form, in which each string came to consist of three identifiable syllables representing the shape, colour and movement of its associated picture. So, for example, a grey square moving in a straight line was represented by the string (here split into syllables for ease of exposition) *n-ere-ki*, whereas a grey circle moving in a straight line was *n-ehe-ki*.

The homonymy filter is the only difference between Kirby et al.'s first and second experiments. It is the addition of this filter that makes the difference between the emergence of a systematically underspecified language and a compositional language. What, then, are we to make of this filter? How might it relate to the expressivity pressure? The answer to this question emerges in three passages, in which Kirby et al. describe the filter, its function and its motivation.

> filtering ensures that underspecification is an *evolutionary dead end*.
> (p. 10684, my emphasis)

This reference to 'evolution' cannot be biological evolution, because this experimental work does not feature any biological evolution, the participants did not 'evolve'. The only evolution in these experiments is cultural, and so this must refer to the cultural evolution of the language. But if this is the case, why should we consider underspecification to be an 'evolutionary dead end'? In fact, the results of experiment one indicate that underspecification, far from being a dead end, is a perfectly viable way for the language to adapt.

As the following quotation indicates, however, Kirby et al. view the introduction of the homonymy filter as posing an additional adaptive challenge for the language:

> [filtering introduces] a new adaptive challenge for the evolving language...a language in this experiment must be *both learnable and unambiguous*.
> (p. 10685, my emphasis)

This seems to signal something of a fundamental shift from the earlier computational work. In the simulations, the pressure to be unambiguous—to be expressive—derived, as we have seen, from the learning biases of the agents. However, Kirby et al.'s first experiment—essentially a replication of those simulations with human participants—seemed to suggest that while the *pre-existing bias explanation* of the expressivity pressure might work in principle, it did not seem to work with human participants. In this second experiment, the role previously played by an *internal* learning bias has come to be taken over by an *external* homonymy filter. What might this filter be meant to approximate? A final quotation supplies the answer:

> [filtering] is an analogue of a pressure to be expressive that would come from *communicative need* in the case of real language transmission.
> (p. 10684, my emphasis)

It should be clear that it is not the *language* that is faced with this communicative need, but rather *language users*. If the language has to adapt in relation to this need, then it is as a knock-on effect of the use which language is serving for its users. It is clear, too, that this relates to the origin of the expressivity pressure. The homonymy filter—in its role of eliminating one-to-many and many-to-one mappings—constitutes a direct analogue of the biases built into the agents in the simulations[11]. Only this time it is operating not as a learning bias but as a proxy for language needing to be used communicatively. In terms of accounting for the expressivity pressure, this might, therefore, be termed the *functional explanation.*

The experimental instantiation of the ILM shows both similarities and differences to the computational instantiation. In terms of the internal functioning of the ILM, they are in complete agreement. Both cite the interplay between the pressures of *compressibility* and *expressivity* as crucial in terms of how cultural transmission functions to create language structure. As such, both provide the same answer to the general problem of linkage: it is the structure-creating process of cultural transmission that links learners and languages. Both also see the pressure for compressibility as something that is inherent to the cultural system itself. Where they differ, however, is in terms of accounting for the expressivity pressure. The computational work saw this as arising from the pre-existing biases of learners. While this was possible in principle, the evidence does not support this explanation in humans. The experimental work, however, traces the expressivity pressure to the functional use of language in communication. In the work cited above

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[11] The formal identity of the agents' biases on the one hand and the homonymy filter—as a proxy for 'communicative need'—on the other, means that one might equally describe the simulated agents as having an in-built *need to communicate.* At the very least, the choice between this description and one couched in terms of 'biases' is a matter of taste.

communication was implemented by a proxy (the homonymy filter). However, the link between communication and the expressivity pressure has been confirmed by more recent work, explicitly involving communication (Kirby et al., in prep, personal communication).

1.3.3 – Summary

We are now in a position to answer the two questions posed at the beginning of this section.

Question 1: What are the processes and pressures involved in the ILM account of language structure?

Language structure emerges as a result of the interplay between the pressure to become *compressible*, which drives language to become ever simpler and easier to learn, and the pressure to be *expressive*, which checks that drive to simplicity. Compositionality can be seen as a compromise between these two pressures. Compositional languages are much more compressible, and thus easier to learn, than holistic languages, but they achieve that compressibility in such a way as to avoid collapsing to completely ambiguous underspecification.

Question 2: Why does the ILM involve those *particular processes and pressures and not other ones?*

The pressure to be compressible is a kind of *informational regularity*, which is inherent to the process of cultural transmission. Systems that are transmitted in this way will tend towards compressibility and simplicity. It is clear, therefore, why a culturally transmitted language should face this pressure. The pressure to be expressive, however, is *not* inherent to cultural transmission. It is contingent. It requires an explanation. The evidence suggests that the expressivity pressure derives from the *use* to which learners put language. The previous explanation, based on the co-option of general, pre-existing biases, was not supported by work with human participants. Instead, the evidence seems to favour the *functional explanation*: the pressure to be expressive derives from the fact that language has to function as a tool for communication.

Given these answers, how does the ILM fare in terms of answering the two linkage problems discussed at the beginning of the chapter? In terms of the general problem —how to link data on learners and languages—the ILM does very well. The process of cultural transmission, with its interplay between the pressures for compressibility and expressivity, outlines a mechanism whereby the capacities and behaviour of individuals is linked to language structure. This is in marked contrast to Pinker and Bloom who failed to provide any answer to the general problem, beyond an assumed isomorphism between UG and language.

In terms of the special problem—how to account for the resulting language structure also being adaptive, from the perspective of language users—the outcome is more mixed. It is clear that a major role is played by the expressivity pressure. This provides a countervailing influence to the inherent tendency for cultural systems to simplify. Or rather, it ensures that when the language does simplify, it doesn't do so in a way that limits expressivity. It is the influence of the expressivity pressure, then, that accounts for why the process of cultural transmission not only links learners and languages, but does so in a way that is also *adaptive* for learners. Despite this vital role, however, there is no reason to expect cultural transmission per se to involve a pressure for expressivity.

Given this, no understanding of how the ILM works can be complete without an account of origin of the expressivity pressure. As noted above, the best account of this origin relates it to the communicative use of language—to its communicative *function*. This takes us some way towards providing an answer to the special problem of linkage. The cultural process produces language that is adaptive for its users because a pressure for expressivity forms part of the adaptive environment of the language. This pressure, in turn, derives from the communicative function to which language is put by its users.

There is still one serious problem, however, which is finds expression in the following two questions:

(a) What determines that *communication* is the function to which the language has to adapt, why not some other function[12]?

In an experiment or model it is the experimenter or modeller who decides the relevant parameters, but who or what decides them in the real case? The *functional account* of the expressivity pressure, at least as described so far, seems to provide no clear answer to this question. Here Pinker and Bloom still have a significant advantage, because in their account it is *natural selection* that determines the relevant function: Language structure is adaptive for communication because it is in relation to *that* function that it has been subject to selection. However, this first question immediately gives rise to a second.

(b) What is meant by 'communication' here?

'Communication' is an incredibly broad term. All living things communicate, using a dazzling array of mechanisms, media and signals. But what is meant by 'communication' in relation to language? The natural starting point would be to look at how linguistic communication itself operates. When Pinker and Bloom did just that, their conclusion was that linguistic communication was primarily code-like, that its function was the "communication of propositional structures over a serial channel". It is highly doubtful, however, whether this represents how linguistic communication actually works (Sperber & Wilson, 1995). Given the centrality of the expressivity pressure to the ILM account of language structure, it is necessary to address these two questions, so I will return to them both when I consider the expressivity pressure in greater detail below (**1.4.5**).

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[12] Why is the relevant function not structuring cognition (e.g. Bickerton, 1990), or to provide the 'narrative centre of gravity' required for consciousness (e.g. Dennett, 1991)? The list of potential functions could be elaborated indefinitely. However, the question remains, why, out of all the possible functions that *could* have played a role shaping the adaptive environment of the language, is *communication* the one that did so?

1.4 – Evolutionary preconditions of the ILM

The previous section presented a critical discussion of the ILM account of compositionality. However, the account of the ILM presented there requires that a range of preconditions be in place for the iterated process to get started in the first place. In this section I shall attempt to detail just what those preconditions might be. I have taken the brief discussion in Smith and Kirby (2008) as a starting point, and combined it with the critical assessment of the ILM presented above. In all, there appear to be five necessary preconditions, which can be split into two groups: individual preconditions and systemic preconditions.

The three *individual preconditions* concern the abilities of individual learners:

I. The ability to acquire new signals
II. The ability to acquire and produce new signal-meaning associations
III. The ability to infer communicative intent

The two *systemic preconditions* concern the nature of the communicative environment:

IV. The existence of a bottleneck
V. The existence of the expressivity pressure

It should be noted that the first four of these preconditions constitute an expanded version of those discussed by Smith and Kirby, and are relatively uncontroversial in discussions of the ILM. The fifth precondition, however, derives from the preceding critical discussion of how the ILM works, and is not something that is usually emphasised in publications on the ILM. Its inclusion is motivated by the fact that while the first four preconditions explain why and how structure might emerge that is adaptive *for the language*, they fail to explain why that structure should also be adaptive for *language users*. To account for that we need to examine the origin of the expressivity pressure, and to do that we need to address the two questions outlined above. Why was *communication* the relevant function? And, what do we mean by 'communication' in this instance? Overall then, in terms of the earlier discussion, preconditions I-IV provide the basis for a mechanism that solves the general problem of linkage, whereas the inclusion of precondition V alters the balance of pressures in that mechanism, such that it also solves the special problem.

In the sections that follow I shall discuss each of these preconditions in turn, making some necessary distinctions and briefly reviewing comparative work regarding examples of these preconditions in other species.

1.4.1 – The ability to acquire new signals

The ILM account of compositionality sees it as emerging from a process in which language itself adapts to the combined pressures of *compressibility* (or learnability) and *expressivity*. It is obvious, however, that the first of these pressures requires that the individuals actually *be capable of learning*. More particularly, that learning play a role in the acquisition of their communication system. This is no trivial requirement given the sparsity of such examples in nature (Janik & Slater, 1997). However, in order to clearly understand this first precondition it is vital to make some distinctions between different kinds of learning. In particular, to make a three-way distinction between *comprehension* learning, *usage* learning and *production* learning (Janik & Slater, 2000; Seyfarth & Cheney, 2010).

Comprehension learning occurs when an individual is able to extract a new meaning or inference from a signal, as a result of their experience of that signal being used by other individuals. This capacity is widespread amongst mammals, with species as varied as primates, dogs, squirrels and bats exhibiting an open-ended capacity to learn the meanings associated with new signals (Seyfarth & Cheney, 2010). Examples of this phenomenon include: the comprehension of other species' alarm calls by several species of monkey (Hauser, 1988; Fichtel, 2004); the recognition of the calls of the adoptive species in cross-fostering experiments (Seyfarth & Cheney, 1997, cited in Seyfarth & Cheney, 2010); and experimental work with dogs in which hundreds of associations between completely arbitrary sounds and objects are successfully acquired (Kaminski, et al., 2004). Sometimes the meanings and inferences extracted can be impressively detailed and complex. For example, playback experiments with baboons have shown that they acquire information about identity, relative rank and matriline from sequences of calls (Bergmann et al., 2003).

Usage learning occurs when an individual learns to modify the production of a signal based on the current situation or context. This capacity is somewhat less common and where it does occur is very restricted in comparison to the open-ended nature of comprehension learning (Seyfarth & Cheney, 2010). One well-known example is the alarm calls of vervet monkeys, which are often glossed as *leopard*, *eagle* and *snake* warning signals. Young vervets initially use these calls in an over-extended manner, for example by issuing an *eagle* call in response to any aerial stimuli. Over time, however, they fine-tune the use of the calls, eventually only producing them in response to the appropriate threat (Seyfarth & Cheney, 1990). One further example concerns the modification of recruitment screams by chimpanzees based on the composition of the audience, particularly in relation to the presence or absence of dominant individuals (Slocombe and Zuberbühler, 2007). Usage learning also occurs when an existing call is used in a novel context.

Production learning occurs when an existing signal is modified or a new signal acquired, and is the rarest of the three forms of learning under consideration. The pattern across mammals, at least as far as vocal communication is concerned, is that most species have a limited repertoire of signals which are generally tied to specific contexts and which are present in their adult form from birth (Seyfarth & Cheney, 2010). The only known exceptions to this generalisation are some species of whales and dolphins (Rendall & Whitehead, 2001; Reiss & McCowan, 1993), bats (Boughman, 1998), seals (Ralls et al., 1985), and possibly elephants (Poole et al., 2005). In terms of other species, the most unequivocal evidence of vocal production learning is in songbirds (Nottebohm & Liu, 2010), parrots (Pepperberg, 2010) and hummingbirds (Baptista & Schuchuman, 1990).

While communication through vocal signals is very widespread in nature, communication through brachiomanual gesture—that is, through "manual communication without touching another individual or a substrate"—is found almost exclusively in apes and humans (Pollick & de Waal, 2007: 8184). The gestural communication of apes is significantly more flexible and less tied to emotional reactions or specific contexts than either their vocal or facial expressions (Pollick & de Waal, 2007). As such, it exhibits all three of the forms of signal learning described above, with both the comprehension and usage of gestures in the wild shifting between contexts (Hobaiter & Byrne, 2011) and new, non species-typical gestures appearing in captivity (Leavens et al., 2005).

From this brief survey, it should be fairly clear that the kind of learning required as a precondition of the ILM is signal production learning. The changes in the language observed in both the computational and experimental instantiations of the ILM are crucially dependent on the capacity of each generation to produce variations on the language that they were exposed to as learners. Of course, in any real world instance comprehension and usage learning would also constitute vital skills; however, these forms of learning are far more widespread throughout mammals as a whole, and so present much less of an explanatory challenge. What does need to be explained, however, is how humans might have shifted from the typical primate pattern of very little production learning, at least as far as vocal signals are concerned, to a state in which production learning was typical. At least some of this shift must have occurred *prior* to the process modelled by the ILM, because the ILM depends on a capacity for production learning.

1.4.2 – The ability to acquire and produce new signal-meaning associations

The comprehension learning of new signal-meaning associations is widespread, and the ability to acquire new signals, although quite rare, is found in a number of different species. However, these capacities considered separately are not sufficient, because what is required as a precondition for the ILM is the *production learning of new signal-meaning associations*. This second precondition represents a subset of the first; it is no surprise, therefore, that it is even less commonly found in other species.

There seems little evidence, for example, that any of the vocal production learners discussed above are learning new signal-meaning associations, or even that their signals have any semantic content at all (Fitch, 2005). Most of the examples consist of either the vocal mimicry of ambient sounds (Poole et al., 2005; Ralls et al., 1985) or of vocal traditions within populations, in which the variation is simply one of acoustic properties (Sanvito et al., 2007; Boughman, 1998; Rendall & Whitehead, 2001). Even in one of the clearest examples of vocal production learning, that of the songbirds, there appears to be no evidence that there is any semanticity to the learned song, or that song elements can be rearranged to yield changes in meaning (Berwick et al., 2011).

The production learning of signal-meaning associations is, however, present in the gestural communication of apes. Apes are known to create new signal-meaning pairs through the process of ontogenetic ritualisation (Tomasello, 1996), whereby new gestural signals emerge through the shaping and anticipation of behaviour between individuals in repeated interactions. For example, an infant may begin to initiate feeding by grabbing directly for its mother's nipple whilst moving her arm. In subsequent interactions the mother may anticipate the infant's desire before this full process has occurred, with eventually a simple touch on the arm being sufficient to initiate feeding (Tomasello et al., 1994).

One final example of the production learning of new signal-meaning associations comes from the findings of ape-language research. The most prominent example of this work is that with the bonobo Kanzi (e. g. Savage-Rumbaugh et al., 1998). Much of the hype surrounding this study has focused on Kanzi's ability to comprehend and appropriately respond to spoken English sentences, at a level comparable to that of a three year-old child (Savage-Rumbaugh et al., 1993). However, the most important feature of this work for present purposes is that Kanzi can use lexigrams communicatively (Savage-Rumbaugh et al., 1986; Lyn, 2007). This clearly represents an example of the production learning of new signal-meaning associations. Kanzi is also not an isolated case in this regard, with various other bonobos and chimpanzees (Savage-Rumbaugh et al., 2005) and a gorilla (Tanner et al., 2006) having acquired similar sets of lexigrammatic or gestural signal-meaning pairs.

1.4.3 – The ability to infer communicative intent

Language is unusual in that it is both *learned* and *symbolic* (Deacon, 1997), with the result that the link between form and meaning is neither innately specified nor inherent in the form of the signal (Oliphant, 2002). This greatly complicates the task of acquiring new signal-meaning pairs, because it requires not just *associative* learning between items, but also the capacity to *infer* one from the other. In philosophical terms, this has been cast as the *Gavagai* problem (Quine, 1960). Quine considers the situation of a naïve linguist attempting to understand what is meant by a speaker of an alien language, who on pointing to a rabbit utters *gavagai*. Does gavagai mean 'rabbit', 'furry thing', 'running animal', 'dinner', or any other of the potentially infinite number of possibilities? This is a problem of determining reference, of working out the *meaning* associated with a given *signal*. Furthermore, this problem must be solved in a way that scales to making large numbers of such inferences, otherwise there will be no bottleneck on transmission and no pressure to generalise.

The examples of signal-meaning production-learning in the previous section fail to meet these criteria. Impressive as the results of ape-language research are, they still only demonstrate the acquisition of around 250 or so lexigrams. More importantly, the acquisition of these signal-meaning pairs takes place in an environment that has been structured and scaffolded by another organism, humans, that is already heavily involved in learned symbolic communication. This environment—understandably described as a hybrid pan-homo culture (Savage-Rumbaugh et al., 2005)—is one that greatly lightens the 'inferential burden' of acquiring learned symbols. As a model for the emergence of language in humans, ape-language research is more of a 'skyhook' than a 'crane' (Dennett, 1995). Our solution to the Gavagai problem cannot appeal to the near-miraculous structuring of our environment by an external agency.

Ontogenetic ritualisation, on the other hand, might be seen as a method of preventing the Gavagai problem from arising at all. There is no doubt as to the referent of a particular signal because the signal-meaning association grows out of a history of shared interaction between the individuals concerned. However, for this very reason, ontogenetic ritualisation may simply be the wrong *kind* of process. Rather than the inferential learning of a new signal-meaning pair, ontogenetic ritualisation represents something of a *constructive* process, whereby two individuals shape each other's behaviour through repeated interactions (Tomasello, 1997). Neither ape-language research nor ontogenetic ritualisation can stand, then, as examples of the kind of inferential capacity required by the ILM.

In language, the inferential acquisition of signal-meaning pairs is probably most clearly exemplified by word learning. Many different processes are likely involved in word learning, including simple associative learning (Samuelson & Smith, 1998), pre-existing cognitive constraints (Markman, 1994), statistical learning (Saffran, 2003) and cross-situational learning (Smith et al., 2006). However, in this section I will focus on the social-pragmatic account (e.g. Tomasello, 2000), because it has a great deal to say about Quine's gavagai problem and because the core cognitive skills it requires will be of great importance when we come to consider precondition V, regarding the expressivity pressure (**1.4.5)**.

From around the age of one, children come to understand others as intentional agents (Tomasello, 1999). As development proceeds, this capacity is built upon, such that children come to be able to engage others in joint-attentional activities (Tomasello et al., 2005). That is, to engage in activities with others, against a background of *mutually shared* knowledge, expectations and goals. In this context, the range of potential referents, and therefore the potential scope of the Gavagai problem, for a given utterance is drastically reduced. Note briefly, too, that this is much the same nexus of capacities cited by Smith (2004) in his account of the pre-existing bias (see **1.3.1**), a point I will return to later. The following account provides a good example of how this works:

> In the context of a finding game, an adult announced her intentions to "find the toma" and then searched in a row of buckets all containing novel objects. Sometimes she found it in the first bucket searched. Sometimes, however, she had to search longer, rejecting unwanted objects by scowling at them and replacing them in their buckets until she found the one she wanted. Children learned the new word for the object the adult intended to find (indicated by a smile and termination of search) *regardless of whether or how many objects were rejected during the search process*
> (Tomasello et al., 1996, cited in Tomasello, 2000, emphasis in original).

The familiar context here is obviously that of a 'finding game'. The mutually shared knowledge relates to how such games are played: that there is something to find; that it might be in a variety of locations; that the goal, and thus the end of the game, is reached when that thing is found; etc. Given this joint attentional situation, the child is able to infer that the adult's utterance is interpretable in light of both participants' shared understanding of that situation. This allows the child to make the simple inference that the signal *toma* refers to the focus of the joint-attentional situation, the to-be-found object. These skills allow one individual to infer the communicative intent of another, to infer the *meaning* associated with a particular *signal*. As a result, they permit just the kind of rapid and reliable signal-meaning pair acquisition required by the ILM.

This third precondition seems to be exceedingly rare—perhaps even entirely absent—in non-human animals. There is little evidence that any of the known vocal learners, for example, are able to engage in joint attentional activities, although some of the component skills have been found in some vocal learning species (Tomasello et al., 2005; Pack & Herman 2006). With regard to the great apes, a previous consensus that they are unable to conceptualise others as intentional agents (Heyes, 1998) has been altered by a wide variety of new studies suggesting that they do in fact understand some mental and perceptual states (Call & Tomasello, 2008). However, the balance of the evidence still suggests that they are unable to engage in joint attentional activities (Tomasello et al., 2005), although suggestive hints of such abilities have been observed in the wild (Boesch, 2002, 2005).

There is, however, an even more basic form of this precondition, which stands as a requirement for the social-pragmatic account—or indeed *any* account of learned symbols—to be possible in the first place. This concerns the recognition that an action or behaviour was meant communicatively *at all* (Scott-Phillips et al., 2009). In contrast to inferring the meaning of a *particular* signal, we might call this a general *sensitivity to communicative intent*. This form of social-pragmatic awareness is the key starting point for the wider set of socio-cognitive skills that underpin the capacity to infer the communicative intent—the meaning—of learned symbolic signals.

1.4.4 – The existence of a bottleneck

The examples of the ILM discussed in **1.3** used toy languages with artificially imposed bottlenecks. In real language learning, however, the bottleneck stems from the infinite number of possible utterances and the very large number of signal-meaning pairs. The existence of a bottleneck is of vital importance to the ILM, because it is this that creates the pressure for the language to compress, to become more learnable.

The existence of the bottleneck is dependent on all three of the preconditions discussed above. It is necessary that signals be learned (precondition I), because the bottleneck is, by definition, related to limitations on learning: either the logical limitation of needing to learn an infinite set from a finite subset, or cognitive limitations of memory and processing capacity. More specifically, however, the bottleneck is dependent on those learned signals being paired with meanings (precondition II), because the crucial pressure to generalise is a pressure to generalise from a subset of the signal-meaning pairs to the (potentially) infinite full set of all such pairs: if the signals had no semantic content, as with birdsong, there would be nothing to generalise *about*[13]. However, it is not enough simply that there be a few signal-meaning pairs to learn. The emergence of a bottleneck depends on there being a large enough number of signal-meaning pairs that the learning limitations described above come into play. This, in turn, requires that there exist a rapid and reliable process for the acquisition of such pairs (precondition III).

1.4.5 – The existence of the expressivity pressure

The four preconditions discussed so far set up the possibility of a culturally transmitted system of signal-meaning pairs. The combined effects of these four preconditions is to produce a system in which, in order to be successfully transmitted, language would have to adapt to be compressible. What they fail to do, however, is provide an account of why that resulting language should also be expressive, and thus adaptive from the point of view of language users. The first four preconditions fail to address the special problem of linkage.

The ILM solution to the special problem of linkage depends on the *expressivity pressure*, which in turn derives from the communicative function of language. However, this *functional explanation*, at least considered alone, provides no account

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[13] It should be noted that the important point here is not meaning per se but the pressure to generalise that meanings introduce. There is no reason to think that semanticity is the only way in which this pressure to generalise could be introduced.

of why *communication* happened to be the relevant function. One possible solution might be to take the best aspect of Pinker and Bloom's argument—their appeal to natural selection—and ground the choice of communicative function in that. I will argue that this is indeed the correct solution, but that it needs to be applied carefully otherwise we run into seemingly insurmountable theoretical difficulties.

In addition, it was left unclear what was meant by 'communication'. Here, too, we might simply follow Pinker and Bloom in adopting the code-model of linguistic communication. However, we shall see that many of the difficulties faced in appealing to natural selection actually derive from problems inherent in the code model. Once we shed the code model of communication, it becomes much clearer how selection can account for the expressivity pressure.

1.4.5.1 – Why *communicative* function? Natural selection as a seductive solution.

The question of why language has to adapt to pressures arising from its communicative function—rather than some *other* function—is not a problem for Pinker and Bloom. For them, language structure comes to reflect its role in communication because it is in relation to *that* function that it has been subject to selection. As another example, the heart both pumps blood around the body and makes thumping sounds. However, the *structure* of the heart reflects the former pressure and not the latter, because its functional role in circulation is the one relevant to selection (Wright, 1976). To reverse the point, the reason the functional demands of producing thumping sounds are *irrelevant* to the structure of the heart, is that its capacity to fulfil that function has been largely, perhaps entirely, irrelevant to selection. Natural selection provides, then, a powerful solution to the question of determining the relevant function: The structure of a trait will come to reflect those functions for which it is under selection. This is what is meant by the phrase 'form follows function'. The application of this logic, integrated into the ILM account of compositionality, would, at first blush, go something like this:

The ILM account relies on the interplay between the pressure to be *compressible* and the pressure to be *expressive*. The first one of these pressures is inherent to cultural transmission. As a result, cultural transmission also has an inherent structure-creating capacity. Unchecked, however, the resulting structure will become continually more simplified and compressed. In the case of language, it is the second pressure—expressivity—that serves to check the first, such that simplification does not occur at the expense of communicative efficacy. The expressivity pressure is *not* inherent to cultural transmission—it is contingent—and an account of its origin is, therefore, required. The *functional explanation* links the expressivity pressure to the communicative use of language by its learners. The reason that *communication* is the relevant function in this connection is because, like with the heart pumping blood, that is the function under selection in language learners.

1.4.5.2. – Problems with that seductive solution: bootstrapping and foresight

The problem with invoking natural selection is that it is not clear exactly *what* is being selected. Natural selection requires heritable variation. If the relevant function is set by natural selection, then there must be some kind of heritable variation underlying language's role in communication. We might call this variation the *language faculty*. Such a faculty might take the form of highly specified UG (Pinker & Bloom, 1990), a language-specific bias (Smith, 2004), or certain computational processes (Hauser et al., 2002; Di Sciullo & Boeckx, 2011). Regardless of the form that faculty takes, however, it is vital to remember that we are not talking about a faculty for the production and comprehension of a set of signals, but rather a faculty to *acquire a culturally transmitted language* (Origgi & Sperber, 2000). This leads to a kind of 'bootstrapping' problem: what use is a faculty to acquire something that does not yet exist?

This same problem can also be recast in terms of natural selection lacking foresight. Natural selection is 'blind' and algorithmic (Dawkins, 1986; Dennett, 1995). In modelling terms, it represents a hill-climbing process (Beasley et al., 1993), each step of which must produce an increase—in the here and now—of the quantity which it tries to maximise, inclusive fitness (Hamilton, 1964; Grafen, 2009). Theoretically speaking, then, natural selection cannot put something in place *today* with a view to its being adaptive *tomorrow*. More specifically, modelling work indicates that, in situations with no established form of communication, a benevolent period of genetic drift is required in order for a language faculty to emerge (Smith, 2004). Selection simply cannot favour a language faculty unless the population is already converged on a language.

The bootstrapping problem arises because the language faculty is one of a class of adaptations whose 'proper domain' does not exist in the environment before they appear (Origgi & Sperber, 2000). This contrasts with things like vision, whose proper domain—the information available in light—was present in the environment long before the first eye ever developed. Unsurprisingly, then, this problem has arisen in connection with many different approaches to language evolution. It will be useful to consider some of those examples here, together with how they attempt to solve or avoid the bootstrapping problem.

Recall, firstly, the computational instantiation of the ILM, discussed in **1.2.1**. In this work the expressivity pressure was argued to derive from the influence of a *pre-existing* set of learning biases, which were later co-opted for language. This co-option hypothesis side-steps the need to account for language-specific biases—that is, for the language faculty—in the absence of language itself. The relevant biases need not arise 'today' *in order* to be used for language 'tomorrow', because they were already present for some other reason. In this way, the bootstrapping problem is avoided. However, while this explanation works in principle, it has not been supported by work with human participants.

Consider next Pinker and Bloom's view of the language faculty as an innately specified UG. How might this faculty have got there in the absence of language?

Pinker and Bloom's solution consists of a combination of the *parity thesis*—the idea that for many aspects of language it doesn't matter *which* form is chosen, as long as we all choose the *same* form—and the *Baldwin effect* (Baldwin, 1896, Godfrey-Smith, 2003), a process by which traits that were once learned become nativised. This two-step process means that the language faculty is actually a collection of now-nativised, but once-learned, signal co-ordinations. Such a faculty does not have appear *prior* to language but instead appears *because of* language, thus solving the bootstrapping problem. The weak link in this solution, however, is the Baldwin effect, which remains a largely theoretical notion, that can only function under a very restricted set of circumstances (Yamauchi, 2001, 2004).

The final example comes from biolinguistics (see Di Sciullo & Boeckx, 2011), and concerns the role of *self-organisation* and *emergence* in accounting for a language faculty comprised of various computational routines. These computational competencies are argued to arise as a consequence of self-organising regularities in the laws of physics, mathematics or developmental biology (Uriagereka, 1998). This approach takes the conventional evolutionary position that 'form follows function' and turns it on its head, arguing that 'function follows form'. Self-organising processes produce a computational *form*, which only later goes on to 'find' a *function*. This inversion of the form-function relationship solves the bootstrapping problem in a similar way to the co-option of pre-existing biases, by removing the need for form to emerge *in order* to fulfil a function that only appears later. What remains somewhat obscure, however, is why such self-organisation should consistently result in *adaptive* outcomes, unless paired, in some way or other, with a process of selection (Weber & Depew, 1996).

The bootstrapping problem presents, then, as a challenge to any evolutionary account of language, yet none of the solutions just considered are wholly adequate. This leaves us in something of a dilemma. The expressivity pressure is a key component of the ILM account of compositionality. It seems to derive from the use of language for communication. Yet the clearest naturalistic explanation of why *that* function, rather than another, should be the one that mattered—natural selection—seems to lead inexorably into the bootstrapping problem.

The key to solving this apparent dilemma is the realisation that it is not natural selection per se that leads us into the bootstrapping problem, but the combination of natural selection and a particular conception of linguistic communication—the *code model*. In order to see how selection on communication can give rise to the expressivity pressure, then, it is necessary to first get clear what we mean by 'communication' in this instance.

1.4.5.3 – Models of linguistic communication I: The code model

The code model, most explicitly formulated by Shannon and Weaver (1949), views communication in terms of the bi-directional mapping of meanings and signals. Under this model, communicators map the concepts they wish to convey onto an external, shared code. This encoded message is then transmitted to their audience, who then perform the process in reverse, by decoding the message and recreating the encoded conceptual content.

There are many reasons to think the code model a wholly inadequate conception of linguistic communication (Sperber & Wilson, 1995). Despite this, many approaches to language evolution have adopted the code model, if only for methodological reasons (Scott-Phillips, 2010). In the present context, however, I want to describe two problems arising out of this conception of language, which together account for the subsequent slide into the bootstrapping problem.

- **Problem 1 --** *The code model alienates language from other aspects of communication*: The view that linguistic communication consists, in essence, of the successful manipulation of a shared language-code tells us very little about how language relates to other aspects of communication. This matters because human communication is fundamentally multi-modal (McNeill, 2000). These other modalities, including co-speech gesture and facial expression, are tightly coupled with linguistic communication temporally (Mayberry & Jaques, 2000), semantically (McNeill, 2005) and neurally (Hubbard et al., 2009). None of these modalities function like a code, and their tight relationships to language suggest that language, too, should be seen primarily as part of this wider communicative whole, rather than an isolated, one-off system of code.

- ***Problem 2 --*** *The code model makes the ongoing evolution of a language faculty difficult to account for*: Simply put, what use is a faculty that permits the acquisition of a more elaborate code if that code is not shared by others (Origgi & Sperber, 2000)? Evolution is unable to 'experiment' with additional codes (Sperber & Origgi, 2012), as code mismatches cause communication to fail.

The bootstrapping problem arises from the conjunction of these two points. If the language faculty is the capacity to acquire a code, then its emergence and subsequent elaboration is difficult to account for. This is further exacerbated by the opaque relationship between language-as-code and other aspects of communication, as we cannot appeal to them to bootstrap language either. Finally, it is no co-incidence that many of the unsatisfactory solutions to the bootstrapping problem come from perspectives that endorse a code model of language. This is certainly true of Pinker and Bloom, who characterise language as the “communication of propositional structures over a serial channel.” Similarly, the computational routines emphasised by biolinguistics represent computations *over the code*. Much work in the ILM also assumes the code-model, if only as a methodological simplification.

The effect of the code model, then, is to obscure the relationships between language and other aspects of communication and between language and the evolution of the language faculty. These outcomes are likely in any approach to language evolution that adopts the code model, and go some way to explaining the ILM's apparently inevitable slide into the bootstrapping problem when attempting to account for the expressivity pressure. What is needed, therefore, is another conception of language that avoids the problems associated with the code model.

1.4.5.4 – Models of linguistic communication II: The ostensive-inferential model

The ostensive-inferential conception of communication sees it as a process in which senders provide evidence—*ostensions*—from which receivers can draw *inferences* regarding the sender's intended meaning. On this view, a linguistic utterance is not primarily something to be decoded (although some decoding is involved), but a piece of evidence from which inferences can be made regarding the sender's intended meaning. Consider the following example, from Sperber and Wilson (2012a: 11):

a. ALAN JONES: Do you want to join us for supper?
b. LISA: No, thanks. I've eaten.

Some decoding is, of course, required in order to understand Lisa's reply. However, taken *simply* as a target for decoding it is a total *non sequitur*. Taken as a target from which inferences can be drawn, however, it makes perfect sense. For example, Lisa is assuming that her reply will be interpreted in light of their shared awareness that people normally only eat once on any given evening. In contrast to the code model, it is uncontroversial that linguistic communication is well characterised as ostensive-inferential. Indeed, language has been described as the “archetypal example” of ostensive communication (Scott-Phillips & Kirby, 2013: 429).

This view of communication is based on the foundational work of Grice (1957, 1968) and has since been elaborated by a range of work in philosophy and pragmatics (e.g. Levinson, 1983; Horn, 1984). For the rest of this section, however, I want to focus on one particular account of ostensive-inferential communication, *relevance theory* (Sperber & Wilson, 1995), because it not only grounds language in the broader context of human communication (addressing problem one) but also grounds communication in cognition, and cognition in evolution (thereby addressing problem two).

1.4.5.5 – Relevance theory

The 'relevance' in relevance theory is a potential property of external stimuli, internal representation, or indeed anything that might serve as an input to cognitive processes (Wilson & Sperber, 2006). The relevance of an input represents a trade-off between its *positive cognitive effects*—the extent to which it enhances an organism's representation of the world—and the *processing cost*—the cognitive effort—involved in deriving those effects. The main claims of relevance theory are stated in the following two principles (Sperber & Wilson, 1995):

> *Cognitive Principle of Relevance*:—
> Human cognition tends to be geared to the maximisation of relevance.
>
> *Communicative Principle of Relevance*:—
> Every act of overt communication conveys a presumption of its own optimal relevance

To flesh out these principles and to see how relevance theory grounds language, communication and cognition in evolution, it helps to lay out the argument in such a way as to 'work forwards' from basic biology to complex linguistic utterances.

- **The brain is metabolically expensive**: The brain is the organ of cognition. It also very metabolically expensive (Mink et al., 1981). Evolution will, therefore, favour anything that reduces the brain's energy demands or that makes it more efficient.

- **Evolution will favour cognitive efficiency**: Cognitive efficiency is a matter of the balance between costs and benefits. The cost is the mental effort required to process inputs, retrieve memories, make connections, etc. The benefits are the cognitive effects of this processing: the extent to which such processing enriches and changes an organism's knowledge, understanding, beliefs and plans (Sperber & Wilson, 1995). Cognitive efficiency is a matter of being able to select what information—from the environment or from memory—is worth processing at any given time (Sperber & Wilson, 2012b).

- **The Cognitive Principle of Relevance is the generalised case of cognitive efficiency**: The most relevant inputs to cognition are those that provide the greatest cognitive effects for the least processing cost (Sperber & Wilson, 2012b). If cognitive efficiency is a matter of selecting which inputs to attend to, relevance is the quality being maximised in that selection (Sperber & Wilson, 2012b). The tendency to maximise relevance is a universal feature of human cognition, with perceptual, mnemonic and inferential processes all focused towards this end (Sperber & Wilson, 2012a). The maximisation of relevance presents, then, as a kind of 'cognitive regularity'.

- **Ostensive-inferential communicative exploits this cognitive regularity**: For communication to be successful, communicators require the attention of their audience. If the attention and processing efforts of the audience are generally directed to relevant stimuli, then communication can best succeed by being relevant (Sperber & Wilson, 2012a). As a result, and assuming communicators *wish* to succeed, the very act of communicating itself indicates that a communicator desires the audience to see the communication as relevant. The Communicative Principle of Relevance can, therefore, be seen as a consequence of the Cognitive Principle. Communicators will make their ostensions as relevant as possible in order to succeed, while their audience will seek to make the most relevant inferences from those ostensions (Sperber & Wilson, 2012a).

- **Ostensions can take almost any form**: Ostensions need not be linguistic, they can take the form of gestures, facial expressions, deictic points, etc. This fact should be seen in light of the tight coupling of language and other forms of communication discussed above (**1.4.5.3**). Indeed, *any* alteration to the shared environment has the potential to act as an ostension. Consider the following two examples, extracted from Sperber and Wilson, (2012b):

(1) Peter opens the latest issue of *Time Out*, intending not only to see what films are on but also to provide Mary with evidence he would like to go out that evening.

(2) Peter establishes eye-contact with Mary and then taps the issue of *Time Out* before opening it, to indicate that he would like to go out that evening.

In both these examples, Peter is providing ostensive evidence—opening or tapping the magazine, gaining eye contact—from which he wishes Mary to draw certain communicative inferences. These inferences depend, amongst other things, on a shared knowledge of the environment (the content of the magazine) and of its role in their life (that they use that content to plan evening activities).

- **Language is an enhancement of ostensive-inferential communication**: Language is simply one further tool of inferential communication (Sperber & Wilson, 1995). However, language is capable of providing uniquely precise and unambiguous evidence of a communicator's meaning. Consider these linguistic counterparts to the examples above:

(3) PETER: Shall we do something this evening?

(4) PETER: Shall we go and see the 8:30 screening of the new Steven Spielberg film?

The evidence provided in both (3) and (4) differs from that in (1) and (2), in that it comes in the form of a linguistically *coded* utterance. I shall return to this distinction below, when I consider what the ILM and relevance theory have to offer one another. For now, however, it is enough to note that any decoding done here—the retrieval of *utterance meaning*—simply serves to provide one more piece of evidence for a wider inferential process, the retrieval of *speaker meaning* (Sperber & Wilson, 2012b), a process which also draws on shared aspects of background knowledge. For example, by 'do something' in (3) Peter likely means 'leave the house and engage in an activity we both enjoy', rather than, say, 're-arrange the cutlery'. However, in both cases, and especially (4), it is possible to draw much more precise and detailed inferences than it is from either (1) or (2). It is this potential for greater precision that renders language an *enhancement* of this type of communication, rather than simply an additional modality.

- **This enhancement *requires* pre-existing ostensive-inferential communication**: Much like money could only have emerged in the context of a pre-existing economic system, language—as an enhancement of ostensive-inferential communication—only makes sense in the context of a pre-existing system of such communication (Sperber & Wilson, 1995). As Sperber (1990: 758) puts it:

  > ...a language faculty and languages are of adaptive value only for a species already deeply involved in inferential communication.

  In other words, the general form of inferential communication has to be in place prior to its subsequent enhancement through the emergence of a linguistic code. Indeed, it may well be that this embedding in the pre-existing, non-arbitrary aspects of inferential communication, such as gesture, represents a necessary condition for the emergence and integration of a system of arbitrary, learned symbols like language (Garrod et al., 2007; Fay et al., 2010; Brown, 2012).

The relevance theory approach solves both of the problems that seemed to follow from the code model. Firstly, it provides a clear account of the relationship between language and others aspects of human communication. Language, gesture, facial expressions, etc., form one general system of ostensive-inferential communication. That system is also grounded in aspects of human cognition, which in turn are grounded in fundamental evolutionary considerations. The expressivity pressure, then, can be seen as the pressure on language to function expressively within this wider system of communication and cognition. Secondly, it also solves the apparent problem of how a language faculty might become more complex. Under a code model, changes to the faculty that allowed the acquisition of a larger or more complex code would be useless, and likely detrimental, because mismatches in the code cause communication to fail. On an inferential model, there is no need for individuals' representations to coincide, as different decodings may provide evidence for the same inferential interpretation (Origgi & Sperber, 2000; Sperber & Orrigi, 2012; Smith, 2005).

1.4.5.6 – The expressivity pressure in light of relevance theory

It is now time to revisit the origin of the expressivity pressure, in light of the ostensive-inferential model of language as exemplified by relevance theory. To recap briefly, the ILM account of language structure emphasises the interplay between the pressure to be *compressible* and the pressure to be *expressive*. The first of these pressures is inherent to cultural transmission and thus needs no further explanation. The second, however, is not, and so an account of its origin is required. The best supported of these accounts links the expressivity pressure to the use of language for communication. The problem with this *functional explanation*, however, was that it provided no clear account of why *communication*, and not some other function, should be the one that influenced language structure. The obvious solution to this problem, in evolutionary terms, seemed to be that natural selection determined the relevant function. However, this also seemed to leave us in the unrealistic position of proposing that a language faculty could be favoured by selection before there was any language to learn.

The clear problem here lies in the conception of 'communication' that is being employed. Much of the work on the ILM implicitly assumes a code-model of communication, if only as a sensible methodological simplification. As we have seen, however, the adoption of the code model has consequences. One of these is to obscure the relationship between language and other aspects of human communication. Once linguistic communication is ghettoised as operations over a code, it becomes easy to view the evolution of language as the evolution *of that particular code*—or, more properly, the faculty that permits its acquisition. From here, it is but a short step to the bootstrapping problem, and the question of how selection might come to favour a code-acquiring language faculty in the absence of the code itself.

The ostensive-inferential model of language avoids this problem by situating language in the wider context of a multi-modal system of inference-based communication. This allows for the possibility that selection might act not on a code-acquiring faculty, but on the wider capacities underlying inferential communication in general. In doing so, it would favour anything that might enhance the power of that form of communication. As we have seen, language represents just such an enhancement. Another way of looking at this is that it changes the functional question from “Is language well designed for information transfer?” to “Is language well designed to provide the evidence necessary to convey the intended speaker meaning?” (Scott-Phillips, 2010: 297). In other words, we should expect natural selection to influence the specific details of language structure—the code—only inasmuch as it impinges on its capacity to convey evidence for inferential communication. As I shall argue in section **1.5**, this is exactly what we see on the ILM account of structure.

We are now in a position to trace fully the origin of the expressivity pressure. As the iterated models and experiments suggest, its initial source lies in language's communicative function. The reason, however, that language structure had to adapt to fit *this* function rather than another one is, indeed, traceable to natural selection; but not selection for a language-specific, code-acquiring faculty, but rather for enhanced ostensive-inferential communication. This should not be surprising, as from an inferential, relevance-theoretic viewpoint this is simply what language *is*: one further tool of inferential communication, tightly coupled with other modalities such as gesture, which serves as an enhancement of inferential communication by virtue of the specificity of ostensions and inferences it supports. It is from this source that the expressivity pressure originates, and its influence on the cultural system—countering the pressure for compressibility—is to ensure that language remains sufficiently expressive to serve its function as an enhancement of that wider system of inferential communication. The arguments made here should be seen as echoing other calls for the inferential nature of linguistic communication to be more fully integrated into the ILM approach to language evolution (e.g. Scott-Phillips & Kirby, 2013).

1.5 – The role of natural selection in cultural accounts of language structure

The juxtaposition of relevance theory and the ILM brings out one further point, which gets to the heart of what Pinker and Bloom got wrong: *our understanding of language structure can be partially decoupled from our understanding of language function*. This decoupling means that natural selection should not be seen as determining the *specifics* of language structure, but rather as setting the 'boundary conditions' under which structure is produced by the cultural system. To better see what this means, it may help to consider the following two tables, 1.1 and 1.2.

A. All possible language structures			
S^c	S^1	S^2	S^3
S^4	S^5	S^6	S^7
S^8	S^9	S^{10}	S^{11}
S^{12}	S^{13}	S^{14}	S^n

Table 1.1: Natural selection in Pinker and Bloom's model

The set of all possible language structures. Natural selection picks between structures based on functional considerations.

Table 1.1 approximates the picture provided by Pinker and Bloom. There is one overall set of possible language structures, A. Natural selection determines which of these structures language takes on. If language ends up with a compositional structure (S^c), this must be because that structure serves language's communicative function better than the other available structures (S^1...S^n). As a direct corollary, that structure itself must be encoded in the genome. There is, in other words, a very tight coupling between language structure and language function, with the *specific details* of the former following directly from the latter. This tight coupling is required for the code-like communication hypothesised by Pinker and Bloom, because even small structural discrepancies can have profound functional implications.

B. Communicatively ineffective languages			
U	U^1	U^2	U^3
U^4	U^5	U^6	U^7
U^8	U^9	U^{10}	U^{11}
U^{12}	U^{13}	U^{14}	U^n

C. Communicatively effective languages			
C	C^1	C^2	C^3
C^4	C^5	C^6	C^7
C^8	C^9	C^{10}	C^{11}
C^{12}	C^{13}	C^{14}	C^n

Table 1.2: Natural selection in a combined ILM and inferential model

Language structures fall into two possible sets. Those that are ineffective for communication (**B**) and those that are communicatively effective (**C**). Natural selection determines the choice of set **C** over set **B**, but has no role in determining which of the specific structures in set **C** language comes to exhibit.

In contrast, table 1.2 illustrates the picture provided by the union of relevance theory and the ILM. The set of possible language structures is divided in two. Set **B** contains all the communicatively ineffective structures ($U...U^n$). Set **C** contains all the communicatively effective structures ($C...C^n$). This second set includes compositional structure (C), but also any other structure ($C^1...C^n$) that might serve an inferential system of communication equally well. As we have seen, cultural transmission is capable of delivering either communicatively effective (e.g. compositional) or ineffective (e.g. systematically underspecified) structures.

The role of natural selection, via the expressivity pressure, is to influence the cultural process such that the resulting structure comes from set **C**, rather than set **B**. This is what is meant by 'setting the boundary conditions'. However, natural selection has no direct influence at all on *which* of the structures in set **C** language comes to posses. If language ends up with a compositional structure (C), rather than an equally effective alternative (C^n), then this is simply a reflection of the overall dynamics of the cultural process.

The only influence on this process that natural selection can possibly have is the functional demands of the expressivity pressure. If those are satisfied, there is simply no way for selection to determine the outcome in more detail. As a corollary, there is no reason to assume that the specifics of linguistic structure be genetically encoded. This partial decoupling of function and structural details is possible for an inferential system, because its success is not dependent on the genetic micromanagement of the linguistic code. Indeed, one might suggest that it is this very fact that makes the offloading of control to a system of cultural transmission possible in the first place (see chapter two, **2.6**).

It is now possible to bring some clarity to the distinction often made between 'biological' and 'cultural' accounts of language structure. Pinker and Bloom's account is 'biological' not because they invoke natural selection, but because of *what* they thought was being selected. They assumed that the *specifics* of language structure—the choice of structure from set **A**—had a biological base. This assumption follows directly from their code-like view of linguistic communication. Pinker and Bloom's account is 'biological', then, because of their appeal to an exclusively biological *mechanism*. Conversely, the ILM is a 'cultural' account not because it doesn't involve natural selection, but because it ascribes the specifics of language structure—the choice of structure from set **C**—to the overall dynamics of cultural transmission. The role of natural selection—by introducing a pressure for expressivity—is simply to bias those dynamics towards the set of communicatively useful structures (**C**), rather than the set of communicatively ineffective structures (**B**). The ILM is a 'cultural' account, then, because it posits a largely self-organising cultural *mechanism.*

1.6 – The complementarity of the ILM and pragmatic approaches to language

The major contribution that a pragmatic conception of language—as exemplified here by relevance theory—can offer the ILM, then, is to place language in a wider communicative, cognitive and evolutionary context. This is vital, because without this wider context we are unable to think clearly about the interrelationships between communication, cultural evolution and natural selection. The difficulty the ILM faced in providing a comprehensive account of the expressivity pressure is a direct testimony to the need for this wider context. That difficulty stemmed, fundamentally, from the tacit adoption of the code model of communication. This was done, I think, largely for methodological reasons. The good news, however, is that there is nothing about the ILM that requires it to adopt the code model of communication (e.g. Smith, 2005).

However, the ILM also has something of great value to offer relevance theory. The central insight of pragmatic approaches to linguistic communication is that language forms one part of a larger, multi-modal system of inferential communication. This system includes gestures, facial expressions, and non-linguistic vocalisations, as well as language itself. Nevertheless, language still stands out because, although the code model is an inadequate characterisation of linguistic *communication*, language itself *is* a code. This fact in itself is not a problem for relevance theory: decoded utterances simply represent one potential piece of evidence from which inferences can be drawn (Sperber & Wilson, 1995, 2012a). However, relevance theory itself has nothing to say about *how this code might have come into existence*. The ILM, in contrast, most definitely does: the code is the product of an iterated process in which language has to adapt to the circumstances of its transmission.

1.7 – Conclusions

This chapter had two principle aims. The first was to assess the ILM with a critical eye, to try and tease apart exactly how it functions to deliver compositional structure. The second, bearing that critical assessment in mind, was to clarify the necessary evolutionary preconditions for the ILM.

1.7.1 – How does the ILM work?

This question can be given two different readings. The first concerns how the ILM works *internally*. The results of both models and experiments suggest that the principle dynamic here is the interplay between the pressure to be *compressible* and the pressure to be *expressive*. Language has to adapt to both these pressures in order to be successfully transmitted. Language has to compress, therefore, in such a way so as not to sacrifice its expressive power. Compositionality represents a compromise solution that delivers a language that is both compressible and expressive.

However, this kind of internal account is simply not sufficient from the perspective of the present thesis. It shows us *how* such a system of interacting pressures might operate to produce language structure, but it does not tell us *why* the system is composed of those particular pressures and not other ones. The second reading, then, is *external* and concerns the origin of the two pressures identified above.

First consider the pressure to be compressible. Language faces the pressure to compress as an inevitable consequence of it being culturally transmitted. This is a general result of models of cultural transmission (Brighton, 2003; Kirby, 2012) and applies to birdsong (Ritchie, 2008) as much as language. One outcome of this result is that cultural transmission is itself an inherently *structure-creating* process. Given a random system, the sheer fact of cultural transmission will itself impose structure, such that it becomes simpler, more compressed and thus easier to learn. To reiterate, this is a point that goes well beyond language, it is something fundamental about cultural transmission itself. This fact constitutes a powerful extra-biological, *informational regularity*. This regularity should be seen as something akin to the regularities of physics and mathematics discussed in relation to frog embryology and human locomotion in **1.2.3**. Like those regularities, it stands as something ripe to be exploited by the evolutionary process.

Unlike the regularities of physics, however, the informational regularities of cultural transmission do not exist independently of organisms with the capacity to implement them. However, once such organisms appear and begin culturally transmitting their communication systems, those systems can become more structured simply as a result of the regularities of cultural transmission. The language will face the inherent cultural pressure to compress. There is no guarantee, however, that the resulting structure will be adaptive from the *organism's* point of view. Unless, that is, there is also a countervailing influence in the system, such that the structure it produced also had to meet some other criteria.

The expressivity pressure constitutes just such a countervailing influence. This pressure does not arise simply from the nature of cultural transmission. Work in the ILM suggests that it traces to the communicative function of language. This still left open the question of why language had to adapt to a pressure stemming from *that* function rather than another one. The clear evolutionary solution here would be to appeal to natural selection. However, under the code model this answer seemed to lead inexorably into the bootstrapping problem. Once we recognise, however, that language is best conceptualised in inferential terms this problem disappears. Natural selection can be seen to act on this wider system of inferential communication, rather than on an implausibly prescient code-acquiring faculty. Potential language users are, therefore, under selection for enhanced ostensive-inferential communication. This is why language has to adapt to a pressure—expressivity—relating to communication, rather than some other function.

For the ILM, then, the role of biological evolution and natural selection is firstly to create organism's capable of culturally transmitting their communication systems. And, secondly, to pair the regularities that emerge from such transmission with another influence, the expressivity pressure, that sets the boundary conditions within which those regularities operate. Once this is in place, the cultural mechanism—the *internal* workings of the ILM—can deliver a structured language.

1.7.2 – What are its necessary preconditions?

In section **1.4**, five preconditions for the ILM account of language structure were identified:

I. The ability to acquire new signals

II. The ability to acquire and produce new signal-meaning associations

III. The ability to infer communicative intent

IV. The existence of a bottleneck

V. The existence of the expressivity pressure

The final task of this chapter is to recognise that these five preconditions are actually reducible to two underlying factors. The first of these is that the communication system must be learned—be *traditionally transmitted*—rather than unlearned and present from birth (preconditions I and II). In many respects, this precondition is obvious: iterated *learning* can only have an influence on systems that are actually learnt.

The second concerns the presence of certain skills of *social cognition*: the ability to conceptualise others in intentional terms, to share intentions with others in joint attentional situations, and, most basic of all, the *sensitivity to communicative intent*. These abilities underpin the acquisition of large numbers of signal-meaning pairs, and thus the creation of the bottleneck (preconditions III and IV). Importantly, however, these *very same abilities* also underpin a general capacity to engage in ostensive-inferential communication. Indeed, the inference of communicative intent *is* the inferential half of ostensive-*inferential* communication. In other words, an organism capable of precondition III—inferring communicative intent—would also likely be capable of some kind of inferential communication, perhaps non-linguistic in form. As we have seen, language itself only makes sense against the backdrop of such pre-existing inferential communication.

The cognitive skills underlying precondition III, then, also bring about the wider functional context which explains the existence of the expressivity pressure (precondition V). Finally, note how this is also the same set of skills, relating broadly to theory of mind, that were invoked by Smith (2004) to account for a pre-existing bias in favour of one-to-one mappings (**1.3.1**). We can now see, however, that the relationship between language structure and theory of mind is somewhat less direct than Smith envisaged. The importance of theory of mind lies not in its introduction of a domain-general pre-existing bias, but in its underpinning of the form of communication—inferential communication—of which language constitutes an enhancement. Language faces the pressure to be expressive, then, to the extent that its users are under selective pressure for enhanced ostensive-inferential communication.

In conclusion, the ILM account of compositional structure itself requires an account of the following two factors:

1. The evolutionary conditions in which **traditional transmission** might come to play a greater role in a species' communication system

This first precondition puts in place the structure-creating regularities of cultural transmission. Assuming learners with finite time and cognitive resources, a system of signals transmitted in this way will inevitably become more structured over time.

2. The evolutionary conditions which might favour the emergence of those skills of social cognition, most basically the **sensitivity to communicative intent**

This second precondition is important in two different ways. Firstly, it enables the inferential association of signals with meanings, such that the culturally transmitted system is a system of signal-*meaning* pairs. This is what distinguishes language from other culturally transmitted systems such as birdsong. Secondly, it underpins the wider capacity for inferential communication. Language is part of that system of inferential communication. The expressivity pressure is the pressure on language to function *expressively* as part of that wider system. It arises to the extent that communicating organisms are under selective pressure for enhanced ostensive-inferential communication.

The combined effects of these two preconditions, then, is that a *culturally transmitted* system of *signal-meaning pairs* becomes progressively more structured in such a way so as not to sacrifice *expressivity*. In the next two chapters I will take each of these two factors in turn and explore in detail a comparative example with the potential to illuminate what these evolutionary conditions might be.

Chapter 2

Traditional Transmission and the Bengalese Finch

Chapter one presented a critical examination of the Iterated Learning Model (ILM), a body of work which shows that language structure can emerge as an outcome of repeated instances of cultural transmission. The key advantage of the ILM over other accounts of linguistic structure is that it provides an explicit mechanism linking facts about language to facts about individual learners. The major problem for the ILM account, however, is that the very possibility of that mechanism—change in the language itself through a cultural evolutionary process—stands in need of explanation. How might this process have got going in the first place? What, minimally, does a cultural account of linguistic structure such as the ILM need to get started? In addressing these questions, the discussion in chapter one identified two key preconditions. It may be useful to briefly recap these here.

The first precondition is that the communication system needs to be *traditionally transmitted.* The structure of a communication system cannot emerge through a process of iterated learning unless it is actually *learned* from a previous generation, and yet in most species, including our closest great ape relatives, the communication system is not learned in this way. This raises the question of the evolutionary conditions under which cultural transmission might come to take on a greater influence on a species' communication system. The second precondition concerns the emergence of the socio-cognitive skills that underpin the possibility of acquiring a large system of signal-meaning pairs, most fundamental among these skills is the *sensitivity to communicative intent*. The importance of this second precondition is twofold. Firstly, it is crucial that it be a system of signal-*meaning* pairs—as opposed to a system merely of signals, such as birdsong—to permit a generalisation to be made, on the basis of meaning, from the subset of the system that makes it through the bottleneck to the system as a whole. Secondly, those same socio-cognitive capacities underpin the possibility of inferential communication, of which language is an enhancement. Under what conditions, then, might these cognitive skills emerge?

In this chapter and the next I will take each of these in turn and discuss in detail a comparative example in which aspects of one of these preconditions can be seen emerging over evolutionary time. The context in which these preconditions emerged in other species may then illuminate how and why they emerged in humans, and thereby begin the process of filling in the 'missing half' of the cultural account of linguistic structure, as discussed in the introduction. In this chapter I will focus on the first of these preconditions, relating to traditional transmission, and consider the case of the Bengalese finch. In chapter three I will turn to the second precondition. First, however, it is necessary to say something about the logic of these kind of evolutionary comparisons.

2.1 – The logic of evolutionary comparisons

Comparative studies search for similarities between organisms. Such similarities fall into two broad categories. The first category concerns those that derive from a shared ancestry, which are known as *homologies.* Opposable thumbs, for example, are shared by humans, the great apes and old-world monkeys, all of which also share a relatively recent common ancestor. The value of homologies lies in their being a clue to the relatedness of different species, for the purpose of reconstructing phylogeny (Gould, 1976). The main limitation of homologies is that any set of related similarities only constitutes a single data point (Fitch, 2010). We can learn nothing about *why* humans came to have opposable thumbs by looking at the opposable thumbs of chimpanzees: in both cases they were simply inherited from a common ancestor.

The second category of comparative similarity concerns resemblances in form or behaviour that emerge in distantly related species, in what is known as convergent evolution. These similarities are known as *analogies*[14]. The camera eyes shared by vertebrates and cephalopods, for example, were not present in their very distant common ancestor, but evolved independently in the two lineages. The similarities between the vertebrate and cephalopod eye reflects similarities in the 'design problem' (Dennett, 1995) to which those eyes present as a solution. In this case the detection and processing of information available in a certain form of electromagnetic radiation—light. The weakness of analogies lies in their potential to mislead in terms of relatedness. It would clearly be a mistake to see the similar eyes of humans and octopuses as indicating close evolutionary kinship. The strength of analogies, however, lie in the separation of data points that they provide. Crucially, this means that the answer to the question of how and why the cephalopod eye evolved *can* shed light on how and why the vertebrate eye evolved, because their functional similarity suggests they likely evolved in response to a similar set of selective pressures.

To complete a cultural account of linguistic structure along the lines laid out in the introduction, it is necessary to explain *how* and *in what context* the preconditions discussed in chapter one are likely to emerge. It is evolutionary analogies that will prove most enlightening in providing this explanation. As such, the comparative studies described in this chapter and the next are both analogies. In both cases, the broad context in which the relevant precondition emerges is during the process of *domestication.* The purpose of this chapter and the next is to explore how and why domestication might lead to the emergence of these analogous preconditions.

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[14] The distinction between homologies and analogies, at least as utilised in the present chapter, is unaffected by the notion of *deep homology* (Shubin et al., 1997, 2009), in which seemingly analogous structures or behaviours turn out to be based on similar, and thus homologous, genetic and developmental mechanisms. This is because what deep homology really represents is the idea that structures or behaviours that *evolved independently* can be based on shared developmental resources, pathways and genetic bases (Fitch, 2010). It should be clear, of course, that the value of evolutionary analogies lies in their ability to shed light, in a way that homologies cannot, on the shared conditions leading to that independent evolution. The concept of deep homology leaves this unchanged.

2.2 – The Bengalese finch and the white-rumped munia: the differences

2.2.1 – Brief historical account

The Bengalese finch is a domesticated strain of the white-rumped munia (Okanoya, 2002). To appreciate the interest in this particular domestication it helps to have some historical background on the Bengalese finch itself. Its naming in English as the *Bengalese* finch is thought to derive from the fact that the traders who first bought the birds to Britain picked them up in India. The birds are not, however, Indian in origin, with the original domestication tracing to either China or Japan (Svanberg, 2008). One clue suggesting a Japanese origin is the fact that Chinese bird-breeders have historically favoured good singers—not, as we shall see, a trait possessed by the wild munia—whereas Japanese breeders have long favoured white plumage (Svanberg, 2008), a trait for which the *white*-rumped munia is named, and which had come to be much exaggerated in the domesticated finches.

Whatever its origin, it is known that the Bengalese finch has been bred in Japan for at least 250 years, primarily for its white colouration (Okanoya, 2004). What is most interesting, however, is that despite being bred for its plumage, and *not* as a singer, the song of the Bengalese finch has also changed significantly relative to its wild ancestor (Okanoya, 2002). The song has become more complex, less predictable and, most importantly in the present context, learning has come to play a greater role in determining song structure. Learning, that is, from members of the previous generation, or *traditional transmission*. However, because 'learning' is such a broad term, it is useful to place the differences between the two species in the context of a wider discussion of the role of learning in birdsong.

2.2.2 – Dimensions of learning in songbirds

In this section I will describe six dimensions along which song learning differs across species (Beecher & Burt, 2004; Beecher & Brenowitz, 2005; Beecher et al., 2010; Soma, 2011). For each dimension I will give a brief overview of the range of observed variation, together with a comparison of the domesticated Bengalese and wild munia.

2.2.2.1 – When song is learned

The first dimension concerns the time-frame in which songs can be learnt. The basic distinction here is between *closed learners*, who can only acquire their song during a limited sensitive period early in development, and *open learners*, who can continue to learn during adulthood (Brainard & Doupe, 2002). Within this basic distinction sits a range of variation. Some closed learners, such as many species of sparrow (Brainard & Doupe, 2002), have a two-phase sensitive period: a first phase for exposure to conspecific song (the sensory phase), and second for practice and auditory feedback (the sensorimotor phase). In other closed learners, such as Zebra finch, the sensory and sensorimotor phases overlap.

The sensitive period is not tied to chronological age as such, but rather to the extent of experience. Once a certain level of exposure to conspecific song has occurred the bird then becomes 'fixed' and subsequent exposure has little effect. Among open learners, some, such as the canaries (Brainard & Doupe, 2002), exhibit a seasonal pattern, acquiring a new song every year; whereas others, such as European starlings (Hultsch & Todt, 2004), can acquire new songs at any time of the year, and can even acquire songs as adults having been reared in isolation as chicks (Chaiken & Böhner, 2007). Finally, the closed-open dichotomy is probably better thought of as a continuum, as even closed learners are able to modify aspects of song such as amplitude during adulthood (Hultsch & Todt, 2004), despite being unable to acquire new song elements.

Finch vs. Munia: Both the Bengalese finch and the white-rumped munia are closed learners (Okanoya & Yamaguchi, 1997; Soma et al., 2006), as indeed are most other species of Estrilid finch (Soma, 2011). Therefore, while much of the discussion in this chapter focuses on the differences in the roles of learning in the two species, this does not imply that one continues to learn throughout life while the other does not.

2.2.2.2 – The necessity of early experience

The second dimension concerns the importance of early experience to the development of normal song. There are two forms of early experience, each of which is associated with one of the two phases described above. The first concerns the auditory exposure to conspecific song, which is usually investigated by rearing birds in isolation and thus disrupting the *sensory phase*. The second concerns auditory feedback during the *sensorimotor phase*, and can be investigated through experiments in which birds are deafened. If reared in isolation most species of songbirds develop an abnormal 'isolate' song, which differs significantly from the song of their conspecifics (Beecher et al., 2010). In some species, however, such as the grey catbird (Kroodsma et al., 1997) and the European sedge warbler (Leitner et al., 2002) normal song repertoires are generated even when the birds are reared in isolation. As far as I am aware, all birds, including those who develop normal song in isolation (although this has not been explicitly tested; Beecher et al., 2010), require auditory feedback to develop normal song.

Finch vs. Munia: Members of both species also require some exposure to conspecific song (during the sensory phase) and the auditory feedback of their own singing (during the sensorimotor phase) in order to develop normal species-typical song (Bao et al., 2003; Peng et al., 2012). It is not the case, therefore, that one species learns while the other one does not. This similarity brings out an important point. Namely, that the focus of this case study is not the emergence of vocal learning per se—both species are vocal learners—but rather the conditions under which such learning, and the channel of cultural transmission it enables, comes to play a more important role in determining the structure of a species' communication system.

2.2.2.3 – The importance of social experience

The third dimension concerns the nature of that early experience. Much of the work regarding the role of experience and the duration of the sensitive period has been carried out within the 'tape tutor' paradigm (Beecher & Burt, 2004), in which birds learn from recordings of conspecific song. This allows precise experimental control over what learners are exposed to, but omits any social dimension. This omission is important. Some birds, such as the white-crowned sparrow will happily learn from a tape tutor, while others, such as the sedge wren will not (Baptista & Gaunt, 1997). The presence of a live tutor has also been found to influence the duration of the sensitive period. For example, although, as just noted, white-crowned sparrows will learn from a tape tutor, they fail to learn any new song presented after about fifty days, but if presented with a live tutor they can continue learning beyond this point (Baptista & Petrinovich, 1984).

Finch vs. Munia: Both species, again like Estrilid finches more generally, are considered 'social' learners (Eales, 1989; Soma, 2011) in that they learn better from socially interacting with a tutor than they do from tape-tutoring, although it is not clear exactly what it is about the social interaction that accounts for this difference (Soma, 2011). The difference between the two species is not, then, that one needs the social interaction with a tutor while the other does not.

2.2.2.4 – The number of songs learned

The fourth dimension concerns the size of the song repertoire. This varies enormously between species. Some, such as the white-crowned sparrow, only have a single song; others, such as the sedge wren have several hundred songs, while the brown thrasher has over 1000 (Kroodsma, 2004). It should be noted, however, that there are two widely used methods to quantify the size of any given species' repertoire (Gil & Gahr, 2002). In some species songs can be classified into distinct *types*, and so the repertoire size is given by the number of these song types. In other species, songs consist of sequences of elements that are repeated in multiple orders, and the total number of these elements is used as a measure of repertoire size. This gives rise to what has been termed the 'comparability problem' (Gil & Gahr, 2002), in which the repertoire size given for one species may be the result of measuring something completely different than the repertoire size given for another species.

Finch vs. Munia: The Bengalese finch and white-rumped munia do not differ in absolute repertoire *size* under either of the measures discussed above (Honda & Okanoya, 1999), with both species only learning a single song type and differing little regarding the number of elements—with 9.3 and 8.4, respectively. What is interesting, however, is that they differ significantly in terms of the complexity and unpredictability of the transition *between* notes and note groups (Okanoya, 2002, 2012). In other words, while the number of elements has remained unchanged the complexity of the relationships between those elements has greatly increased in the Bengalese finch. Bengalese finches are, in effect, doing much more varied things with the same amount of material. This, then, is the first significant difference between the two species.

2.2.2.5 – Copying fidelity of learners

The fifth dimension concerns the degree to which birds faithfully copy the song of the particular model to which they are exposed. Species lie somewhere on a continuum that ranges from the complete and total imitation of a tutor's song, through improvisations based on the tutor's singing, right up to the individual invention of a species-typical song-type that has no clear connection with the details of any individual tutor (Beecher & Brenowitz, 2005).

Finch vs. Munia: The differences in copying fidelity represent the second significant difference between the two species. The clearest evidence for these differences comes in the form of cross-fostering experiments (Takahi & Okanoya, 2010), in particular from the comparison between the two species when reared by conspecific parents. Munia chicks learning to sing from munia fathers display a very high degree of fidelity. In contrast, the Bengalese chicks are much less accurate in their copying of Bengalese song. The song of Bengalese chicks still resembled that of their particular tutor, but not in the form of an exact replica. In the white-rumped munia, then, song learning is characterised by the very close and faithful copying of a tutor; whereas in the Bengalese finch aspects of the tutors song are combined with improvisations and variations introduced by the learner.

2.2.2.6 – Degree of canalization

The final dimension concerns the degree of canalization, in particular the range of possible songs that a species is able to copy. Some species, such as the white-crowned sparrow, will only copy songs that fit within a narrow, species-specific range (Beecher et al., 2010); whereas others—most famously the mynah bird—are able to mimic any number of environmental sounds (Kelley et al., 2008). The concept of canalization is going to be important throughout the rest of this chapter, as such it will be useful here to provide a more detailed discussion of what it means to say that something is canalized.

A phenotypic trait is said to be canalized to the extent that it appears during the course of development regardless of conditions, and thus exhibits a robustness in the face of developmental perturbations (Flatt, 2005). Another way of putting this is that organisms can arrive at similar phenotypes despite variation in either their genotypes or developmental environments. As a result, the concept of canalization can be further subdivided into *genetic canalization* and *environmental canalization* (Wagner et al., 1997).

Genetic canalization refers to the insensitivity of the phenotype to genetic perturbations, such as mutations, that might otherwise have had a phenotypic effect (Meikeljohn & Hartl, 2002). As such, genetic canalization can be seen as an epistatic phenomenon (Flatt, 2005), in the sense of interactions between genes, and especially the blocking of the effect of one allele by an allele at another locus (Phillips, 2008). The factors involved in genetic canalization are numerous and varied (see Flatt, 2005 for an extensive list); however, a few examples will serve to illustrate the general principle. For instance, in cases where there is a fully dominant allele, the phenotype of heterozygous and the homozygous-dominant individuals will be identical despite differences in their underlying genetics. Another example concerns the so-called 'protein chaperones' that act to mask the effect of mutant polypeptides by assisting in the process of protein folding (Rutherford, 2003). This assistance allows polypeptides with incorrect amino acid sequences, as the result of a mutation in the coding segment of DNA, to successfully fold into the correct three-dimensional structure to function as a protein, for example an enzyme. Again, this mechanism ensures phenotypic similarity despite genotypic differences.

Environmental canalization, by contrast, refers to the insensitivity of the phenotype to variations in the environment. These can either be macroenvironmental variations such as climactic conditions, or random fluctuations in an organism's internal or external microenvironment (Flatt, 2005). In many cases this environmental insensitivity is mediated by some of the same mechanisms as genetic canalization. For example, the protein chaperones described above are also involved in the repair of proteins damaged by environmental stress (Rutherford, 2003). This overlap in mechanisms has led some to argue that there is only a single 'mode' of canalization (Meikeljohn & Hartl, 2002), which serves to buffer development from all kinds of variation in conditions that might otherwise result in deleterious outcomes.

Finch vs. Munia: This is perhaps the most important way in which song-learning between the two species differs. The white-rumped munia exhibits a much greater level of canalization in respect to song learning than the Bengalese finch. The evidence for this is, again, drawn from the cross-fostering experiments, but this time the best illustration comes from what happens when chicks are raised by non-conspecific parents. Munia's are very faithful copiers of munia song, but poor copiers of Bengalese song (Takashi & Okanoya, 2010). Fostered Bengalese chicks, however, are just as faithful in their copying of munia song as they are of Bengalese song. This difference suggests that munias are more constrained—exhibit a greater degree of environmental canalization—in what they will copy than are Bengalese finches (Takashi & Okanoya, 2010). Munias, it seems, are highly constrained learners who will only learn from a narrow range of species-specific songs. In the Bengalese finch, however, this constraint seems to have somewhat broken down.

2.2.3 – Summary

There are, then, three ways in which the song-learning of the Bengalese finch differs from that of its wild ancestor, the white-rumped munia: Bengalese finches, although working with the same number of elements, order those elements in more complex, less predictable ways; they also copy their models less faithfully, often introducing their own variations; and are much less constrained in terms of what they are able to copy, their song-learning is less canalized.

Three important points follow from these differences. The first is that the reduction in learning constraints seen in the Bengalese finch means that the specifics of experience during development (e.g. particular tutor used as model) have a much greater influence on the structure of the resulting song. The second is that the reduction in high-fidelity copying combined with the broader range of what Bengalese chicks will copy has resulted in a much greater variation in song between different finches than is seen in their munia ancestors. Finally, all three of these differences combined have meant that many Bengalese finches have come to sing songs of much greater complexity than seen in white-rumped munias (see Okanoya, 2012: 46, for an account of how this sequential complexity was measured), especially in terms of the decreased predictability of how elements are ordered within a song.

In the wild-living white-rumped munia, we have an example of a stereotypic, highly canalized communication system in which learning plays a minimal role. In its domesticated descendent, the Bengalese finch, song learning is less canalized, the songs themselves are less stereotypic and the influence of traditional transmission on song structure has increased. We see in this example, then, a parallel with the first of the preconditions identified in chapter one: an increase in the role of traditional transmission in relation to the communication system. This change occurred in the context of domestication. Recall, however, that despite this context it cannot be attributed to artificial selection for more complex song.

In the next section I will explore two hypotheses which attempt to account for why this change occurred under domestication. Both the hypotheses discussed below place the shift to a domesticated environment at the centre of the explanation, but they differ as to what the key effect of that shift was likely to be. The first, associated with the work of Kazuo Okanoya, places the emphasis on sexual selection, and the female preference for more complex song. The second, associated with Terrence Deacon, places the emphasis on the global lifting of selective pressure afforded by the domesticated environment and the subsequent shift in the role of epigenetic[15] processes in the context of development.

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[15] Throughout this thesis the term 'epigenetic' is used very generally to refer to *all* non-genetic inputs to the process of development, rather than in its more specific usage denoting a particular kind of non-genetic, physical inheritance, such as patterns of DNA methylation (e.g. Jablonka & Lamb, 1995).

2.3 – Okanoya's hypothesis: sexual selection

The first hypothesis concerns the role of sexual selection, and is outlined in Okanoya (2002: 56) in the following way:

> ...females of the ancestor species [white-rumped munia] preferred more complex songs, but the ability of males of the ancestor species to develop and sing complex songs was limited by constraints in nature, including predation risk and foraging costs
>
> ...[white-rumped munias] developed a finite-state syntax after domestication freed them from predation pressure and other pressures associated with life in the wild. In such a protected environment, song structure can develop as a result of female choice.

The core of this hypothesis is that once the white-rumped munia had shifted to a safer, domesticated environment, the only pressure influencing song structure was sexual selection, in the form of a female preference for more complex song. As a result, the song of the domesticated strain became more complex.

It should be clear, however, that this hypothesis actually requires two strands of evidence to be fully supported. The first is evidence that Bengalese and munia females *actually prefer more complex songs*. This is a claim about mate choice. It needs to be demonstrated that song complexity constitutes a proximate mechanism of mate-choice. The second is evidence showing *why* mate choice based on song complexity might have evolved in the first place. What is the ultimate explanation for the existence of this female preference? Does, for example, song complexity function as a signal of mate quality, and if so how?

2.3.1 – Do Bengalese females use song complexity in mate choice?

The first question to explore in examining Okanoya's hypothesis is whether females actually use song complexity in choosing a mate. One line of evidence that suggests they might concerns differences between male and female finches in their responses to song. Ikebuhci et al. (2003) compared the heart rate responses of male and female finches to novel songs. When presented with a novel song the heart rate of female finches increased, whereas that of male finches did not. Neither males nor females showed any heart rate increase when presented with a novel zebra finch song, suggesting that the female response is to species-specific novelty and not novel sound per se. This result is certainly consistent with the sexual selection hypothesis, but as it deals with song novelty rather than complexity it says nothing about whether female finches respond more to songs of greater complexity. Several studies have, however, investigated this directly.

Okanoya and Takashima (1997; cited in Okanoya, 2004) compared the effects of song complexity on the nest building behaviour of female finches. Three groups of finches were caged separately with a supply of nest building materials. One group was stimulated with a complex song, consisting of a shifting pattern of phrase units; a second group was stimulated by a simple song, consisting of one repeated phrase, while a control group received no stimulation. The females stimulated with complex song retrieved significantly more nesting material than either those stimulated with simple song or the control group. A random ordering of notes, that sometimes produced complex sequences, also failed to elicit the increased nesting behaviour. Okanoya and Takashima also measured levels of the sex hormone estradiol in the three groups. Females stimulated with complex song showed a far greater increase in estradiol levels than the other two groups. There is evidence, then, that more complex song has a greater stimulating effect on female reproductive behaviour and physiology. However, interesting as these findings are, they concern the passive reaction of females to hearing song stimuli. What is needed is evidence that active female mate-choice is influenced by song complexity.

Morisaka et al. (2008) conducted an experiment in which females had to make a choice between perches. Picking one perch caused the playback of a complex song; picking the other resulted in the playback of a simple song. Given the results discussed above, it might have been expected that the birds would exhibit a significant preference for the perch associated with the more complex song. The actual results, however, were somewhat less clear. While half the birds did exhibit a preference for the complex song, most of the rest appeared to choose between the perches randomly, with one bird showing a preference for the simple song. As the authors conclude, the overriding finding of this study was that there was considerable variability in the preferences of female finches. Kato et al. (2010) also examined the active choices made by females. They used an operant selection task, in which touching a response key resulted in the playback of a song stimulus. Females showed a significant preference for their father's song over an unfamiliar song. However, they showed no such preference for a complex over a simple song. The finding here, then, was that females preferred familiar rather than complex song.

It should be noted, of course, that neither of these studies replicated the naturalistic choice *of a mate*, however both do involve females actively choosing between alternatives, and so it is interesting to observe how their results differ from those studies that recorded physiological responses. The major distinction between the two, at least on present evidence, seems to be that there is a much less clear and direct link between female choice and song complexity, than between song complexity and certain physiological reactions that likely contribute to that choice-making process. This assessment fits with the wider literature on song complexity and repertoire size, which has many findings *consistent with* the notion that song complexity is sexually selected, but lacks much clear evidence that females *actually use* complexity as a criteria in the selection of a mate (Kroodsma, 2004). Soma and Garamszegi (2011) conducted a meta analysis of studies into the relationship between song complexity and reproductive success, finding as small but significant effect. This effect was reduced in studies that controlled for confounding factors through the use of multivariate analyses, suggesting that many apparent associations between reproductive success and song complexity might actually reflect other variables such as age or quality of territory.

In terms of the proximate question, then, there seems to be good evidence that hearing complex song is associated with some sexually related physiological changes. The evidence that female Bengalese finches use complex song in mate selection is less secure, but this is in line with the wider literature on sexual selection and song complexity. It is quite possible that the Bengalese finch fits the pattern identified by Soma and Garamszegi, with song complexity playing a small but significant role in determining mate choice.

2.3.2 – Why do Bengalese females have a preference for more complex song?

Female Bengalese finches seem, then, to exhibit some level of preference for more complex song. But the demonstration of this preference is only one half of a complete account in terms of sexual selection. It is still necessary to explain why it is that females have these particular preferences in the first place. Why should song complexity have come to play a role in mate choice?

There exist some disagreement about how best to divide up the various models of the evolution of mate choice, with 'lumpers' suggesting that many of the distinctions are illusory (Kokko et al., 2003) and 'splitters' pointing to the heuristic value of dividing up the various models (Jones & Ratterman, 2009). In this section I will be something of a splitter, as the distinctions seem useful in the context of the present argument. Perhaps the key distinction is between *condition-dependent* and *condition-independent* models (Jones & Ratterman, 2009). In the former, mate-choice preferences are explained by the preferred trait serving as a reliable signal, or *indicator*, of mate quality—in terms of genotype, capacity to invest in offspring, or a combination of the two (see below for further discussion). In the latter, there is no necessary connection between mate quality and the preferred trait. I will first briefly discuss condition-independent models, before turning to one particular condition-dependent model that has received considerable attention in relation to song complexity.

2.3.3 – Sexual selection I: Condition-independent models

One potential explanation for mate preferences is that the selected sex comes to exploit certain sensory biases of the selecting sex (Ryan, 1990), biases which may have evolved for reasons other than mate selection (Fuller et al., 2005). In such a situation female preference may be unrelated to mate quality. Another possible condition-independent explanation for mate preferences is the Fisherian runaway process, in which preferences emerge as a result of a genetic correlation between a preference and a trait (Andersson, 1994). The key point here is that females with a preference for a certain trait are likely to have offspring that exhibit both the trait and the preference (depending on the sex of the offspring). This sets up a spiralling, runaway process in which both the preference and the trait are exaggerated until impinged upon by some other selective pressure (Andersson, 1994; Jones & Ratterman, 2009).

It should be noted, of course, that both these models are only potentially condition-independent. For example, Fisherian-style correlations between trait and preference are also an inevitable part of any condition-dependent model, and sensory biases may play a role in enabling any kind of preference-trait cycle of evolution to get going in the first place (Kokko et al., 2003). The heuristically valuable point, however, is that such condition-independent explanations only posit two factors, a preference and a trait (Jones & Ratterman, 2009), with no necessary link to genetic quality or viability.

2.3.4 – Sexual selection II: Condition-dependent models

In contrast, condition-dependent models posit three factors: a preference, a trait and differences in mate-quality for which the trait functions as an indicator (Jones & Ratterman, 2009). The central question in these kind of models—indeed, the central question in the whole field of animal signalling—is how such indicators are kept reliable, how is *honesty* in signalling maintained? This question relates to the evolutionary stability of the system. There needs to be some mechanism by which the link between the favoured trait and the genetic quality of its bearer is maintained. Without such a mechanism every individual might come to exhibit the favoured trait and it would then cease to function as an indicator of quality, resulting in the breakdown of the signalling system.

Maynard Smith and Harper (1995) survey three mechanisms that are capable of maintaining honesty in animal signalling. The first is what they term a *minimal signal*, which owes its stability to the fact that signaller and receiver have aligned interests, and there is, therefore, no pressure for the signal to become dishonest. The second is when the signal is an *index*, which they define as a “signal that is physically associated with a quality of interest”. For example, when tigers mark their territory by scratching as high as they can on a tree, the height of the scratches is physically linked to their size. The third mechanism is when signals are *cost-added*, which they define as a signal that is “more costly to make than the minimum required to transmit the information”, this is an idea that goes back to Zahavi's (1975) concept of a handicap. The honesty of cost-added signals is maintained because only those individuals of sufficient quality are able to afford the cost of producing the signal. The most famous example of this is the tail of the peacock: only males of the highest quality are able to sustain the cost of maintaining the most impressive tails. As a result, an impressive tail serves as a reliable indicator to peahens of a potential mate's quality.

Which of these mechanisms might be relevant in the case of the Bengalese finch? Minimal signals are an unlikely explanation because of the inherent conflicts of interest between males and females in any sexually reproducing species. Indices may be relevant to some aspects of birdsong, for example differences in fundamental frequency correlate with body size (Ryan & Brenowitz, 1985). However, by far the most investigated possibility is that birdsong can serve as an honest signal of quality because of the costs associated with its production. But what might those costs be in relation to learning and song complexity? Gil and Gahr (2002) survey a variety of different costs that are likely to be associated with various features of birdsong. For example, aspects of song performance such as singing louder or for longer periods carry increased energetic costs and put birds at greater risk of predation. It seems unlikely, however, that repertoire size or song complexity incur the same kind of costs as singing loudly (Gil & Gahr, 2002). One potential mechanism that might maintain the honesty of song complexity as an indicator concerns its relation to stressors during development. This view has been termed the *developmental stress hypothesis*.

2.3.5 – The developmental stress hypothesis

Unlike many of the proposed costs associated with birdsong, the developmental stress hypothesis links the honesty of song complexity as an indicator to costs paid in early development rather than at the time of singing as an adult. This idea was initially put forward by Nowicki et al. (1998: 179):

> ...learned features of song can provide an accurate indicator of male quality because they reflect variation in the development of brain areas mediating the learning process, which in turn reflects variation in the response of individuals to nutritional stresses faced early in life.

In this original formulation it was termed the 'nutritional stress hypothesis', but it has since been expanded to include other potential stressors during development (Buchanan et al., 2003), hence the more general name. The central idea, however, remains the same: exposure to stressors during early life affects brain development, which in turn impacts on song-learning capacity. In this way adult song provides an honest indicator of male quality. The central logic of this hypothesis has recently been generalised to other examples—such as musical production in humans—where the capacity to acquire complex behaviours through learning might signal something about mate quality. This extended form has been termed the *investment in learning hypothesis* (Kirby, 2012).

Returning to the specific case of birdsong, if the developmental stress hypothesis were correct it should be possible to demonstrate the following:

1. That developmental stress impacts adult song
2. That developmental stress affects the development of the song system in the brain

In the sections that follow I will take these two points in turn and discuss the evidence in relation to them both from songbirds more generally. I will then turn to studies investigating whether the developmental stress hypothesis works in the case of the Bengalese finch.

2.3.5.1 – Developmental stress and adult song structure

There is a range of evidence showing that early developmental stress does seem to affect the nature of adult song. Nowicki et al. (2002) found that food restriction during the development of the swamp sparrow resulted in reduced copying accuracy. Buchanan et al. (2003) found that European starlings raised under a regime of unpredictable food deprivation started singing later, spent less time singing and sang fewer bouts as adults. Zebra finches raised under conditions of dietary stress or with elevated levels of the hormone corticosterone have been found to produce shorter songs (Spencer et al., 2003). And European starlings, again raised in conditions of food deprivation or increased corticosterone levels, show shorter song motifs and reduced complexity of song (Spencer et al., 2004).

2.3.5.2 – Developmental stress and the avian song system

A comprehensive survey of the neural underpinnings of bird song is beyond the scope of the present thesis; however, it will be necessary to have a rough idea of the overall architecture of the avian song system. This system comprises two major pathways: the *song motor pathway* (SMP, shown in red in figure 2.1, below) and the *anterior forebrain pathway* (AFP, shown in blue), finally there are a series of sensory and motor feedback connections (shown in green) (Mooney, 2009; Olveczky & Gardner, 2011). Typically, lesions to the SMP disrupt or destroy song entirely, whereas lesions to the AFP have little effect on established song but destroy vocal plasticity, and with it the capacity to learn new song (Mooney, 2009).

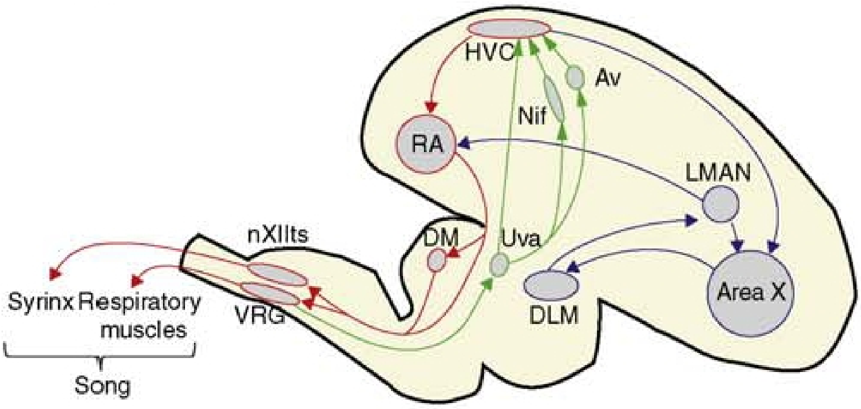

Figure 2.1: The avian song system
(Taken from Ölveczky & Gardner, 2011)

Much of the detail in figure 2.1 can be safely ignored; however, there are three areas I will especially flag up here because they are referred to in the discussion below.

- **HVC** (acronym used as a proper name): this is common to both pathways and is also a target for much of the sensory and motor feedback

- **RA** (Robust Nucleus of the Arcopallium): an important part of the motor pathway

- **Nif** (nucleus interfacialis): an important part of the circuits sending auditory and motor feedback to the HVC

Nowicki et al. (2002) found that food restrictions during development in swamp sparrows were associated with an absolute reduction in size of the HVC, together with a general reduction in the size of the telencephalon (the avian equivalent of the mammalian neocortex). Furthermore, the reduction in size of the RA was greater than that seen in the telencephalon as a whole. In other words, the song nuclei seemed to be disproportionately affected. This finding is echoed by work with zebra finches that also found a disproportionate reduction in the volume of the HVC in response to food restrictions and also to raised levels of corticosterone (Buchanan et al., 2004), together with an association between fledgling weight and the mass of the adult HVC. MacDonald et al. (2006) found that food restrictions in song sparrows resulted in the size of the HVC being reduced at the beginning of the song-learning period in both males and females. Similar findings of reduced HVC volume have been found in canaries (Spencer et al., 2005a) following early parasitic infection, and in zebra finches following raised levels of corticosterone (Spencer et al., 2005b).

2.3.5.3 – Developmental stress in the Bengalese finch

Soma et al. (2006) conducted a study into the effects of early rearing experience in the Bengalese finch. However, unlike earlier studies that used experimental manipulations—such as food restrictions or raised levels of stress hormones—Soma et al. examined the effect of different brood sizes and brood sex-ratios on the subsequent adult song in semi-naturalistic conditions (breeding pairs monitored in a large indoor aviary). Song length was found to be related to body size (itself causally related to brood size). The total number of notes used was also related to brood size. However, the most intriguing result in the present context was that song *complexity* was related to brood size. Soma et al. (2009a), in a similar semi-naturalistic setting, also found that song complexity varied with laying order within a clutch, with those earlier in the sequence having more complex song, a finding the authors suggest may reflect differences in maternal investment. Finally, Soma et al. (2009b) found some evidence that chicks' tutor selection is influenced by song complexity.

2.3.6 – Summary

It seems, then, that there is a good level of evidential support for both the predictions of the developmental stress hypothesis. In the interests of completeness, however, it should be mentioned that there have been some negative results. Gil et al. (2006) and Naguib et al. (2006, 2008) both found that brood-size manipulations had no effect on song complexity or neural development. Brood-size is, however, a somewhat indirect developmental stressor (MacDougall-Shackleton & Spencer, 2012), and other manipulations of brood-size have found an effect on subsequent song (e.g. Holveck et al., 2008; Soma et al., 2006).

Finally, it is important to realise that the developmental stress hypothesis interacts in complex ways with the dynamics of cultural transmission. As discussed in chapter one, models suggest that culturally transmitted systems will tend towards simplicity, or compressibility (Brighton, 2003), in response to the requirement to be learnable, and thus successfully passed between generations (Kirby, 2012). These results, in principle at least, apply to *any* kind of culturally transmitted system, including birdsong. When culturally transmitted systems fail to simplify in this way, it is necessary to explain why.

In chapter one we saw just this dynamic in relation to linguistic structure and the ILM, especially in those examples where there was no pressure on communication, or a proxy thereof, and in which the language became systematically underspecified. In the case of language, it is the functional demands of communication that explain why the system doesn't simply collapse to its most compressed possible state. Models of the developmental stress hypothesis (e.g. Ritchie et al., 2008) indicate that complex, hard-to-learn songs are evolutionarily stable—despite being culturally transmitted, and thus expected to simplify—because it is the very fact of their *being hard to learn* that allows them to function as reliable indicators of mate quality. In both cases, it is these functional demands that prevent the culturally transmitted system from collapsing to its simplest form.

2.3.7 – Developmental stress: some issues

It seems, then, that a sexual selection account of the differences between munia and Bengalese song—based proximally in female preference, and ultimately in indicators of developmental stress—has much to recommend it. In the next section I will consider a second, possibly compatible, explanation proposed by Terrence Deacon. However, before considering Deacon's proposal it should be acknowledged that there are a number of unanswered questions surrounding the developmental stress hypothesis (see MacDougall-Shackleton & Spencer, 2012 for a wider discussion), one of which in particular stands out as important in the present context: Does adult song reflect good genes or good upbringing?

This question arises because an adult bird's song is a reflection of both its inherited genotype and its developmental conditions (plus the interaction between the two). However, the relative influence of these two factors remains unclear. To see why this matters it is important to realise that all models of sexual selection posit, in varying proportions, two kinds of benefits associated with mate-choice (Andersson, 1994; Jones & Ratterman, 2009). The first are termed *direct* benefits, and concern the immediate help that a selected mate can provide, such as defending territory or provisioning food. Variation in the capacity to provide direct benefits may relate to genetic differences, differences in developmental experience, or a combination of the two.

The second concerns *indirect* benefits, where the selected sex—typically the male—provides nothing but their sperm. In these circumstances the female's fitness is increased as a result of her offspring inheriting the genes of the favoured male. It should be clear, therefore, that indirect benefits only reflect genetic differences. The important point in the present context, however, is that for any species in which the developmental stress hypothesis is invoked it is going to be unclear to what extent adult song constitutes an honest signal of conditions of upbringing, and to what extent an honest signal of a good genotype. While it is likely that both are important in most cases, it is also true that the relative importance of each—and the balance of direct and indirect benefits—may well vary between species.

This point is well illustrated by the case of the European sedge warbler, which has one of the largest, most complex song repertoires of all songbirds, a trait that has been driven by sexual selection (Leitner et al., 2002; Kroodsma, 2004). As noted above, however, the European sedge warbler doesn't need to be exposed to singing models during development to acquire this song, and can reach, and even exceed, normal repertoire sizes when raised in isolation (Leitner et al., 2002). Furthermore, there is no difference between the sizes of song system nuclei such as the HVC and RA between warblers reared in isolation and those exposed to singing models. Intriguingly, the great variety of song produced by isolate sedge warblers suggests that, rather than inheriting whole song repertoires, what they inherit is a powerful capacity to *improvise* (Leitner et al., 2002).

The original formulation of the developmental stress hypothesis particularly emphasised *learned* features of song as an indicator of condition, but in the sedge warbler no learning is required. Instead, song complexity reflects the condition of the highly heritable song system, and its potential to support improvisation. In the European sedge warbler, then, while song complexity and variety certainly serve as honest signals of genetic quality, they fail to differentiate between individuals with a normal developmental experience and those whose experience was as aberrant as total isolation. It seems, then, that a demonstration of a capacity to learn is not the only way in which song complexity can serve as an honest signal of condition. I shall return to this point at the conclusion of the chapter.

2.4 – Deacon's hypothesis: relaxed selection and degeneration

Deacon (2003b, 2009) has proposed an alternative hypothesis to explain the changes in the song of the Bengalese finch. Like Okanoya's hypothesis, Deacon's has a central role for domestication. Where it differs, however, is that Deacon argues that the changes in song could occur in the absence of positive selection, which in Okanoya's account is driven by female preference. Indeed**,** for Deacon the song of the Bengalese may have changed *as a result of* that absence of positive selection. The thinking here is that much of the action of natural selection concerns the maintenance of current structures and behaviours through the elimination of mutations (Powell, 2011), a process known as purifying or stabilising selection (Barton et al., 2007). As such, natural selection can often act as something of a conservative force, which actually prevents the emergence of novel structural or behavioural configurations.

Deacon's arguments raise a range of issues relevant to this thesis: including, the relationships between natural selection, external regularities and self-organization; how to best think about multiple forms of evolutionary inheritance; and the contexts in which new complex behaviours are likely to emerge. As such, this section presents a detailed description, investigation and evaluation of Deacons views. In order to provide a target for that wider discussion, I shall begin with a condensed presentation of Deacon's hypothesis:

The shift from the wild to the domesticated environment introduced a wide-ranging *relaxation of selection* on the structure of the munia song, this included sexual selection as birds were now exclusively paired up by breeders. In other words, many of the selective pressures influencing song structure in the wild were no longer relevant under domestication. Selection had, in effect, ceased to operate on song structure. In this context, mutations affecting the munia's song-learning biases, which would previously have been eliminated by selection, would now be free to accumulate, resulting in the breakdown, or *degeneration*, of those biases. Another way of looking at this is that the shift to a domesticated setting caused variation in the biases to be *masked*, to become *invisible to selection*.

For Deacon, this breakdown of previously constraining biases is the key part of the explanation. If, following this breakdown, song learning becomes less canalized—less restricted to a narrow, species-specific range—then a variety of factors that had previously only had a minor influence on song structure might be free to increase in importance. These might include early auditory experience, social context, general learning biases or the propensity to improvise. This shift in influences would then come to be reflected in changes in the brain, with areas that had previously had little role in the song system, coming to have a greater involvement in song formation. Finally, there is likely to be a *redistribution of selection* away from the maintenance of strong biases and towards capacities related to those new influences.

The changes in Bengalese song following domestication are, on this account, not explained by any selective pressure in favour of greater variation and complexity, but instead result from a lifting—a relaxation—of selective pressures that had previously maintained the song as simple and stereotypic, through the exclusion of other potentially complexifying and diversifying influences. Maintained, that is, munia song in its highly canalized form. The rest of this section presents a detailed breakdown of this hypothesis, with a particular emphasis on the terms in italics, above.

2.4.1 – The visibility of variation: masking and unmasking

Deacon's argument starts from two basic facts of evolution. The first is that natural selection can only act on phenotypes, meaning that selection can only eliminate variation if it is phenotypically expressed. The second is that selection operates through differential reproductive success, meaning that only variation that actually influences reproductive success can be selected for or against. As a result, variation is only *visible to selection*—that is, can spread or be eliminated through selective processes—if it is both phenotypically expressed *and* has an influence on fitness. Of course, evolution per se can still occur in relation to variation that does not meet these two criteria, through processes such as genetic drift, but what cannot occur is evolution *by natural selection*.

It follows, then, that there are two ways in which variation can be *in*visible to selection. The first is for variation to have no phenotypic effect. This is part of the phenomenon of developmental canalization, discussed above, in which many of the processes operate by preventing variation from finding phenotypic expression. Recall the example of dominance relationships among alleles, which mean that the phenotypes of homozygous-dominant and heterozygous individuals are identical, despite underlying variation in their genotypes.

The second way for variation to be invisible is for it to be phenotypically expressed but have no effect on fitness. This is related to an organism's environment and the selection pressures it faces in that environment. For example, it is quite possible that the precise size and shape of the human earlobe is of so little consequence in terms of reproductive success that the genetic variation underlying it is practically invisible to selection. However, perhaps the most interesting possibility concerns shifts from one situation to the other: Either from a position in which visible variation becomes invisible, a process Deacon terms masking; or from a position in which invisible variation becomes visible, which Deacon terms unmasking. Deacon considers the move from the wild to domesticated environment to have initiated just such a shift.

2.4.2 – Masking through functional redundancy

These kind of shifts, in which masking or unmasking occurs, can be found in relation to both of the ways that variation can be invisible to selection, but the consequences of the shift differ between the two. In both cases the possibility for such shifts derive from the existence of *functional redundancy*. The different consequences depend on whether that redundancy is internal or external to the organism in question. The following examples, taken from Deacon (2009), illustrate this distinction.

Consider first the phenomenon of gene duplication (Zhang, 2003), in which a segment of DNA is accidentally copied, often by being inserted into another chromosome as a result of an error during meiosis. Prior to the duplication event, any mutations affecting the single copy are liable to have serious phenotypic consequences, perhaps resulting in the organism being unable to synthesise a vital species of protein. After the duplication event, however, the existence of *two* copies mean that any mutations that might accumulate in one of them are actually invisible to selection, they are masked by the presence of the second copy, which can ensure they have no phenotypic effect.

This masking is the result of a kind of functional redundancy: there are now two genes performing the same function. Intriguingly, this functional redundancy can actually be an important step towards the production of new kinds of functional complexity. Perhaps counter-intuitively, this possibility exists *because of* the potential build-up of mutations such redundancy allows. In most instances these mutations are likely to be neutral or deleterious, eventually resulting in the production of a non-functioning pseudogene. However this need not always be the case, especially as the duplicated segment begins as a fully functional coding sequence of DNA. Indeed, just this kind of process is thought to account for the existence of multiple forms of haemoglobin (Storz et al., 2013). In this case, however, the redundancy is internal to the organism. This is important because it means that the organism *does not lose the original function*. The end result is either one functional copy plus a pseudogene, or a functional copy of the original gene plus a novel functional configuration in the second copy.

In contrast, consider the case of vitamin C acquisition in primates. Unlike most mammals, primates, including humans, are unable to endogenously synthesise their own vitamin C (Ha et al., 2004). Primates are entirely dependent on exogenously obtained, dietary vitamin C. This is not the result of any dramatic genetic difference between primates and other mammals; all the required genes are present in the primate genome. However, the gene for one vital enzyme involved in the later stages of vitamin C synthesis, known as GULO, has degenerated to pseudogene status. Such a vital biochemical pathway would, presumably, be under strong selection to be maintained, so how have these mutations managed to accumulate?

Deacon's (2009) answer is that the availability of dietary vitamin C in food items such as fruit masked variation in the effectiveness of endogenous synthesis. Note that this variation would still be phenotypically expressed: some individuals would still synthesise vitamin C endogenously, whereas others would not. But with adequate dietary vitamin C, this phenotypic difference would cease to have fitness consequences. With this variation thus invisible to selection, there would be no way for any mutations to be eliminated, resulting in an eventual degradation to pseudogene status.

This example also involves functional redundancy, in the form of two sources of vitamin C. The key difference, however, is that one of these sources is *external* to the organism. The importance of this is that once the ability to synthesise vitamin C endogenously had been lost, primates effectively became 'addicted' to food items such as fruit, with diet now the only source of the still-necessary vitamin. When the redundancy is external there is the possibility that the internal function can be lost entirely. A further corollary is that this internal loss can result in the unmasking of variation related to the capacity to exploit the external source. In terms of vitamin C, this might include variation underlying traits associated with the acquisition of fruit, such as colour vision, digestive tolerance and foraging techniques.

2.4.3 – The two faces of Deacon's hypothesis: degeneracy and parsimony

It should be clear now that Deacon's hypothesis regarding the Bengalese finch shares some similarities with both the gene-duplication and vitamin C examples, just discussed. As in gene-duplication, the emergence of new complexity was initially dependent on variation coming to be invisible to selection. However, like the vitamin C example, this variation was masked extrinsically by a change in the environment. In relation to vitamin C, the environmental change related to the supply of the vitamin in the diet, which specifically masked variation underlying endogenous synthesis. As such, the degeneration observed was also specific. In the Bengalese finch case, however, the relevant environmental change is the shift to the domesticated setting.

Domesticated environments differ in a wide variety of ways from their wild equivalents (Price, 1999, 2002; chapters four **4.5.1.3** and five **5.1**), presenting the possibility of a more wide-ranging relaxation of selection. Deacon (2010: 9004) terms this phenomenon *global redundancy*, but it might be better thought of in terms of domesticated environments *buffering* organisms from a wide range of selective pressures (Price, 1999, 2002). One way of reading Deacon's account, then, is that the Bengalese finch is actually a *degenerate* white-rumped munia, whose species-specific song-learning biases have broken down in the highly buffered context of domestication, with increased complexity following as a kind of side-effect of this degeneration.

There is, however, a more positive way to read Deacon's hypothesis, which connects it with the discussion in chapter one (**1.2.3**) of how evolution can exploit extra-biological regularities. This involves what Deacon terms an *epigenetic parsimony principle*, which he (2009: 742) describes in the following way:

> ...we should not assume genetic micromanagement of epigenetic processes, but rather only genetic regulation of the boundary conditions affecting processes that have the potential of arising by self-organization

> Epigenetic biases and constraints that are reliably present or that reliably emerge during development, due to adaptive flexibility or extragenomic influences, will tend to mask selection maintaining corresponding genetically inherited information. Thus the genome will tend to offload morphogenetic control, in the course of evolution, in a way that takes advantage of the emergent regularities that characterise many epigenetic processes.

On this view, the Bengalese finch could be described as a munia that has offloaded the control of the details of its song structure to epigenetic processes; offloaded them, that is, to a non-genetic, cultural form of inheritance. The role of genetic inheritance could then be seen to have shifted away from tightly controlling song structure and towards setting the boundary conditions under which those epigenetic processes self-organize. The differing role of learning in the munia and Bengalese might be seen, then, as reflecting the differing degrees to which each species' song was open to being shaped by non-genetic, heritable influences. In the highly canalized munia, the tight genetic control of song structure restricts the role of non-genetic influences such as cultural transmission. In the less canalized Bengalese, those aspects of non-genetic inheritance are free to have a much greater influence. Rather than a simple case of degeneration, might the breakdown of biases be seen instead as an example of evolution exploiting the properties of cultural transmission?

This question opens up a range of issues that are important not just in understanding the Bengalese finch but also in relation to the role of culture in evolution more generally. This relationship was a major theme of the last chapter, as part of a very focused discussion of the ILM. The conclusion there was that the ILM is best viewed as exploring a set of extra-biological, informational regularities, whose structure-creating dynamics can be exploited by evolution, in much the same way as can regularities deriving from the laws of physics. It is time now to return to that line of thought, but with a much wider focus. Once this survey is completed, I will apply its conclusions to the Bengalese finch.

2.4.4 – Epigenetic parsimony: evolution and multiple inheritance

To fully appreciate Deacon's position it helps to view it in the light of other perspectives on evolution, inheritance and development. Like all discussions of evolutionary theory, this has to begin with the union of Darwinian natural selection and Mendelian genetics known as the *Modern Synthesis* (see Mayr & Provine, 1980 for a historical overview). The outcome of this synthesis, stated in a single line, is as follows:

> adaptation is the result of natural selection on Mendelian variation
> (Barton et al., 2007: 32).

A fuller unpacking of this terse statement, cast in present-day terminology, might go something like this (drawn from Futuyama, 2005; Barton et al., 2007):

With regard to evolution, a clear distinction can and should be made between an organism's observable characteristics—its *phenotype*—and its complete set of genes, its *genotype*. Phenotypic variation between organisms is attributable to both genetic differences and environmental influences, plus the interaction of the two. However, the kind of variation required for adaptive evolution, *hereditary variation*, is underpinned by the transmission between generations of particulate Mendelian units of inheritance, or genes. The influence of the environment on the phenotype, and the changes the phenotype undergoes during its lifetime, often termed acquired characteristics, are not inherited. The source of evolutionary variation is genetic mutation. Mutation is random with respect to adaptation: appropriate beneficial mutations do not arise in response to need. This variation is further amplified, at least in sexually reproducing species, through the processes of recombination during meiosis. As a result, populations of organisms contain a large amount of diversity in their genotypes. Evolutionary change is the result of alterations in the frequencies of different genotypes in the population. This can occur either as a result of random fluctuations (e.g. genetic drift), or as a result of non-random changes resulting from the differential reproduction of some variants rather than others (selection). This non-random process of selection is what accounts for the emergence of adaptive complexity, the appearance of design.

This summary illustrates three important aspects of the modern synthesis view of evolution. The first is that inheritance is identified solely with genetic material, with DNA. The second, following from the first, is that, from the perspective of evolution, development can be 'black boxed' (Hall, 2012). If genes are the only developmental resource that is also heritable, and thereby relevant to evolution, then the rest of the developmental process can be ignored, can be viewed as an example of the 'internal', functional biology of an organism, in contrast to the 'external' biology of evolution in the lineage over time (Mayr, 1982). Finally, evolution can be seen as consisting of two distinct phases: an entirely *random* phase—of mutation and recombination—by which variation arises; and an entirely *non*-random phase—of natural selection—by which the relative proportions of different variants in the population change over time. All three of these points, and by extension the adequacy of the modern synthesis, have come under increasing attack in recent years (e.g. Pigliucci, 2007; Jablonka & Lamb, 2005; Rose & Oakley, 2007).

There is insufficient space here to consider all of these attacks. However, one point made by many of those critical of the modern synthesis is that the heritable inputs to development are more than simply DNA—and also include non-genetic forms of physical inheritance[16] (Jablonka & Lamb, 1995), together with behavioural (Avital & Jablonka, 2000), cultural (Jablonka & Lamb, 2005; Richerson & Boyd, 2005) and ecological (Odling-Smee et al., 2003; Mameli, 2004) kinds of inheritance. Given this variety of inputs to development, and the fact that it is the developmental process itself that produces the phenotypes that undergo selection (West-Eberhard 2003), the idea that development can be black-boxed has come to seem less and less tenable, a view that has contributed to the rise of *evolutionary developmental biology*, or evo-

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[16] In much of the literature this is referred to as *epigenetic inheritance*, however as the term 'epigenetic' is beset with multiple uses—one of which has already been employed in this thesis—I thought it best to avoid confusion.

devo (Carroll, 2008; Hall, 2012). These developments need to be taken seriously. The question is not whether they are going to be incorporated into evolutionary thinking, but what form that incorporation is going to take (Hall, 2012, Pigliucci, 2007). What, in other words, is the best way to conceive of the relationship between genetic and other forms of inheritance? This question is important because both language and birdsong represent forms of non-genetic inheritance, and Deacon's concept of epigenetic parsimony directly concerns the relationship between different forms of inheritance.

One potential answer to this question would be to treat all the inputs to the developmental process equally, and not to 'privilege' one input—typically the genetic—over any of the others. This is the answer advocated by *developmental systems theory* (DST) (Griffiths & Gray, 1994; Oyama, 2000). According to the DST approach it is not possible to identify particular units, or 'replicators', as specially responsible for variation being *heritable* variation. Instead, what replicates is the developmental system as a whole, including the full range of inputs and their interactions (Griffiths & Gray, 1994, 2005). The various inputs to the developmental system, while not seen as necessarily identical or equally important, are viewed as being similar *in kind*, such that no major distinctions, metaphysical or otherwise, can be made between them (Griffiths & Knight, 1998).

This view has been criticised for its commitment to a vague holism and for failing to provide criteria for what does and does not belong to any particular developmental system (Sterelny et al., 1996). I want to pursue a somewhat different objection, however, because it presents a challenge not just to DST but to any attempt to incorporate non-genetic inheritance into evolutionary theory.

2.4.5 – Intrinsic and extrinsic inputs to development

This challenge concerns the distinction between *intrinsic* and *extrinsic* developmental inputs (Dickins & Dickins, 2008). At the core of this distinction is the fact that inputs can only function as such for systems whose intrinsic design prepares them to make use of those inputs. For example, infra-red light cannot function as an input to human vision—although it can for various insect species—because the intrinsic design of the human ocular system does not permit it. This same logic, argue Dickens and Dickens (2008: 47), applies to the process of development as well:

> Genes are not only intrinsic features but they are also inherited, and they are consistently brought to each developmental situation, and therefore consistently set the agenda for other inputs.

It should be noted how this parallels Deacon's position outlined above. Where Dickens and Dickens have 'set the agenda', Deacon has 'regulation of the boundary conditions'. Indeed, a further quote from Deacon (2009: 743) illustrates that he was thinking along very similar lines:

> This does not mean, however, that we should treat genetic and epigenetic inheritance as simply parallel...Although gene expression depends upon epigenetic processes and epigenetic processes depend on conditions produced by genes, the genetic information is embodied in a structural artifact whereas epigenetic information is dynamical in origin and must emerge anew in each developing organism.

In both these views, then, the role of genetic inheritance, embodied as it is in a 'structural artifact', is to set up the conditions—based on some aspects of intrinsic design—that permit the influence of other inputs to development.

Following this line of argument, Dickens and Dickens discuss claims made by Lickliter and Honeycutt (2003: 823) regarding the role of various factors, including the light-dark cycle, in determining levels of gene expression. It should be obvious how the argument applies to this example: the light-dark cycle can only serve as an input to development—exercising, as it does, some influence on gene expression—because of the intrinsically inherited preparedness of the system to respond to this input. As such, it makes little sense to consider genes and cyclical variations in illumination as equivalent *kinds* of input to the process of development.

2.4.6 – Intrinsic and extrinsic forms of inheritance

Some have claimed that the existence of multiple forms of inheritance requires, in and of itself, that our understanding of evolution needs to be reformulated (e.g. Mameli, 2004; Jablonka & Lamb, 2005; Bonduriansky & Day, 2009). Bonduriansky and Day (2009) present a survey of non-genetic forms of inheritance[17], including non-genetic forms of physical inheritance, behavioural inheritance and cultural inheritance. They argue that the evolutionary importance of these forms of inheritance lies in the 'decoupling' they introduce:

> nongenetic inheritance decouples phenotypic change from genotypic change and, in so doing, can overcome some of the limitations of genetic inheritance.
> (Bonduriansky & Day, 2009: 120)

At first sight this may seem persuasive. However, the distinction explored above between intrinsic and extrinsic inputs to development should make us wary of this position. It is not enough simply to demonstrate that there *are* multiple forms of non-genetic inheritance, it is also necessary to show that these various forms of inheritance are similar *in kind* to genetic inheritance, that they play a similar role. A consideration of the forms of non-genetic inheritance discussed by Bonduriansky and Day shows, however, that this is not the case, that they do not play a similar role to genetic inheritance.

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[17] Bonduriansky and Day (2009: 106) define non-genetic inheritance as: “any effect on offspring phenotype brought about by the transmission of factors other than DNA sequences”.

The first step in making this clear lies in the realisation that all the forms of non-genetic inheritance listed above are actually aspects of *phenotypic plasticity*. Ironically, this point is made rather well by Bonduriansky and Day themselves (2009: 108):

> Nongenetic inheritance can be viewed as a transgenerational form of phenotypic (developmental) plasticity...Indeed, because variation in the expression of a nonplastic trait can reflect only genetic variation by definition...only phenotypically plastic traits are susceptible to nongenetic inheritance.

I will return to the question of transgenerational transmission below. For now, however, the most important point is that the mechanisms underlying phenotypic plasticity are themselves the product of adaptive evolution (Schmitt et al., 1995, 1999; De Jong, 2005). Phenotypic plasticity allows organisms to respond to changes in their environments that occur during their lifetime, to respond to novel environments and to modify and adjust aspects of their physiology and behaviour in light of experience. While the precise changes and challenges an organism is likely to face in its lifetime are not predictable ahead of time, the fact that it *will* face such changes is predictable. Phenotypic plasticity is an evolutionary response to this fact.

Phenotypic plasticity represents, then, the mirror image of the concept of environmental canalization discussed above (**2.2.2.6**). Where environmental canalization describes the *insensitivity* of the phenotype to environmental variations, phenotypic plasticity refers to the *sensitivity* of the phenotype, its ability to respond, often but *not always* adaptively to variations in the environment (Flatt, 2005). This last point is vital and is worth elaborating further. The following quote from West-Eberhard (2003: 36) sums up the situation nicely:

> While...we should not assume that observed phenotypic plasticity is adaptive, both continuously variable and discrete plasticity are products of switches whose thresholds are subject to genetic variation and adaptive adjustment by natural selection

This quotation makes two points very clearly. Firstly, the notion that plasticity represents an adaptation to the predictability of unstable environments in no way entails that every plastic response should itself be adaptive. The various mechanisms of phenotypic plasticity (discussed below) are favoured because statistically—on average—they produce adaptive responses, but neutral and maladaptive responses should be expected in relation to all aspects of plasticity. Secondly, while natural selection is not directly responsible for the details of any particular plastic response, it is responsible for the mechanisms that deliver those responses.

This last point represents the distinction between the *direct* and *derived* functions of a trait (Millikan, 1984). The direct function of phenotypic plasticity is to allow organisms to respond to changes in their environments. The derived functions are all the particular plastic responses to particular environmental changes or experiences. For example, the direct function of learning mechanisms is to allow us to acquire knowledge and skills during our lifetime. My *particular* instance of learning to play tennis in this *particular* lifetime represents an example of a derived function. Derived functions, then, are particular instantiations of direct functions.

Phenotypic plasticity serves, therefore, to 'tailor' the phenotype in light of environmental circumstances (Dickens & Rahman, 2012). The 'decoupling' of genotypic and phenotypic change noted by Bonduriansky and Day is thus a natural consequence of this tailoring. The mechanisms by which this phenotypic tailoring occurs are many and varied. The following represents a partial list, drawn from West-Eberhard's (2003) major overview of the topic.

- Exploratory growth in plants, for example growing towards light or *phototropism*
- Response of skin pigment cells to light
- Remodelling of bone and muscle
- Somatic selection, as seen in the overproduction and then culling of both neurons and antibodies

- Behavioural flexibility
- Learning both individually and from others[18]

Crucially, however, these mechanisms of phenotypic plasticity are only possible at all because organisms are intrinsically structured in such a way as to permit their tailoring role. This intrinsic structuring includes the capacity of aspects of the body, such as the musculature, to alter in response to experience, the capacity to produce a range of flexible behavioural responses and the capacities that permit learning both individually and from others. All these capacities have a genetic basis—the 'switches' noted by West-Eberhard—and it is only as a result of that genetic basis that phenotypic plasticity is possible at all.

Nothing about this last point is changed in any way by the fact that some aspects of phenotypic plasticity can be inherited. Heritable aspects of phenotypic plasticity are only heritable at all because organisms are intrinsically structured to permit that inheritance. That intrinsic structuring is provided by genetic inheritance. Non-genetic inheritance is, then, *extrinsic* inheritance, and shares much in common with developmental influences such as the light-dark cycle. In both cases they can only influence development to the extent that the intrinsic structuring of the organism permits that influence.

It should be made clear that I am not denying the existence of non-genetic inheritance, nor am I denying the possibility that it can have very interesting effects on development and possibly evolution (West-Eberhard, 2003). What is being argued, however, is that it is simply untenable to treat genetic and non-genetic inheritance as similar *in kind*. Genetic inheritance is intrinsic. It is responsible for structuring organisms in such a way as to 'pick out' which aspects of the environment

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[18] Culture, or more properly, the capacity to learn culturally transmitted behaviours, should also be seen as part of phenotypic plasticity, both in humans and other species. I will discuss cultural inheritance in more detail below, as I think it represents a particularly complex instance of non-genetic inheritance.

and which forms of extrinsic inheritance to which an organism is able to respond.

Indeed, the balance between canalization and plasticity struck by different genotypes can be seen, in part, as differing responses to the question of how much and what kind of influence extrinsic, non-genetic inheritance should have on the phenotype. Selection acting on genes, therefore, influences not only those aspects of the phenotype that are strongly canalized and thus under close genetic control, but also the extent to which other non-genetic aspects of plasticity are able to modify the phenotype. It is for this reason that genetic inheritance can be seen as the place where the 'buck stops' (Dickens & Rahman, 2012).

To put this point more broadly, the rejection of a strongly constraining innate or modular explanation does not in and of itself entail that natural selection is no longer relevant. Strongly constraining innate modules are simply one *mechanism* natural selection can use to bring about adaptive outcomes. Similar adaptive outcomes can also be produced through the enabling, biasing and 'boundary setting' influence natural selection can have on non-genetic inheritance and other self-organising developmental influences. While it makes sense, therefore, to distinguish between plastic and 'hard coded' responses, it makes little sense to distinguish between aspects of plasticity and natural selection. The mechanisms of plasticity are themselves produced and—just as crucially—*maintained* through a process of 'adaptive adjustment by natural selection' (West-Eberhard, 2003: 36). It is this adjustment that accounts for why plastic responses, heritable or otherwise, are statistically—on average—non-random with respect to adaptation. Phenotypic plasticity represents, then, an alternative *mechanism* whereby adaptive outcomes can be produced.

In the next section, I shall argue that exactly this same analysis applies to those aspects of plasticity associated with culture. It is for this reason that the ILM should not be viewed as an alternative to natural selection. Rather, it presents as an alternative to the kind of innate, highly modular *mechanism* outline by Pinker and Bloom.

2.4.7 – Cultural inheritance as a complex example of extrinsic inheritance

It is likely that some who accept the wider characterisation of non-genetic inheritance outlined above, as extrinsic and best considered part of phenotypic plasticity, will baulk at the idea that *cultural* inheritance[19] should be considered in the same way. The likely basis for this objection is that culture has its own temporal and historical dimension, in which it exhibits many aspects of an evolutionary process (Mesoudi et al., 2006). However, I want to suggest that this objection is rooted in a failure to distinguish clearly between the process of cultural *evolution*—in which cumulative culture emerges through the differential spread, reproduction and elaboration of cultural variants—and the role played by cultural *inheritance* as one form of non-genetic inheritance passed between generations of organisms.

2.4.7.1 – Cultural *inheritance* vs. cultural *evolution*: the seeming dilemma

Considered in the wider perspective of evolution, cultural *inheritance* is clearly a form of extrinsic inheritance and an aspect of transgenerational phenotypic plasticity. Much like the other forms of non-genetic inheritance discussed above, the very possibility of cultural inheritance is itself dependent upon certain aspects of intrinsic design, such as particular cognitive processes (Tomasello, 1999; Boyd & Richerson, 1996). Only those organisms whose intrinsic, genetically based structuring permits the kind of social learning required for cultural transmission can possibly be influenced by cultural inheritance. As we have seen, these learning capacities are one mechanism of phenotypic plasticity. This point remains unchanged by recent arguments suggesting that social learning capacities may themselves be culturally

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[19] Some have objected that culture is not really *inherited* at all, but rather *inferentially reconstructed* (e.g. Sperber, 2000). For present purposes, however, I will continue to treat cultural inheritance as falling under the umbrella of non-genetic inheritance, in the sense advocated by Bonduiransky and Day (2009; see footnote 17).

acquired (e.g. Heyes, 2012). Even if accepted, this would simply alter *what* we took that intrinsic structuring to consist in—directly encoded social learning capacities vs. the preparedness to acquire those capacities during development—rather than the *role* played by that intrinsic structuring per se.

The fact that culture is part of phenotypic plasticity can be seen most clearly through a consideration of the nature and origin of the variation involved in cultural inheritance. The generation of genetic variation through mutation is an entirely random process, at least with respect to adaptation (**2.4.4**). In contrast, there is no analogue to this random process in the generation of cultural variants (Henrich et al., 2008; Dickens & Rahman, 2012). Instead, the possible variation in cultural inheritance is always related to aspects of intrinsic design. Cultural variants that fit the model and content biases of human learners (Henrich & McElreath, 2003), together with those that fit other kinds of 'attractors', including those related to memory and other cognitive capacities (Henrich et al., 2008), are more likely to appear and spread than other variants.

The argument here is not that the content of culture can simply be 'read off' from human cognition (indeed, see below), but rather that the composition of the pool of cultural variants is skewed *from the outset* by the biases and capabilities of cultural organisms. This is quite unlike the random origin of genetic variants, but exactly what we should expect if culture is part of phenotypic plasticity. As discussed above, mechanisms of phenotypic plasticity are calibrated as a 'best guess' at how to respond to the certainty of *some* change without any foreknowledge of *what* that change will be. This is precisely the role played by the biases and attractors associated with the social learning of cultural variants. In some cases these will reflect strategies that statistically—on average—provide adaptive outcomes, such as 'copy the majority' or some aspects of content biases. In other cases they will reflect more general memory or cognitive limitations.

However, if our analysis were to stop here, we would miss something very important.

While the capacities and biases underlying social learning in humans are indeed mechanisms of phenotypic plasticity, they can have results unlike those of the other aspects of plasticity or extrinsic inheritance discussed above. By enabling cumulative transgenerational transmission, they set up a new process with its own historical dynamics. This is the process of cultural *evolution*. It concerns the way that cultural variants themselves change in response to repeated acts of transmission and can have a range of surprising and powerful effects.

To take an example from the study of language evolution, the evolutionary plausibility of a strongly constraining, innate language faculty is reduced by the presence of cultural transmission, whose internal dynamics can amplify the effects of weak biases, thereby masking the strength of those biases from selection (Smith & Kirby, 2008). In other words, the process of cultural transmission can produce variants that while consistent with the biases of learners, could not possibly be deduced or 'read off' from those biases. More generally, cultural evolution can be seen as Darwinian in its own right, exhibiting many parallels to biological evolution (e.g. Mesoudi et al., 2004). There are, for example, large numbers of cultural variants that compete for space in human brains and exhibit differential reproduction. Once again, the outcome of this process is not one that can be 'read off' from a consideration of the properties of individuals.

This leaves us with what might be taken as something of a dilemma. When we look at cultural *evolution*, its temporal nature and the fascinating, unpredictable outcomes it can produce have suggested to some that culture should occupy a similar position to genetics in a 'dual inheritance' model of evolution (e.g. Richerson & Boyd, 2005). However, when we step back and look at the role of cultural *inheritance*, the view that it is similar in kind to genetic inheritance is unsustainable. It is clearly an aspect of phenotypic plasticity and clearly a form of extrinsic inheritance, and yet this position seems to ignore the importance of cultural evolution.

2.4.7.2 – Epigenetic parsimony resolves this dilemma

Deacon's conception of epigenetic parsimony provides an insightful resolution to this dilemma. Under this view, genetic inheritance—as intrinsic and embodied in a structural artefact—sets the agenda regarding which other potential inputs can and cannot have a developmental influence. Some of those other inputs, particularly cultural inheritance, will themselves derive from temporally extended, dynamical processes that can be exploited by evolution, and lead to results that could not have been predicted without a consideration of the nature of those systems. This allows us to see why there should be such an apparent mismatch between the status of culture as seen from the perspective of cultural *evolution* as compared to that seen from the perspective of cultural *inheritance* and its wider role in evolution. The modification of the phenotype through cultural inheritance represents an aspect of phenotypic plasticity, much like the other forms of non-genetic inheritance discussed above. However, this particular aspect of plasticity also creates an emergent system with its own evolutionary dynamic.

The temporal dynamics of cultural evolution should be thought of as a system of informational regularities, regularities that derive from the way in which cultural variants themselves have to change in order to be transmitted. These regularities can then be exploited by evolution—much like physical or mathematical regularities—through the production of organisms whose intrinsic design permits such regularities to function as inputs to development, and whose biases steer those regularities in particular directions. The generationally repeated exploitation of these regularities can produce something that resembles a kind of 'cumulative phenotypic plasticity', in which individuals can draw on the flexible responses of previous generations as well as their own. Thus while cultural inheritance differs in kind from genetic inheritance, it also differs in kind from developmental inputs such as gravity or temperature, because it derives from a process that has its own historical dimension with its own dynamics. Nevertheless, these extra complexities aside, cultural inheritance is just as much a form of extrinsic inheritance as the other kinds discussed above. While the mechanism may be more complex, exhibiting its own historical dynamics, it is unmistakably a facet of phenotypic plasticity. Indeed, the fact that this aspect of plasticity gives rise to such self-organising dynamics is one of the consequences that can bear on the adaptive adjustment of the 'switches' described by West-Eberhard (2003).

2.4.8 – Epigenetic parsimony as a general organising principle of multiple inheritance

Deacon's notion of epigenetic parsimony, in which genes regulate the “boundary conditions affecting processes that have the potential of arising by self-organization”, is actually an alternative way of characterising the exploitation of extra-biological regularities, discussed in chapter one. It is worth revisiting some examples considered there, but recast in Deacon's terminology. In human locomotion, the down-step is delivered 'for free'—is self-organized—as a result of a minimal setting of the boundary conditions by genes in order to exploit the physical regularities of gravitation. This view allows for the fact that gravity constitutes an input to the human developmental system, but avoids the mistake of treating very different kinds of inputs as the same. Similarly, the form of symmetry breaking seen in the embryological development of the frog depends upon a genetically co-ordinated exploitation of self-organization arising from the laws of physics.

The discussion of the ILM in chapter one also concluded that it was best understood in similar terms. The specifics of language structure are the outcome of a process of cultural evolution. This process is a self-organizing dynamical system of structure-creating informational regularities. The boundary conditions under which this self-organizing process operates are set by the intrinsic design of language learners, in the form of the genetically inherited pragmatic capacities and biases underlying inferential communication. These boundary conditions ensure that the language has *some* structure that is communicatively useful, but have no direct influence over exactly what structure eventually emerges.

Deacon's perspective also allows us to situate in a wider evolutionary context the finding that cultural transmission amplifies weak biases, and thus prevents the emergence of strong ones (e.g. Smith & Kirby, 2008). This outcome is sometimes glossed as culture acting to 'shield' the strength of the bias from selection. However, the discussion in this chapter and the last provide an alternative viewpoint from which to describe this same result. Strong biases fail to emerge because they are *unnecessary*, given that the same outcome can be produced more easily through the exploitation of regularities inherent in cultural transmission, an exploitation for which weak biases will suffice. Once the environment includes cultural transmission, weak biases that set the boundary conditions for the self-organising properties of cultural transmission, can come to be preferred over strong biases that micromanage the details genetically.

The 'shielding' and 'regularity exploitation' views are not mutually exclusive, but the alternative presented here allows us recognise that the presence of cultural transmission—and thus the regularities with which it is associated—itself forms part of the environment in which adaptation occurs. In an environment with gravity, there is no need to genetically encode much of the details of the down-step in human locomotion. Similarly, if the plasticity of an organism permits cultural transmission, there is no need to encode strong biases if weak biases will produce the same result through cultural amplification. In each case, selection is putting in place the capacity to exploit a reliably present extra-biological regularity, rather than tightly encoding the trait in the genome.

The concept of epigenetic parsimony can be seen, then, as the general form of the account of the ILM presented in chapter one. Before moving on to apply this line of reasoning to the Bengalese finch, it may be useful to place this general form beside the more specific argument made in the last chapter.

Epigenetic parsimony: General form

Evolution will favour the exploitation of reliably present, non-genetic regularities in order to produce an adaptive outcome over the 'hard coding' of that same outcome in the genome. The role of genetic inheritance is to set the boundary conditions under which those non-genetic regularities can successfully self-organize to deliver that adaptive result.

Epigenetic parsimony: Language structure

Once there are organisms engaged in the cultural transmission of their communication system, the structure-creating capabilities of cultural transmission represent a reliably present, non-genetic regularity. If the genetically inherited, intrinsic structure of those organisms also renders them capable of and under selection for inferential communication, then this acts, through the expressivity pressure, to set the boundary conditions such that the self-organizing process of cultural evolution delivers a language that is not only structured but structured in such a way as to also be communicatively useful.

2.4.9 – Epigenetic parsimony and regularity exploitation in the Bengalese finch

We are now in a position to apply this reasoning to the Bengalese finch: The shift to the domesticated environment provided a context in which something that had previously been tightly specified intrinsically by the genome—song structure, as limited by tightly constraining biases—was partially offloaded onto an extrinsic channel of inheritance, namely learning during early auditory experience. Something that had once been transmitted through the genetic inheritance system, came to be transmitted through the behavioural inheritance system (Jablonka & Lamb, 2005), with song structure coming to be much more determined by early auditory experience. Or, to be more precise, the relationship between the two inheritance systems shifted: rather than tightly constraining song structure, the role of genetic inheritance came to be to set the boundary conditions that enabled the exploitation of the possibilities inherent in cultural transmission.

In Deacon's terms, there was a *redistribution* of selection, away from the maintenance of strongly canalizing biases and towards an intrinsic design that facilitated the exploitation of the extra-biological regularities in cultural transmission. Rather than create a degenerate munia, domestication may have laid the grounds for the epigenetically parsimonious offloading of the control of song structure. I shall return to this argument towards the end of the chapter, where I will outline a Bengalese counterpart to the general and language-structure forms of epigenetic parsimony described above. For now, however, with Deacon's hypothesis fleshed out in some detail, it is time to consider a range of evidence relating to its plausibility in the case of the Bengalese finch.

2.4.10 – Evidence for Deacon's hypothesis

Several lines of evidence bear on the plausibility of Deacon's hypothesis. The first concerns other contexts in which selective pressure might come to be relaxed. For Deacon, the role played by domestication centres on the breakdown of wild-type biases in a buffered context where selective pressure was relaxed. By this logic, similar changes to song structure should also occur in other contexts where selective pressure becomes relaxed. Kagawa et al. (2012) compared the songs of three wild populations of white-rumped munia on the island of Taiwan. The syntactical complexity of munia song was found to vary in relation to the number of sympatric, closely related species. One of the key functions of song is species recognition, which is important in order to avoid the infertile hybrids that often result from cross-species matings. This is best achieved through the use of simple, stereotypic songs that exhibit little variation. In locations with fewer sympatric close relations, however, the selective pressure on species recognition is relaxed. The greater song complexity found in areas with fewer sympatric species could well be another example of song complexification following a relaxation of selective pressure.

The second strand of evidence relates to the levels of stress hormone in white-rumped munia and Bengalese finches. Suzuki et al. (2012) report measurements of fecal corticosterone, a hormone known to be directly involved in the development of the song system (Suzuki et al., 2011). Bengalese finches were found to have lower levels of corticosterone than white-rumped munia, regardless of whether the munia had been wild-caught or captive raised, indicating that it is domestication of the lineage that matters here and not simply the conditions in which an individual bird was raised. Indeed, changes in hormonal regulation are known to commonly follow from domestication more generally (Price, 2002; Trut et al., 2009; chapters three and five, this thesis). As discussed above, a range of work shows that higher levels of corticosterone negatively affect the development of the song system and can reduce the complexity of the resulting song (Spencer et al., 2003; Buchanan et al., 2004). If this is the case, then the finding that domestication can reduce levels of corticosterone in finches—perhaps through consistently reduced levels of stress in a buffered environment—might well provide a physical mechanism whereby the relaxation of selection following domestication could induce song complexification.

A third line relates to the impact of lesions to various parts of the song system. Bilateral lesions to the Nif (see figure 2.1) in the Bengalese finch have been found to significantly disrupt their ability to sing more complex songs (Okanoya, 2004; Hosino & Okanoya, 2000), rendering the songs of lesioned birds more like that of the white-rumped munia. Similar lesions performed on Bengalese finches that already sang simpler, munia-like songs failed to produce this disruption. This finding echoes work with zebra finches (Vu et al., 1995, cited in Okanoya, 2004), whose fairly simple song showed no detectable changes following bilateral lesions of the Nif. The Nif is part of the auditory and motor feedback circuits and is, therefore, just the kind of brain area that, on Deacon's hypothesis, should be expected to become more involved in the song system in a situation where strong, species-specific biases had begun to degenerate, and learning and auditory experience become more important.

Finally, Ritchie and Kirby (2007) present modelling work that supports the logical coherence of the idea that increased complexity can follow simply as a result of relaxing selective pressure. The formal support for Deacon's view provided by the modelling work combines well with the identification of an actual selective pressure (species recognition) that might be relaxed; a mechanism (reduced levels of stress hormone) that could produce increased song complexity following domestication; and neural changes (the recruitment of new areas to the song system) that might reflect that complexification. There is, then, good evidence that song complexification *could* have occurred simply as a result of the relaxation of selection following domestication. However, there is one major problem with Deacon's hypothesis.

2.4.11 – A weakness in Deacon's hypothesis: sexual selection and breeding efficiency

Perhaps the greatest weakness of Deacon's hypothesis is the claim that *sexual selection* was also relaxed following domestication, as a result of birds being paired up by breeders. If this claim were true, then all the evidence regarding female preference and developmental stress, while independently valid, could not possibly apply under domestication. There are, however, two arguments that suggest this claim cannot be supported. Firstly, the idea that humans have controlled *every* Bengalese finch mating over the last 250 years seems both unrealistic and impossible to verify. Secondly, even if we assume that human breeders did have complete control over all matings since domestication, this would still not eliminate sexual selection as a possible explanation. If female finches prefer more complex song, then a female paired with a male who sings a complex song will be more receptive and aroused than a female paired with a male singing a simple song. There are, in other words, differences in the 'breeding efficiency' (Okanoya, 2004) of different pairings that could permit a role for sexual selection even if all those pairings were entirely determined by human breeders.

It is not possible, therefore, to rule out a role for sexual selection on the grounds that, once domesticated, all pairings were made by breeders. This means that although there is good evidence supporting a role for relaxed selection, those who hypothesise such a role have to find an accommodation with arguments relating to sexual selection. The obvious question arising from this, of course, is whether the two hypotheses should be seen as alternatives or as complementary.

2.5 – How compatible are the two hypotheses?

In recent publications, Okanoya seems to have begun integrating aspects of both hypotheses, arguing that domestication masked various selection pressures, particularly species recognition, thereby permitting increased variation and complexity, and that this process was then reinforced by female preferences (e.g. Kagawa et al., 2010; Okanoya, 2012). In other words, the two explanations *just happen* to be pushing in the same direction. This is a reasonable union of the two positions. However, the logic behind the evolutionary exploitation of regularities discussed in chapter one, and Deacon's concept of epigenetic parsimony discussed above, hints at a more intriguing relationship between the two hypotheses. To make this possible relationship clearer, consider the following simple question: Why should a demonstration of fitness through song complexity necessarily involve *learning*?

To appreciate the force of this question, consider again the case of the European sedge warbler, discussed several times previously in this chapter. These birds sing complex songs with large repertoire sizes that are the result of sexual selection (Kroodsma, 2004). However, as discussed above, sedge warblers reared in isolation are able to develop full song repertoires (Leitner et al., 2002). Quite obviously, then, the complexity of an adult warbler's song does not reflect its capacity to *learn*, but rather, as Leitner et al. report, its capacity to *improvise*, which in turn is related to highly heritable aspects of the neural song system. It is true that the original formulation of the DSH referred to 'learned features of song', but it did so with reference to nutritional and other stressors that might impair the development of the neural structures that underpin that learning.

What matters is not learning per se, but the *capacity* for which learning serves as evidence, a capacity which is dependent upon the healthy development of neural structures. But in the sedge warbler, the evidence for this capacity is not provided by learning but by *improvisation*. As Leitner et al. point out, this has important implications for our understanding of how sexual selection works in relation to both birdsong and brains. However, the immediate question here is, why, when the song of the Bengalese finch complexified after domestication, did it not do so in a way similar to the sedge warbler? Why did the female preference for complexity not drive male Bengalese finches to become virtuoso improvisers? Why, instead, did song complexity come to reflect the capacity to learn, rather than the capacity to improvise?

One potential answer to this question seems to follow directly from Deacon's hypothesis, in particular its emphasis on relaxed selection. If the wide-ranging relaxation of selective pressure following domestication were sufficient to cause an increase in song variation and complexity—and there is evidence that it is—then selective pressure stemming from female preference might be most easily satisfied by exploiting the breakdown of biases, reduction in canalization, and the increased role of learning and traditional transmission thereby enabled. Put simply, did the complexity of song in the Bengalese finch—serving as an honest indicator of neural condition—come to be demonstrated through a capacity to learn, rather than to improvise, because the relaxation of selection accompanying domestication had *in and of itself* already provided the conditions under which learning might come to play a greater role?

This question allows us to present a Bengalese counterpart to the general and language-structure forms of Deacon's epigenetic parsimony principle:

Epigenetic Parsimony: Bengalese finch

Once cultural transmission, as a result of relaxed selection under domestication, had come to play a more prominent role in the birds' communication system, the structure-creating capabilities of cultural transmission also represented a reliably present, non-genetic regularity. If the genetically inherited, intrinsic structure of those (female) birds also makes them favour *complex* song, then this acts, contra the tendency for culturally transmitted systems to simplify, to set the boundary conditions such that the self-organizing process of cultural evolution delivers a song that is not only structured but also complexly structured.

2.6 – Comparison with the ILM and language

This view of the Bengalese finch has some intriguing parallels with the discussion of the ILM account of language structure in chapter one. Consider first the Bengalese finch. Once domesticated, it would have been quite possible for selection to have favoured an increased capacity to improvise and then utilise the complexity of song produced by improvisation as the signal of mate quality, much like in the sedge warbler. Deacon's arguments suggest, however, that song complexity came instead to reflect the capacity to learn—the capacity that is, to engage with a culturally transmitted form of inheritance—because domestication had already introduced the circumstances where such cultural transmission could take on a more prominent role. In other words, the increased complexity of Bengalese song was achieved through the exploitation of the structural possibilities and regularities inherent in cultural transmission. Recall, however, that the structure produced by cultural transmission tends towards simplicity and compressibility, at least if unchecked by some countervailing pressure. It is the female preference for complex song that provides this counter-pressure. Once this female preference is 'plugged in' to the cultural dynamic, cultural transmission not only creates structure, but complex structure directed towards a particular functional end.

Next consider the case of language, which exhibits some striking parallels. Work in the ILM sees language structure emerging through a cultural process. In this case, too, the inherent regularities of cultural transmission are able to generate structure. However, the same caveat applies: unless the inherently simplifying dynamics of cultural transmission are balanced by some counter-pressure, that structure will tend towards increasing simplicity and compressibility. As argued in chapter one, in the case of language this counter-pressure derives from its use in communication. In particular, from the demand that language function effectively as an enhancement[20] of the wider, multi-modal system of inferential communication of which it forms a part (Sperber, 1990; Sperber & Wilson , 1995). This functional demand could have been satisfied, at least in logical terms, through the kind of detailed genomic specification of a UG advocated by Pinker and Bloom (1990). Instead, however, work in the ILM suggests that this same functional outcome can be achieved simply through 'plugging in' the functional pressure for enhanced inferential communication into the cultural dynamic. Once this union has occurred, cultural transmission not only creates structure, but complex structure directed to some functional end.

The most intriguing aspect of the parallel, however, is that in neither case do the specifics of that structural complexity actually matter that much, at least when viewed from a functional standpoint. For language, as long as the structure produced by the cultural system forms an effective enhancement to inferential communication, the details of the structure produced by the cultural process don't matter that much. In the terms used in chapter one (**1.5**), it doesn't matter whether the language becomes structured in line with compositionality as we know it (C) or in line with an

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[20] As discussed in chapter one, language can be seen as an *enhancement* of inferential communication by virtue of the high degree of precision it grants its users with regard to the ostensions and inferences that can made using linguistic evidence.

alternative (C^n) that provides an equally good compromise between the pressure for learnability, deriving from the sheer fact of cultural transmission, and the pressure for expressivity, deriving from communicative need. The fact that language is structured to reflect the need for expressivity *at all*, and not just learnability, is down to natural selection introducing the competing pressure into the cultural system; the form taken by that compromise structure is the result of the overall dynamics of the cultural process.

Equally for birdsong, the exact pattern of notes and note transitions that together make a given song complex really don't matter; as long as the song *is* complex, then the capacity to learn it can serve as a reliable indicator of quality. The fact that culturally transmitted birdsong is complex *at all* is down to natural selection introducing a pressure which competes with the simplifying tendency inherent in cultural transmission; the form of that complexity reflects the dynamics of the cultural process that gave rise to a particular song.

This point about the exact form of structure not mattering is important. It makes sense of why evolution was able to produce these systems—language and birdsong—by exploiting the potentialities inherent in a set of extra-biological regularities—cultural transmission—over which it could have only ever have had limited control. This works because, in Deacon's terms, all evolution by natural selection needs to do is set the boundary conditions under which the exploitation of such regularities can occur; the self-organizing nature of the regularities themselves does the rest. In the case of language those boundary conditions might be glossed, following arguments in chapter one, as, 'the resulting system has to possess sufficient expressive power to enhance the capacity to provide evidence, in the form of *ostensions* from which others can draw *inferences*'. In the case of birdsong, the boundary conditions might be glossed as, 'the system must be complex enough that the capacity to learn it can serve as an honest indicator of quality'. Within these wide remits, the exact form of the system can be left to the dynamics of the self-organising cultural process.

2.7 – Conclusions

Two preconditions were identified in chapter one for the very possibility of a cultural account of linguistic structure. In this chapter a comparative case study was examined which saw the first of these preconditions—an increased role for traditional transmission—emerging in a species of songbird, the Bengalese finch. Both the major hypotheses for how and why this change is likely to have occurred put the concept of domestication central to their explanation. In particular, both focus on the buffered nature of domesticated environments, which allows for the relaxation of various selection pressures that may have prevented traditional transmission from increasing in importance in the wild. The buffering provided by domesticated environments and the relaxation of selection it enables will form a major theme in later chapters of this thesis. It is also likely that this process was further driven by selective pressure from female preferences. Furthermore, the degeneration of biases permitted by the buffering under domestication may have interacted with this pressure from female preference in interesting ways. Or, to put it another way, such pre-existing pressure may have been satisfied by exploiting possibilities inherent in a situation in which such biases broke down.

Chapter 3

Sensitivity to Communicative Intent and the Domestic Dog

Chapter one identified two preconditions for the possibility of a cultural account of linguistic structure: an increased role for *traditional transmission* and the emergence of the *sensitivity to communicative intent*. The possible conditions surrounding the first of these were examined in chapter two, through an extended discussion of the domesticated Bengalese finch and how its song has changed in comparison to its wild ancestor. In this chapter I will turn to the second precondition, with an examination of how domestication may have lead to the emergence of a sensitivity to communicative intent in dogs.

Before turning to this task, however, it may be helpful to consider some differences between the two preconditions. Considering the first, it is easy to see how traditional transmission might be important: if structure is produced through iterated instances of learning, then it is necessary that the communication system actually *be learned*, rather than simply present from birth. In the case of the sensitivity to communicative intent, however, the relationship is somewhat less direct. This second precondition relates to the need for signals to be paired with meanings, specifically the learning of a large system of *arbitrary* signal-meaning associations. Such a system cannot be acquired without the capacity to *infer* the meaning associated with a given signal.

As discussed in chapter one (**1.4.3**), this kind of inference relies on a wide-range of socio-cognitive skills, such as theory of mind and the capacity to engage in joint-attentional activities, many of which may be unique to humans. This full suite of skills is unlikely to be found in other species, making it hard to identify any analogous cases. As a result, the focus of this chapter is on one specific skill—the ability to recognise that an action was meant communicatively *at all*—that represents a necessary foundation for all the more advanced inferential capabilities.

3.1 – The domestic dog and communicative intent

Starting in the late 1990s a number of studies appeared describing how domestic dogs were particularly adept at using human communicative cues, such as pointing (e.g. Hare et al., 1998; Soproni et al., 2001). Of particular interest was the fact that dogs seemed to outperform chimpanzees and other apes (Miklósi et al., 1998; Hare et al., 2002), and indeed seemed more similar to human children in this respect (see Povinelli et al., 1999). Of course, these findings immediately raised a whole range of questions.

- How might we explain the presence of this ability in dogs?

- In what way did dogs utilise these cues, did they understand them as communicative or did the cues merely function as a form of stimulus enhancement?

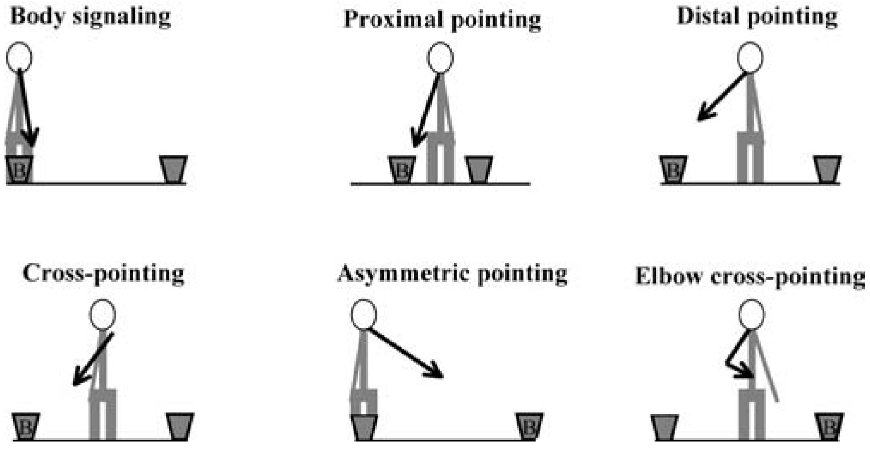
- To what extent is this ability present in other species?

In the discussion that follows I will address these questions amongst many others. However before moving on to this discussion it is necessary to have a clear understanding of the methodology used in these experiments, for much of what follows will depend on the details and subtle variations of this methodology, the *object-choice task*.

3.1.1 – The object-choice task

The basic procedure of the object-choice task is very simple. Out of sight of the subject, a piece of food or other desirable item is placed in one of two or more locations. The location with the food is then indicated to the subject, through pointing or some other cue, and the subject is then allowed to choose between the locations (Miklósi & Soproni, 2006). The question of interest, of course, is whether the subject can use the cues to select the correct location. The details of the implementation vary between studies in ways that will be referred to as and when they arise. However, before moving on to a thorough discussion of the studies themselves it is necessary to have at least an overview of the various pointing cues. This is because the differential patterns of success between species in utilising the various cues is important in comparing their abilities and the nature of their comprehension of the cues.

The pointing cues used in these studies vary along three dimensions: (1) the distance from the target; (2) the relationship between the pointer and the target; and (3) the kinds of arm movements used in the pointing (Miklósi & Soproni, 2006). Figure 3.1 provides a representative, although not exhaustive, sample of the variety found amongst the first two dimensions.



Body signaling

Proximal pointing

Distal pointing

Cross-pointing

Asymmetric pointing

Elbow cross-pointing

Figure 3.1: The object-choice task.
(Taken from Miklósi & Soproni, 2006)

There are three factors to take away from figure 3.1. The first is that pointing cues can be delivered by an experimenter who is equidistant between two locations, in which case it is referred to as *symmetric pointing*, or by an experimenter closer to one location than the other, in which case it is *asymmetric pointing*. The second is that the experimenter can be either close to the locations while giving the point, known as *proximal pointing*, or further away, known as *distal pointing*. Finally there is the way in which the arm is used, with either the ipsilateral arm fully extended, or the contralateral arm used in so-called *cross-body pointing*.

The third dimension—the kind of movement used—divides into the following three categories. *Static pointing*, in which the experimenter is already in the pointing position when the subject enters the test area and remains pointing until the choice is made. *Dynamic pointing*, in which the point is produced in full view of the subject and, again, the arm remains in position until the choice is made. And, *momentary pointing*, in which the experimenter points in full view of the subject but withdraws their arm after a few seconds (Miklósi & Soproni, 2006). In addition to pointing, many of the studies discussed below also utilised a range of other cues such as touching or placing a marker on the correct location, shifting gaze towards the location, and even iconic representations and photographs.

This dry march through the methodology is necessary because the interpretation of the studies that follow depends on the combinations of cues and actions that various species are able to utilise. The most important point here, and one that will be repeatedly returned to in the discussion below, concerns the extent to which a comprehension of the *communicative* nature of the cues is necessary for success on the task. It is quite possible, for example, to be successful with some cues, such as tapping or sustained proximal pointing, purely as a result of stimulus enhancement. As a result, that is, simply of attention being drawn to one location over the other, without any need to recognise the communicative nature of the attention-drawing action. Other cues, however, such as iconic representations and momentary distal points, are much less salient in this regard.

The real test, however, lies in the *pattern* of success and failure exhibited by a given species. If that pattern relates closely to the salience of the cue as a form of stimulus enhancement, then it becomes difficult to ascribe communicative comprehension. If, however, a species were to be successful across a range of different cues, regardless of their stimulus-enhancing saliency, then this would serve as much better evidence that they recognised their communicative nature. Finally, such a recognition is even more strongly confirmed if a species not only utilises cues of varying *forms*, but also modifies that utilisation in response to the *ostensive content* of those cues. For example, by responding differently to intentionally given communications than to very similar physical actions produced 'by accident'.

3.1.2 – Three initial hypotheses

In terms of accounting for this capacity in dogs, Hare et al. (2002) put forward the following three hypotheses:

(a) The *canid generalisation hypothesis*: that this ability is common across canids, and that dogs simply inherited it from their ancestor, the grey wolf.

(b) The *human exposure hypothesis*: that dogs' skills at utilising communicative cues should vary in line with their degree of experience with humans, with the corollary that younger dogs should be less skilful than older dogs.

(c) The *domestication hypothesis*: that dogs acquired this capacity during the process of domestication, with the corollary that dogs should be more skilful than wolves, and that variations in experience with humans should not affect the performance of either species.

Hare et al. then conducted a series of experiments to examine the differing predictions of these three hypotheses. In their first experiment they replicated the finding that dogs outperform chimpanzees in the use of communicative cues. In their second experiment they compared the performance of dogs and wolves on the use of three communicative cues: Gaze+Point+Tap (GPT), in which the experimenter gazed at the correct location, extended their (contralateral) arm and gave the location a tap; Gaze+Point (GP), the same as GPT except that the tap was replaced by a (dynamic, proximal, cross-body) point; and Point (P), in which no gaze was used, only pointing alone. There was also a control condition in which no cue was used. Dogs significantly outperformed wolves on their use of all the cues. In their third experiment there was no difference between dogs and wolves on a non-social food-finding game. Finally, in experiment four they tested puppies aged 9 to 26 weeks under the same conditions described for experiment two. The puppies were able to utilise all the communicative cues above chance, and showed no effect of learning over the trials, or differences dependent on rearing history.

The findings reported by Hare et al. relate to two major issues: the differing abilities of dogs and wolves and the presence of these abilities in even young puppies. Subsequent studies have gone on to explore both these points.

3.1.2.1 – Dogs compared with wolves

Turning first to the dog-wolf difference, Miklósi et al. (2003) compared dogs and wolves that had been socialised with humans to a comparable level. They found that wolves socialised with humans could use touching and, to a limited extent, pointing cues in a food-finding task, although there was significant individual variation between wolves, and they were still inferior to dogs. They then went on to test how dogs and wolves react when faced with a similar but insoluble task. Here a striking difference emerged. The dogs initiated and maintained face and eye contact with the human experimenter to a much greater extent than the socialised wolves. Miklósi et al. argue that this difference goes some way to explaining the inferior performance of wolves, as a reluctance to engage with the human hampered the extent to which the wolves were able to extract information from any communicative cues.

Virányi et al. (2008) related this difference in eye contact to differences in the object-choice task. They compared hand-reared wolves that had been intensively socialised and displayed no wariness of humans, hand-reared dogs that had been specifically bred for the purposes of the experiment and pet dogs recruited from local owners. At age four months both hand-reared and pet dogs were able to utilise a momentary distal pointing cue in order to find food. Hand-reared wolves, however, were unable to utilise this cue. In addition the wolves showed far greater reluctance to engage in eye-contact with humans than either group of dogs.

Virányi et al. then went on to re-test the group of hand-reared wolves at regular intervals. Initially the wolves still failed to utilise distal pointing (momentary or dynamic)—although, again, the wolves exhibited high levels of individual variation—but they were able to use cues where the human hand got much closer to the target, such as touching or proximal pointing. However, over the course of the study their performance on distal pointing gradually improved. Finally, Virányi et al. compared a subset of these highly trained wolves, each of which had by now experienced hundreds of distal pointing trials, with a group of age-matched naïve pet dogs. The highly trained wolves and naïve pet dogs were both able to utilise distal pointing equally well, and both were equally willing to engage the experimenter in eye-contact. The overall finding of this study, then, is that wolves that have been hand-reared, intensively socialised and given months of training can utilise the same kind of cues as four month old dog puppies.

3.1.2.2 – Ontogenetic emergence

Turning now to the ontogenetic emergence of these abilities in dogs, Riedel et al. (2008) compared the ability of puppies aged 6, 8, 16 and 24 weeks to use gestural and other communicative cues in a food-finding game. Puppies in all age groups were tested on their ability to utilise various forms of dynamic cross-pointing and to use a marker placed near the correct location as an indicator of where the food was. Six week-old puppies used all of the communicative cues correctly, as indeed did puppies in the other three age groups. Furthermore, apart from the marker cue, there was no significant difference between the age groups. In the marker condition the only significant difference was that 24 week-old puppies outperformed those aged 6 weeks. In follow-up experiments, Riedel et al. limited the possible role of stimulus enhancement by manipulating the trials so that the puppies couldn't simply select the correct location by approaching the experimenter's hand. These follow-up tests also confirmed the findings of Virányi et al. (2008) that very young puppies could effectively use dynamic distal cross-body pointing.

3.1.2.3 – Non-pointing cues

Dogs have also been tested using a range of other, non-pointing cues. In an early study, Agnetta et al. (2000) found that dogs could utilise the placing of a marker as a communicative cue to the location of food. Perhaps even more intriguingly, Kaminski et al. (2009a) found that dogs could also successfully use iconic 3D representations and photographs as cues for objects to retrieve. Most impressively, when shown a photograph, dogs were able to successfully retrieve the depicted object in preference to a second photograph of that object. Their success in utilising this range of cues is important, because it suggests that there is nothing specific about *pointing* to which dogs are responding, and that this might represent a more general capability. Finally, these last few studies also indicate that dogs can utilise a wide range of cues and are not tied simply to those that provide particularly salient forms of stimulus enhancement.

3.1.2.4 – Summary

It may be useful at this point to make a brief summary of the findings just reviewed. In addition to multiple replications of the original work regarding their sensitivity to human communicative cues, the following points emerge from the studies just discussed:

(1) Dogs outperform great apes in tasks that require utilising a communicative cue

(2) Dogs also outperform their ancestors, grey wolves, in these kind of tasks

(3) Dogs are able to utilise these communicative cues from a very young age, and don't (unlike wolves) seem to be reliant on experience with humans for the ability to emerge

To return to Hare et al.'s (2002) three possible hypotheses, point (2) suggests that the *canid generalisation hypothesis* is incorrect: if this ability is not found in wolves then dogs cannot simply have inherited it. Point (3) suggests that the *human exposure hypothesis* is also incorrect: the fact that very young puppies show such good performance indicates that exposure to humans is not what explains this ability. However, points (2) and (3) do provide support for the *domestication hypothesis.* The ability to utilise these communicative cues is a derived trait in domestic dogs, not present in wolves, although, interestingly, testing reveals significant variation in wolf capacities that might have provided the basis for selection during domestication (Virányi et al., 2008). Furthermore, it seems that its emergence in dogs is not the result of their developing in a human-intensive setting, as even very young puppies with limited exposure to humans can demonstrate this skill. Taken together, these two arguments indicate that dogs' skills at interpreting human communicative cues are likely to have arisen during domestication.

3.1.3 – Challenges to the domestication hypothesis

All three of the points listed above have been contested. I will return to point (1), regarding great apes, in section 3.2, when I discuss the studies of the object-choice task in other, non-canid species. For now, however, I will focus on points (2) and (3)—the claims that dogs outperform wolves, and that exposure to humans during development is unnecessary for the emergence of these skills in dogs.

3.1.3.1 – Challenge I: Dogs *don't* outperform wolves

The claim that the sensitivity to communicative intent is absent in wolves has been challenged by Udell et al. (2008). Udell et al. cite several methodological problems with previous studies, many of which have been discussed above (e.g. Hare et al., 2002; Miklósi et al., 2003; Virányi et al., 2008). In particular, that the testing conditions for wolves and dogs have often differed, with wolves being tested outside—in some instances while inside a fenced enclosure—and dogs being tested inside, with no barrier between them and the experimenter. In an attempt to correct for these methodological flaws, Udell et al. compared the performance of human-reared, socialised wolves, pet dogs, and rescue dogs living in a shelter. With these methodological problems corrected for, they found that both wolves and dogs could use communicative cues equally. They also found that the performance of pet dogs varied depending on the nature of the testing location, whether indoors or outdoors, and with or without a dividing fence. Finally, the shelter dogs were found to perform significantly worse than both pet dogs and wolves.

3.1.3.2 – Challenge II: Dogs *do* require developmental experience

The claim that the emergence of these skills is not dependent on experiences during ontogeny has also been challenged. Wynne et al. (2008) presented a re-analysis of the data from Riedel et al. (2008; discussed above), and argued that, contrary to the its original interpretation, the study *did* show that the older dogs outperformed younger dogs. Wynne et al. focused on Riedel et al.'s first experiment, comparing puppies at four different age groups. In particular, they argue that a much stronger main effect of age could be observed if the (non-cued) control condition was eliminated from the analysis, with the reasoning being that no improvement with age would be expected in the control condition. With this alteration made, Riedel et al.'s data show a significant improvement with age. In addition, Wynne et al. argue that the performance of 6 week-old puppies was significantly better in the second half of the experimental trials than the first, suggesting a learning effect. Dorey et al. (2010) tested the comprehension of momentary proximal pointing in puppies aged 9-12, 13-16, 17-20 and 21-24 weeks, and found an improvement with age, with only the two oldest groups showing above-chance performance.

3.1.3.3 – An alternative: The two-stage hypothesis

Putting both these sets of results together, Udell et al. (2010) present an alternative to the domestication hypothesis, the *two stage hypothesis*. This states that the sensitivity to human communicative cues depends on two kinds of experience during development. The first kind of experience is the exposure and interaction with humans during the canids' sensitive period of socialisation (see section **3.4** for a fuller discussion of the canid socialisation period), in which they learn to accept humans as social companions. The second kind of experience consists in their lifelong learning to use aspects of human limb movement as cues to locate food and other desired items.

The *two stage hypothesis* has several interesting features. Firstly, it emphasises developmental experiences and not phylogeny, in other words *any* canid socialised to humans during the sensitive period and then subsequently exposed to human cues will, according to this hypothesis, learn to utilise those cues. As such, it presents as something of a more domain-general explanation than the domestication hypothesis, which suggests that dogs have become attuned specifically to the kind of communicative cues produced by humans. Secondly, the second component of the two-stage hypothesis involves very low-level learning mechanisms, indeed Udell et al. (2010) explicitly refer to both classical and operant conditioning playing the major role in this second stage. Finally, the two-stage hypothesis makes some interesting predictions: for example, that dogs socialised to other species, such as sheep or cats, should be more sensitive to the social stimuli of those species than of species to which they are not exposed (Udell et al., 2010; 338).

3.1.3.4 – Responses to these challenges

Hare et al. (2010) present a methodological critique of Udell et al.'s (2008) claim that dogs and wolves performed equally well. The centre of this critique is that Udell et al. bundled together non-responses with incorrect responses, such that failure to participate was classified together with incorrect participation. Once this confound was removed no significant difference between wolves and dogs remained, in fact the wolves performed much like the adult wolves in Virányi et al. (2008). In addition, the removal of this same confound showed that the presence of a fence or other barrier between the dog and the experimenter affected *participation* and not the number of correct choices made by those who did participate; dogs tested from behind a barrier were more likely simply not to participate in the experiment at all.

However, even after re-analysis, the shelter dogs tested by Udell et al. (2008) were still not utilising the cues significantly above chance. Hare et al. suggest that this may have been the result of the small sample size (N=8), and report their own experiment with a larger group of shelter dogs, who were found to be skilled at using human cues. Finally, Hare et al. point out that the dogs and wolves used by Udell et al. were not bred for the experiment and so their rearing and developmental histories were unknown. This is important because for reliable conclusions to be drawn regarding the influence of genes on behaviour it is necessary to keep the environmental conditions as similar as possible (Miklósi & Topál, 2011).

Hare et al. (2010) also question the re-analysis of Riedel et al (2008). Wynne et al.

(2008) argued that if the control condition was excluded then a main effect of age became apparent. But as Hare et al. (2010) point out, this main effect is entirely dependent on the marker condition, with there being no difference between the age groups on either of the two pointing cues. However, even with the marker condition this main effect was driven entirely by the difference between 6 and 24 month old puppies. In other words, even after excluding the control condition, the only significant difference between age groups was that reported in the original paper.

3.1.3.5 – Conclusion

We have, then, two theoretical accounts of dogs' sensitivity to human communicative cues: the *domestication hypothesis* and the developmental, *two-stage hypothesis*. Rather than continue with the methodological wrangling, I will now turn to two other sources of evidence that bear directly on the choice between these two hypotheses. The first concerns whether there are differences between the various breeds of domestic dog. The domestication hypothesis would predict that a similar kind of sensitivity to communicative cues should be found across all breeds. In contrast, the two-stage hypothesis, focused as it is on developmental experience, should seemingly predict much greater variation. The second concerns the question of the manner in which dogs understand human cues. This will be investigated through an examination of some of the similarities and differences between the use of cues by dogs and human infants. The domestication hypothesis, in positing a more domain-specific account, might expect to see some similarities, given that we are talking about the same domain in both cases. However, the two-stage hypothesis, in focusing on canid-typical mechanisms of socialisation and general associative learning, provides little reason to expect similarities with human infants.

3.1.4 – Differences between dog breeds

Present-day domestic dogs exist in a profusion of hundreds of different breeds, some of which have been bred as working dogs, others as companions, and each with varying degrees of relatedness to their wolf ancestors. It is important to ask, then, whether there are any differences between breeds in their use of communicative cues.

Wobber et al. (2009) compared the New Guinea Singing Dog (NGSD), a primitive breed that is thought to have had little contact with humans for thousands of years, with two groups of more conventional breeds representing those that had been bred as working dogs (e.g. golden retrievers) and those that had been bred as companions (e.g. toy poodles). All breeds were able to utilise the cues—cross-body distal pointing and a placed block—at above chance levels. The working and companion dogs outperformed the NGSDs on the pointing cue, while the NGSDs outperformed the other two groups in utilising the placed block. These results are re-enforced by work showing that Australian dingoes—a close relative of the NGSD—are also capable of successfully utilising these communicative cues (Smith & Litchfield, 2010), including the 'benchmark' momentary distal point, which goes furthest to eliminating low-level explanations such as stimulus enhancement (Miklósi et al., 2003). Much like the NGSDs, dingoes have an early history of domestication but have lived as free-ranging, essentially wild, animals for the last few thousand years.

In a second experiment, Wobber et al. divided both the working and companion dogs into more wolf-like (e.g. huskies/basenji) and less wolf-like (e.g. German shepherds/toy poodles) groups, to compare the relative contributions of genetic distance from wolves and breed-purpose to the ability to utilise cues. As in experiment one, all breeds were able to use the cues above chance. There was no evidence that genetic distance from wolves made any difference, and the working dogs outperformed the companion breeds overall. It seems, then, that the basic sensitivity to communicative intent is shared across all breeds—even those with little human contact in historical times—but that those breeds subsequently selected to work and co-operate with humans exhibit an enhancement of this basic capacity.

What might explain the differences between breeds? One possibility is related to the findings of Miklósi et al. (2003) that the superior performance of dogs compared to wolves may be related to a greater willingness to direct their gaze at humans. Jakovcevic et al. (2010) compared the willingness of three breeds—retrievers, German shepherds and poodles—to gaze at the human face. Retrievers showed a greater willingness to initiate gaze and slower rates of extinction once gaze had been established than poodles, perhaps suggesting that this might underlie the difference between working and companion dogs. This conclusion has to be tempered, however, by the fact that no such difference was found between German shepherds and poodles. Helton and Helton (2010) found that large dogs performed better than small dogs in their use of human pointing cues. They provide several suggestions as to why this might be so, one of which is that working dogs tend to be larger than those bred for companionship, although by itself this fails to tease apart whether it is being bred to work or larger size that's making the difference.

3.1.5 – What do dogs know about communicative cues: parallels with human infants?

In this section I turn to the question of what dogs know about communicative cues. This is approached through a comparison between dogs and human infants. Three main topics are considered in this comparison. The first concerns the situations in which human cues are most likely to be utilised. The second concerns the ostensive indicators influencing the perception that an action was meant communicatively. Finally, I will consider some parallels between the mistakes made by dogs and those made by human infants that may relate to similarities in their understanding of communicative cues.

3.1.5.1 – Use of cues in competitive and co-operative situations

One interesting question concerns the kinds of situations in which dogs are best able to utilise communicative cues. It is known, for example, that chimpanzees perform better at competitive than co-operative cognitive tasks (Hare & Tomasello, 2004). Herrmann et al. (2006) compared the performance of chimpanzees and human infants in using human gestures driven by either a competitive or co-operative communicative motive. Chimpanzees succeeded in the competitive but not the co-operative condition, whereas children aged 24 months only succeeded in the co-operative, informing condition.

Pettersson et al. (2011) compared dogs' success in two similar conditions—asking, in effect, whether dogs are more like chimpanzees (better in competitive situations) or more like human infants (better in co-operative situations). In the co-operative context dogs utilised the gesture at above chance levels, whereas in the competitive trials they were not significantly different from chance. Furthermore, the latency time before a choice was made was significantly lower in the cooperative condition. It seems, then, that dogs—much like humans infants, but unlike chimpanzees—exhibit a particularly high sensitivity to human cues in *co-operative* situations.

3.1.5.2 – Ostensive indicators to the communicative nature of cues

Of course, the question remains as to whether the similarities between dogs and human infants are based on the same underlying processes. This comes back to the question of what dogs understand about communicative cues and, indeed, how they know such cues are communicative in the first place. Kaminski et al. (2012) report a series of experiments probing this question. In their first experiment they established that dogs respond differently to intentionally given communicative points and gazes than to similar unintentional movements, with only the former being utilised to select the correct location in an object-choice task. It is this sensitivity to the *ostensive content* of a cue—that is, to whether it was provided intentionally and communicatively—that marks dogs out as unusual in comparison to most other species tested on the object-choice task (see **3.2** below).

The ostensive cues used in their first experiment all involved initially establishing eye-contact with the dog. However, in a second experiment, Kaminski et al. found that dogs could successfully use cues provided by somebody facing away from them who called their name (or indeed *any* name in the relevant high-pitched manner). This suggests both that eye-contact is not always necessary for dogs to recognise the communicative nature of human cues and, further, that a human's inability to see the dog, something previous studies have shown dogs can understand (Schwab & Huber, 2006), is no barrier to cues being communicatively interpreted.

In a third experiment, Kaminski et al. compared dogs' responses to gazes and points with and without eye-contact and name-calling, and whether dogs could utilise communicative acts directed at a third party. Eye-contact was found to be the most significant factor, with name-calling being relatively unimportant. However, taken together with the findings of experiment two, it seems that dogs are capable of using a number of different features to diagnose the communicative intent of a human cue. Importantly, many of the ostensive indicators used by dogs are the same as those used by human infants (Kaminski et al., 2012). One difference, however, was that unlike human infants, dogs seem comparatively poor at utilising cues directed at a third party. Finally, they also found that puppies used a similar set of features to discriminate intentionally given, communicative cues from unintentional, but physically similar, non-communicative actions.

3.1.5.3 – Similar kinds of errors in dogs and human infants

One of the most striking parallels between the use of communicative cues by dogs and human infants is the occurrence of similar kinds of *errors* in both groups, with the most notable example being the so-called *A-not-B error*. This error refers to the curious behaviour of human infants (aged 6-12 months), first uncovered by the work of Jean Piaget, whereby after having successfully retrieved a hidden object from one location (*A*) the infant will continue to search for the object at that location, even if they see it hidden, right in front of them, at another location (*B*). In Piaget's (1954) original formulation, this strange error was explained in terms of infants' underdeveloped model of the physical world, in particular their failure to grasp the concept of *object permanence*.

Recently, however, Topál et al. (2008) have shown that the rate at which this error occurs is related to the degree to which the task is social and communicative in nature. Infants make a much greater number of errors when object-hiding is accompanied by a range of ostensive-communicative cues, such as eye contact, pointing and gaze alteration (which Topál et al. term 'communicative context'), than when the hiding occurs without such cues (non-communicative context) or by an experimenter outside the infant's view (non-social context). The A-not-B error can be seen, then, as kind of 'pragmatic misinterpretation', with infants taking the communicative cues in the A-trials as being meant to convey general information about where this *class* of objects are to be found in the world, rather than just as a physical indicator of where this individual object happens to be right now (Topál et al., 2008).

Topál et al. (2009a) tested both dogs and wolves for the occurrence of the A-not-B error and examined whether the frequency of errors differed between communicative, non-communicative and non-social conditions. Dogs showed very much the same pattern of results as human infants, with their continuing to search at location A, even after having seen the object moved to location B, but only in the communicative conditions, and not in non-communicative or non-social controls. Human-reared wolves, on the other hand, showed no sign of this search error in either communicative or non-communicative conditions, and no difference between the two conditions. These differences complement those between dogs and wolves on the object-choice task, discussed above, and would seem a better fit with the domestication hypothesis than the two-stage hypothesis. However, Topál et al. also found an interesting difference between infants' and dogs' use of the cues. When the identity of the experimenter changed between the A- and B-trials, infants continued to search in location A, whereas dogs did not. In other words, infants seemed to generalise beyond the specific communicative situation and partner more readily than dogs.

Of course, these findings with dogs have not gone unchallenged. Fiset (2010) pointed out that Topál et al.'s (2009a) implementation of the A-not-B search task was somewhat atypical. In particular, that the B-trials also involved an initial 'sham baiting' of the A location, as a result of the experimenter taking a 'zig-zag' path that first moved the object to the A location and then finally to B. This more complex route might place greater attentional demands on the dogs than the A-trials. Furthermore, this difference was more pronounced in the communicative than non-communicative conditions. In addition, there is also the possibility that the errors may stem from failure to inhibit a previously rewarded motor act.

Kis et al. (2012) directly addressed these concerns with an experiment designed to control for these procedural and motor-inhibition explanations. They found that the kind of approach on the B-trials—whether zig-zagging and sham baiting, or direct like on the A-trials—made no difference to the occurrence of the A-not-B error, suggesting that this wasn't simply an artefact of the experimental procedure. In a second, watch-only, condition they found that whether the dog searched on the A-trials, or merely watched what the experimenter was doing, made no difference to the frequency of their errors on the B-trials, suggesting that such errors are not explicable in terms of a failure to inhibit a motor response.

In a further experiment, Kis et al. found that the error-rate could be reduced by varying the level of ostensive cues in the B-trials. In particular, if location B was ostensively enhanced—through eye contact, gaze-shifting, etc.—then this reduced, but did not eliminate, the appearance of the A-not-B error. This finding is very much in line with the view that both dogs and human infants make similar mistakes for similar, pragmatic-communicative reasons.

3.1.5.4 – Summary

It seems, then, that dogs resemble human infants in a number of different ways. Firstly, they appear more adept at using human cues in co-operative situations than in competitive contexts. Secondly, they are not only capable of utilising a wide range of communicative cues, but are also sensitive to a range of ostensive indicators, such as eye contact and name calling, that those cues have been given intentionally as communications. This sensitivity seems to parallel that seen in humans infants and to be present from birth. Furthermore, dogs seem to make many of the same mistakes as human infants and to do so for some of the same reasons of pragmatic-ostensive misinterpretation.

3.1.6 – Conclusion

It is now possible to draw some conclusions regarding the relative merits of the domestication hypothesis and the more developmentally oriented two-stage hypothesis. The bulk of the early experimental work (discussed in **3.1.2**) suggests that dogs outperform wolves on the object-choice task and that dogs, unlike wolves, do not require developmental exposure to humans in order for these abilities to emerge. Both these claims have, of course, been disputed. However, the real evidence that distinguishes between the two hypotheses relates to the expanded discussion of these capacities undertaken in the previous few sections.

Firstly, the presence of these capacities across a huge variety of different breeds—from working dogs, through companion dogs, to now-feral species such as the dingo—does not fit well with the developmental account provided by the two-stage hypothesis. The developmental conditions of these breeds vary greatly; what they share is a history of domestication. Secondly, dogs' capacities seem to go well beyond the kind of simple, learned responses to particular human action envisaged by the two-stage hypothesis. Dogs are able to utilise a wide range of human cues, including novel ones to which they have not previously been exposed (e.g. 3d replicas or photographs). Furthermore, dogs are not simply using human *actions* as cues, but seem to be sensitive to whether those actions were *meant communicatively*. Finally, the ostensive indicators they use to discern whether a cue was meant communicatively, together with the pattern of errors they produce, exhibits some striking parallels with human infants. All this makes it difficult to accept that the capacities exhibited by dogs simply represent the outcome of the socialisation period occurring around humans and subsequent re-enforcement learning, as argued by the two-stage hypothesis. It seems, then, that the domestication hypothesis provides the best account of the emergence of these capacities in dogs.

3.2 – Sensitivity to communicative cues in other species

So far the discussion has been almost entirely focused on dogs and their ancestor the grey wolf. In this section, however, I turn to studies examining the sensitivity to communicative intent in other species. These will be dealt with in two groups: *non-canid domesticates* and *non-domesticated species*, including great apes. Findings with both these groups will obviously have some important bearing on the relationship between domestication and the emergence of a sensitivity to communicative intent.

3.2.1 – Non-canid domesticates

One obvious question raised by the domestication hypothesis is the extent to which a similar sensitivity to communicative cues might be found in other domesticated animals. Is it something common across many species, and so potentially part of the domestic phenotype (see chapter four, section **4.2)**, or is it peculiar to dogs? As far as I am aware, only three other domesticated species—goats, horses and cats—have been tested on their ability to utilise human communicative cues. The results lend limited support to the generality of the domestication hypothesis, but are very far from conclusive.

Kaminski et al. (2005) tested domestic goats on an object-choice task similar to those used with dogs. Like dogs, the goats managed to use both a touching/tapping cue and, to a lesser extent, a pointing cue. Also like dogs, young goats were just as adept as adults. However, the goats failed to utilise a gaze cue, despite having demonstrated the ability to follow gaze in an initial experiment. Two further points, both discussed by the authors, need to be made in relation to this study. The first is that this pattern of results is easily explained as a result of simple learning processes such as stimulus enhancement, with the goats' success at using the cues varying in step with the extent to which they drew attention to the correct location. This is unlike the results with dogs who have been shown to use a wide range of cues equally successfully and to be sensitive to their ostensive content in a way difficult to account for in terms of simple stimulus enhancement. The second point is that it is impossible to carry out the ideal comparison because the wild ancestor of the domestic goat is now extinct. This, unfortunately, is true of a great number of present-day domesticated species, and one of the reasons why dogs, with a living ancestor in the grey wolf, make such ideal subjects for comparative studies concerned with domestication (Topál et al., 2009b).

Another domesticated species that has been tested on its use of cues is the horse. Earlier work (McKinley & Sambrook, 2000) found little sign that horses were able to use communicative cues. More recently, Proops et al. (2010) report horses to be successful at using a marker cue and a distal sustained pointing cue in selecting a food bucket. They failed, however, to use momentary tapping, body orientation and gaze alternation cues. Much like the findings with goats, the authors interpret this pattern of results in terms of stimulus enhancement, rather than as evidence that the horses grasped the communicative nature of the cues. This is supported by their observation that all those horses that used the marker cue to choose the correct location inspected the marker itself before going to the bucket.

Miklósi et al. (2005) compared the performance of domestic cats with that of dogs. The cats were found to perform as well as dogs at utilising distal and proximal pointing cues made either momentarily or dynamically. While these results are intriguing, the limited range of cues tested with cats makes it difficult to claim full equivalence with dogs. In particular, there is no way to tell the nature of the cats' understanding of the cues, whether it is rooted in stimulus enhancement, as seems the case for goats and horses, or shows a greater sensitivity to ostensive content as seems the case in dogs. Miklósi et al. report one further difference between dogs and cats that lends weight to a more cautious interpretation. When faced with a similar, but insoluble, object-choice task, dogs showed a greater willingness than cats to gaze at humans and a greater level of gaze alternation between the target and the experimenter. This, recall, is exactly the difference Miklósi et al. (2003) found between dogs and wolves, which they argued might go some way to accounting for their differential levels of success. It may be that cats' reluctance to gaze at the human face could hamper their ability to use more subtle and complex cues.

3.2.2 – Non-domesticated species

Of course, the flip side of the last section is that if evidence of the capacity to utilise human communicative cues were found in species that had never been domesticated, then this would, at the very least, show that domestication was not *necessary* for the emergence of this ability, even if it might still be associated with it in certain cases. This section will be further subdivided into studies with non-domesticated mammals, particularly dolphins and seals; non-domesticated birds, particularly parrots and various species of corvid; and apes.

3.2.2.1 – Mammals

Perhaps the best evidence for the use of communicative cues in a non-domesticated mammal—indeed, the best evidence from any species outside of dogs—comes from work with dolphins (Pack & Herman, 2004, 2006, 2007). Dolphins have shown spontaneous, first trial, understanding of ipsilateral and cross-body points, and gaze direction as communicative cues to a location. Given the necessarily large-scale aquatic nature of the testing environment, all these cues have obviously been presented distally. Furthermore, dolphins are able to take a point to an object as a cue to fetch a similar object, a task that has at least a passing resemblance to the iconic cues successfully used by dogs (Kaminski et al., 2009), and also to show an understanding of the geometry of pointing by grasping that a point refers to a distal object rather than a proximal one along the same line of sight.

The results with dolphins are clearly very impressive, however several points of difference between the work with dolphins and that with dogs needs to be borne in mind. The first concerns the very small number of subjects used in the studies. For example, the results reported in Pack and Herman (2007) come from only two individuals. Furthermore, these individuals tend to have had intense, long-term contact with humans in captivity, often having taken part in numerous other studies or having been engaged in some form of display work. It would, for example, be very interesting to know how young dolphins, or those with much more minimal human contact—perhaps even wild ones—might perform in object-choice tasks. It should be acknowledged, of course, that many of these points derive from inescapable facts about the biology and habitat of the species concerned, and the associated costs and difficulties inherent in their being kept in captivity and thus amenable to experimental investigation. I would also stress that none of this means I'm casting any doubt on the findings with dolphins. The evidence clearly suggests that dolphins *can* utilise a range of human communicative cues with impressive sophistication. Rather, and I shall return to this point below, it is not entirely clear how or why the tested dolphins have come to exhibit this ability. This is particularly important given the findings that socialised wolves can learn how to utilise cues over time (Virányi et al., 2008), eventually reaching comparable levels to domestic dogs, and the relatively better performance of enculturated apes (see below, Itakura et al., 2001).

Several species of seal have also been tested for their ability to comprehend communicative cues. Shapiro et al. (2003) report on a specially captured grey seal pup, who demonstrated the ability to utilise a variety of ipsilateral and cross-body points, given both symmetrically and asymmetrically, in order to select the correct location. However, as the authors acknowledge, this was not a capacity that emerged spontaneously, but rather followed from an extensive period of training, in which the seal learned first to follow a pole, and then a human point, to the correct location. The seal's pattern of success and failure also reflect this early training, with a failure to utilise head turning and gaze cues, and a seeming inability to generalise from a right-or-left pointing task to one in which there were three possible locations (Shapiro et al., 2003). Overall the authors concluded that the results were best explained as a result of simple conditioning rather than any comprehension of the communicative nature of the cues.

Scheumann and Call (2004) report a study with South African fur seals. In contrast to the grey seal study just described, the fur seals had not been specifically trained to utilise communicative cues. All the tested fur seals were, from the first trial, able to utilise a point-and-gaze cue, delivered symmetrically and asymmetrically, and a point-only cue. In addition, all but one of the seals successfully used a gaze-only cue from the first trial onwards. The seals failed, however, to utilise glance, hand point, or iconic replica cues, several of which have been successfully utilised by dogs. These findings are, outside of dogs and dolphins, probably the most impressive demonstration of the use of communicative cues by a non-human species. It should be noted, however, that many of the caveats identified in relation to the dolphin studies also apply here. The fur seals were housed in a zoo and took part in twice-daily public demonstrations, in which they had to respond to the instructions and directions of their caretakers. Although, as the authors state, these seals had never been specifically trained to respond to points, it seems very possible, much like the dolphins, that prolonged exposure to humans is likely to have played a role in their acquisition of this ability.

3.2.2.2 – Birds

Giret et al. (2009) tested the use of cues in African grey parrots. The pattern of results is in many ways similar to that seen in horses and goats. From the first trial, or within 15 or so trials, all the birds managed to use the most salient, stimulus enhancing cue in the experiment, a sustained proximal point. One bird learned to use a sustained proximal gaze cue, although the rest did not. None of the birds ever managed to successfully utilise momentary points or distal points or gaze. In other words, the more obviously the cue drew attention to the target the more easily the birds managed to use the cue, but there seems little reason to conclude that they understood the communicative purpose of the cues.

The most thoroughly studied group of birds, however, are the corvids. Overall the results from this group are mixed and difficult to interpret. Schloegl et al. (2008) found that ravens could use a touch cue, but that they failed to utilise pointing or gaze cues even after over 150 trials. Tornick et al. (2011) found stronger results with Clark's nutcracker's, who could use a touch cue from the first trial and quickly learned to use proximal point and gaze alternation cues, although the order of cues from most to least successfully utilised—touch > point > gaze alternation—is, as the authors point out, fully in line with a stimulus enhancement account.

Schmidt et al. (2011) found that rooks as a group could not utilise gaze cues, although one bird did learn to use such cues during the experiment. Perhaps the most impressive results come from Jackdaws, who were able to successfully use both proximal cross-body pointing and gaze alternation from the first trial, but were unable to use gaze or a gaze and head-turn combination. None of these studies show comparable results to seals or dolphins, let alone dogs. They all show a greater effect for proximal, active cues (e.g. repeated gaze alternation vs. single-instance gaze) compared to distal, one-time cues. And, perhaps with the partial exception of the jackdaws, seem quite adequately accounted for in terms of stimulus enhancement.

3.2.2.3 – Apes

Earlier in this chapter I laid out three broad conclusions that followed from the initial work on the use of communicative cues by dogs. Two of these conclusions—that dogs outperform wolves, and that dogs require very little exposure to humans for these abilities to emerge—have been dealt with above. In this section, I will deal with the third conclusion: that dogs are better than great apes in tasks requiring the sensitivity to communicative intent.

To recap, numerous studies (Hare et al., 2002; Hare & Tomasello, 2005; Gomez, 2005; Miklósi, 2007) have found that, unlike dogs, great apes are not particularly skilled at using human communicative cues to locate food or other desired items. Further, it seems that dogs only outperform apes in social tasks that involve co-operative communication and not in social tasks more generally, at which apes seem the more skilled (Wobber & Hare, 2009). This pattern of results fits neatly into the wider view of ape cognition, which suggests that apes are both highly socially skilled (Byrne & Whiten, 1992)—perhaps exhibiting some aspects of theory of mind (Call & Tomasello, 2008)—but also seem to perform better in competitive rather than co-operative versions of the object-choice task (Hare & Tomasello, 2004). However, recent work suggests that the situation as regards apes and the object-choice task may be somewhat more complex. Three factors seem to have emerged that need to be taken into account when assessing the performance of apes: the nature of the experimental design; the level of contact with humans; and the use of multiple cues, such as a combined pointing and vocal gesture.

The experimental design used with apes seems to play a role in determining their level of success. In particular, it has been found that chimpanzees, bonobos (Mulcahy & Call, 2009) and orangutans (Mulcahy & Suddendorf, 2011) perform better given a peripheral version of the object-choice task—with the two locations placed some distance either side of the subject—than with a central version of the same task, in which the two locations are placed in front of the ape, perhaps on a table. Mulcahy and Hedge (2012), in a review of published studies of the object-choice task with apes, found that the majority of these studies, unlike those with dogs, used the central form of the task. In addition, they also found that most studies with apes failed to establish eye-contact prior to issuing the cue.

Mulcahy and Hedge's explanation for the difficulty apes seem to have with the central version of the object-choice task is that containers, associated as they are with food rewards, are more salient than the cue being issued by the experimenter, with which they share the visual field. As a result, apes choices become somewhat random, relating to their failure to inhibit a motor response to these more salient stimuli. Of course, this fails to address the question of apes' better performance in competitive versions of the object-choice task (e.g. Hare & Tomasello, 2004). Mulcahy and Hedge suggest that this is because *competitive* cues exceed the salience of the containers in a way in which cooperative cues do not. The problem with this is that apes' greater attunement to competitive rather than cooperative cues is, as we have seen, one of the very things argued to contribute to their relatively poor performance on the object-choice task. Similarly, as Mulcahy and Hedge acknowledge, many of the studies with dogs have also failed to elicit eye-contact prior to issuing the cue. They suggest that this may be less important for dogs because they are more willing to initiate eye-contact themselves. It is, however, this very willingness that has been cited as a possible part of the explanation for the superior performance of dogs as compared with, say, wolves (Miklósi et al., 2003).

Mulcahy and Hedge's most important point, however, is probably that statements about the relative capabilities of different species require that those species be tested with comparable versions of the same task, leaving aside unavoidable differences dictated by their biology. Part of this should include testing dogs on a central version of the object-choice task, something not yet reported to date (Mulcahy & Hedge, 2012). The other half involves comparing apes and other species on peripheral versions of the task. In this respect it should be noted that not all studies utilising a peripheral method have found positive results (e.g. Herrmann et al., 2006). Recently, Kirchhofer et al. (2012) compared chimpanzees and dogs in a task in which two (widely spaced) objects were placed behind the subject, who faced the human experimenter. The experimenter then delivered a distal sustained point, combined with gaze alternation and a vocal cue. The dogs as a group performed above chance on this task, whereas the chimpanzees did not. Findings such as this make it hard to ascribe the difficulties great apes seem to have with the object-choice task entirely to their inability to inhibit responses in central versions of the task.

Despite the general finding that apes are poor at the object-choice task, there have always been a few positive results (e.g. Ikatura & Tanaka, 1998), generally involving apes that have been *enculturated*; that is, raised in an environment of intensive social interaction with humans. This kind of exposure is known to have a large effect on their cognitive and social development (Call & Tomasello, 1996) and to result in abilities not seen in the wild (Savage-Rumbaugh et al., 1998). Lyn (2010) conducted an object-choice study comparing enculturated, nursery-reared, mother-reared and wild-caught chimpanzees and bonobos. The enculturated group massively outperformed the other three groups, who showed no significant differences.

Finally, some studies have shown that the performance of apes increases if multiple cues are given. For example, Herrmann et al. (2006) found that apes could use an iconic cue (a picture or replica) paired with a spatial/indexical cue to locate food, but returned to chance performance when the iconic cue was presented alone. Lyn (2010) also found that chimpanzees and bonobos performed better when a pointing cue was accompanied by a vocal cue.

3.2.3 – Conclusions

This brief survey of object-choice studies conducted with non-canid species, both domesticated and non-domesticated, reveals two important conclusions. The first, echoing the work with dogs, is that it is necessary to go beyond the question of whether a given species has 'passed' the object-choice test. If the question of interest is the sensitivity to communicative intent, then it is also necessary to examine *which* cues are being successfully utilised, and whether it is variations in their *ostensive* content that is making a difference. The work with horses and domestic goats provides some minimal support for the domestication hypothesis. However, in both cases the pattern of success and failure is perhaps most simply explained as a result of stimulus enhancement. This same explanation can also be applied to most of the work with birds, which, like that with horses and goats, exhibit a pattern of results largely explicable in terms of stimulus enhancement, and that seems to show little of the varied and flexible capabilities of dogs

The second conclusion concerns those cases in which an explanation based on stimulus enhancement or some form of conditioning seems inadequate. The major example of this is the work with dolphins, together with some of the work with seals. The first thing to note, of course, is that neither of these is a domesticated species. Having an evolutionary history of domestication is not, then, a *necessary* condition for the sophisticated utilisation of human communicative cues. The second thing to note, however, is that, for both dolphins and seals, the individuals that were tested have intensive, long-term contact with humans, often participating in research programs, demonstrations or shows for many years. This is reminiscent of the finding that socialised wolves could acquire the use of human cues after a lengthy period of training. It also fits with the advantage seen for enculturated apes over their mother-reared or wild-caught contemporaries.

Taken together, these findings suggest that there may be multiple routes, each comprised of different proportions of phylogenetic and ontogenetic contributions, that can lead to similar phenotypic outcomes (Miklósi & Topál, 2011). Broadly speaking, the *ontogenetic route*, taken by dolphins, seals and intensively socialised wolves, consists of heavy long-term exposure to humans. In contrast, the *phylogenetic route*, seemingly taken by the domestic dog, means it requires little or no exposure to humans for comparable capacities to become manifest (Miklósi &

Topál, 2011).

The next question to address, then, concerns what it is about domestication that might explain the emergence of these capacities in dogs? The history of dog domestication would seem like the natural place to start looking for an answer.

3.3 – The history of dog domestication: a brief sketch

If domestication has played a role in the emergence of these capacities in dogs, then the obvious next question to ask is how or why domestication might have had this effect. What is it about domestication that has lead to the emergence of these capacities? In this section I will provide a very brief overview of what is known about when and how dogs were domesticated.

The consensus emerging from genetic studies is that the domestic dog is likely to have originated somewhere between 15,000 and 20,000 years ago (Pang et al., 2009; vonHoldt et al., 2010; Ding et al., 2011), although there is disagreement as to whether the locus of that origin was the Mesopotamia (vonHoldt et al., 2010) or south-east Asia (Pang et al., 2009; Ding et al., 2011). The archaeological evidence in the form of both skeletal remains (Galibert et al., 2011) and in relation to dog burials (Morey, 2006, 2010), a key indicator of the importance of domestic dogs in the lives of prehistoric peoples, is broadly in line with the genetic evidence, suggesting a figure of 14,000-16,000 years ago. Collectively, the evidence suggests that dog domestication began subsequent to the last glacial maximum (LGM), the time at which global ice-sheets were last at their maximum extension (26,000-19,000 BP: Clark et al., 2009). There has, however, been a series of findings in recent years (Germonpré et al., 2009; Pionnier-Capitain et al., 2011; Ovodov et al., 2011) of remains dating from 35,000-30,000 BP, and thus prior to the LGM, that differ from wolves in ways similar to the domestic dog. It has been suggested that these remains constitute an incipient or 'proto-dog', although it is unclear to what extent, if at all, these very early dogs are ancestral to later post-LGM dogs (Ovodov et al., 2011).

Current thinking on dog domestication suggests, then, that it may have proceeded in three discernible stages (Galibert et al., 2011). The first stage, starting c35,000 BP, was a form of *proto-domestication*, which is likely to have been unconscious, perhaps with self-selecting groups of wolves hanging around human settlements and adapting to their new niche. The second stage, starting around 14,000 BP, represents the start of domestication as conventionally understood, in which dogs were starting to be actively kept and bred for human purposes. It is this stage that is reflected in the dog-burial findings. Finally, the third stage occurred much more recently, with the first evidence of distinct 'breeds' dating from within the last 3000-4000 years, and the major explosion in breed number from the last 500-1000 years (Clutton-Brock, 1995).

The key point to take from this very brief overview of dog domestication is that it has been a very long process, which took place under an extremely diverse variety of conditions. As such, the task of working out when, why and how a particular trait is likely to have emerged—particularly a behavioural trait that leaves no fossil traces—seems pretty much impossible. Fortunately, however, there is a long-running experiment, expressly designed to investigate the origins of the domestic dog, which provides a very clear indication of just why this capacity is likely to have emerged during domestication. The remainder of this chapter will be dedicated to a discussion of this work, which has come to be known as the farm-fox experiment.

3.4 – The farm-fox experiment: domestication and selection against aggression

The farm-fox experiment (Belyaev, 1979; Trut, 1999) was started in 1959 by the Russian geneticist Dmitry K. Belyaev. The experiment took the Siberian silver fox—a regional variant of the more familiar red fox—as its model animal, and began a selective breeding program, still running today, to investigate the origins of the physical and behavioural characteristics typical of domesticated species, often referred to as the *domestic phenotype* (see **4.2**). Belyaev's hypothesis was that this suite of phenotypic characteristics emerged as a consequence of selection for *tameness* (Belyaev, 1979)—or, to put it another way, selection *against* aggression.

The key to this hypothesis, as noted by Trut (1999), lies in the fact that behaviour is rooted in biology. This means that selecting against a certain behaviour, such as aggression, really means selecting for a whole suite of physiological changes that underlie the control of that behaviour. This nicely captures the essence of Belayev's original argument regarding *how* selection against aggression might result in a range of other physiological and behavioural changes, which he termed *destabilizing selection* (Belyaev, 1979). The key element of destabilizing selection is the breakdown of previously co-adapted groups of traits and ontogenetic trajectories in the face of a new environmental stressor. According to Belyaev, the stressor relevant to domestication was the presence of humans, in particular the change in the social environment of other species that followed from that human presence.

At the core of the experiment is the breeding of three lines of foxes, tame, aggressive, and a control group. In this account of the work I will focus mainly on the tame line, but mention will be made of the other two groups where necessary.

3.4.1 – Selection criteria

The first important thing to note is that selection in both the tame and aggressive lines was entirely based on the level of defensive or aggressive behaviour exhibited by the foxes towards humans. This was tested monthly for the first six or seven months of the fox kits' development. The experimenter would offer the fox food and try to stoke and handle the animal. Once the foxes had reached maturity, at about eight months, they were classified based on the level of tameness they exhibited into one of the categories in the table 3.1, below.

Classification	Animal Reaction
IE 'domesticated elite'	Fox eager to establish human contact, whimpering to attract attention and sniffing and licking experimenters like a dog. Behaviour begins to be displayed before one month old.
I	Fox shows emotionally positive response to experimenter, wagging tail and whining.
II	Fox lets itself be petted and handled, but shows no emotionally friendly response to the experimenter.
III	Passive-protection response; fox avoids experimenter or bites if stroked or handled.

Table 3.1: Classification system for tame-line foxes.
(Adapted from data in Kukekova et al., 2006)

The aggressive line was selected using a different system of classification, based largely on how close the experimenter could get to the fox before eliciting an aggressive response (see Kukekova et al., 2006 for details). The control group was not selected.

It should be noted that this somewhat subjective set of criteria has recently been supplemented by an approach based on the binary yes/no assessment of objectively observable behaviours—such as 'fox touches cage door with nose'—that can be coded from recordings of fox-experimenter encounters (see Kukekova et al., 2008 for full details). The full set of such observations are then subject to statistical tests, such as principal components analysis (PCA), which allows the identification of correlated behavioural variation and provides a more objective method of classifying foxes into groups such as tame or aggressive. This approach has served to confirm the validity of classifications based on the earlier, more subjective criteria; and, for the first time, allowed a single system to be used in the assessment of both tame and aggressive foxes (Kukekova et al., 2008, 2012).

3.4.2 – Behavioural changes

The selective pressure applied to the tame line of foxes was very strong indeed, with only the top 10% of most tame individuals being used as the parents of the next generation (Trut et al., 2009). This resulted in very fast changes. Within two or three generations of this selective regime all aggressive and defensive behaviours had been eliminated from the tame population (Trut et al., 2009). By the fourth generation foxes began to appear who behaved in many ways like dogs, for example by wagging their tails. The subsequent shifts in behaviour observed as the experiment proceeded are well illustrated by the percentage of foxes classified as belonging to the 'domesticated elite' in each generation, as shown in table 3.2, below.

Generation	**% of 'domesticated elite'**
6th	1.8%
10th	17.9%
20th	35%
30th	49%

Table 3.2: Percentage of the 'domesticated elite' in selected generations
(Extracted from Trut et al., 2009)

As can be seen, the shift in behavioural responses was rapid and dramatic, with Trut et al. (2009) reporting that by 2006 almost all the population of tame foxes were classified as belonging to the domesticated elite. The genetic basis of this behavioural change has been demonstrated though a series of experiments. These have included the cross-fostering of newborn tame and aggressive pups and the transplantation of embryos from tame to aggressive lines and vice versa (Trut et al., 2001; Kukekova et al., 2006). The temperament of the resulting fox has reflected its selected linage—tame or aggressive—rather than its individual circumstances of gestation and/or development. More recently, this has been confirmed by the cross-breeding of tame and aggressive foxes, which results in hybrid offspring intermediate between the two lineages (Gogoleva et al., 2009; Kukekova et al., 2006). In addition, foxes in all lineages spent the majority of their time in cages and were only allowed brief, 'time dosed' contact with humans, to ensure that any changes in behaviour were not the result of training or developmental experience (Trut, 1999).

3.4.3 – Other correlated changes

This rapid shift towards tame behaviour should not, however, have been unexpected: very strong selective pressure was, after all, being applied to just this trait. What was perhaps less expected was the range of other changes that also occurred in the tame line of foxes. In addition to their loss of aggressive behaviours towards humans the tame foxes also came to differ from the aggressive and control lines in the following ways (see Trut, 1999; Kukekova et al., 2006; Trut et al., 2009; Bidau 2009 for more details):

- earlier response to sound
- eyes opened earlier
- delayed development of fear response
- extended socialisation period

- play extended into adulthood

- piebald coat
- brown mottling on coat
- floppy ears
- shortened tails
- curly tails
- smaller cranial height and width

- decrease in sexual dimorphism
- earlier sexual maturity
- breakdown of strict mating seasons, with some foxes mating twice a year

The most striking thing about this list of changes is how many of them are typically found in other species that live in close association with humans (Trut, 1999; Price, 2002). Indeed, many of these changes—increased variation in coat colour, shifts in cranial size, breakdown of seasonal mating, accelerated sexual maturation, and reduced sexual dimorphism—form part of what has been termed the *domestic phenotype*, that suite of characteristics that typifies many domesticated species (Price, 1999; chapter four, **4.2**). One remarkable finding of the farm-fox experiment, then, is that many of these typical outcomes of domestication can be produced simply as a by-product of selection against aggression. I shall return to this point at some length in chapter five in relation to humans. In the present context, however, I want to focus on one further change: that the tame line of foxes, like domestic dogs, also came to exhibit a sensitivity to communicative intent.

3.4.4 – Sensitivity to communicative intent in domesticated foxes

Hare et al. (2005) conducted an object-choice task, similar to those described at length with dogs and other species above, comparing the abilities of dog pups, tame-line domesticated fox kits and control fox kits. The three groups were tested on their ability to use a point-and-gaze cue to select the correct location of some hidden food. The two major findings were that tame-line fox kits performed as well as dog puppies, and that the tame-line kits outperformed kits of the control population. There was also no evidence of learning during the experiment, as the tame-line kits performed as well in the initial trials as in later ones.

This finding is remarkable and provides the strongest support yet for the domestication hypothesis regarding the emergence of these capabilities in dogs. However two caveats need to be mentioned. The first is that while the tame-line foxes did significantly outperform the control foxes, the control foxes were able to utilise the human cues at an above-chance level. The second is that only one cue, point-and-gaze, was used in the experiment. As discussed above, the most impressive finding with dogs concerns the range of cues they can utilise and their apparent sensitivity to the ostensive content of those cues, neither of which were explored in the experiment with foxes.

However, these caveats aside, the finding that tame foxes also show sensitivity to communicative intent is important in the context of the present chapter because it provides an insight into what it is about the domestication process that might explain the emergence of this capacity in dogs. It had previously been argued that the capacities exhibited by dogs had been directly selected for: that selection, both natural and artificial, following domestication could have favoured those individuals best able to read human communicative cues (e.g. Coppinger & Coppinger, 2001). And, indeed, this may be part of the story, as suggested by the differences between working, companion and now-feral breeds such as the dingo (**3.1.4**).

The foxes in this long-running experiment have not, however, been bred for this purpose. As described above, their contact with humans has been carefully controlled, and their response to cues formed no part of the criteria for selection. The fact that the sensitivity to communicative intent has emerged in the tame fox line, on which the only active selection was against aggression, lends support to what has been termed the *emotional reactivity hypothesis* (Hare et al., 2005; Hare & Tomasello, 2005). This is the view that cognitive changes, particularly those involving co-operative behaviour, may not always requires direct selection, but can appear as a by-product of selection acting on systems of emotion or aggression that had previously prevented the use of pre-existing skills in these kinds of co-operative contexts.[21]

Recall the question in section **3.3**: how and when in the long course of dog domestication is the sensitivity to communicative intent likely to have emerged? The answer arising from the farm-fox experiment is that such capacities are likely to have emerged as a by-product of selection targeting defensive and aggressive behaviours, and that this could, dependent on the strength of selective pressure, have happened very rapidly, although it is almost certain to have taken longer than the 45 years between the start of the farm-fox experiment and the tests conducted by Hare et al. (2005).

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[21] This kind of view is exemplified by the work of Melis et al. (2006), who found that chimpanzees that were seemingly unable to solve a co-operative dyadic task could do so if dyad-pairing was manipulated such that individuals with mutually high tolerance were placed together. When subsequently placed with a less tolerant partner, these same individuals reverted to being seemingly unable to solve the task. The case of dogs and foxes—and indeed bonobos (see **5.2.1**) and humans (see **5.2.5**)—may represent a similar kind of 'freeing' of cognitive potential from its temperamental shackles, but on a permanent, species-wide basis.

3.4.5. – Underlying physical basis for these changes

How might we explain the emergence of this correlated group of seemingly unrelated changes that appeared in the tame line of foxes? One possible answer lies in the fact that many of these changes relate to shifts in the *timing* of development (Trut, 1999; Trut et al., 2004). In some instances this is obvious. For example, the earlier age for sexual maturity and the extension of the juvenile socialisation period represent changes that *are themselves* shifts in developmental timing. In other cases the link is less obvious but still present. The appearance of a piebald pattern on the coats of tame-line foxes has been related to the action of a particular gene, termed *Star*, which delays the development of pigment cells (Trut, 1999). Other examples include the retention into adulthood of traits that are typical of newborn kits, such as floppy ears (Trut, 1999). I will return to the discussion of shifted developmental trajectories, or *heterochrony*, in the next chapter (**4.3.3**); for now, however, I will consider some of the physiological changes that are likely to have mediated the developmental shifts seen in the farm-fox experiment.

One key physiological change relates to levels of hormone activity, particularly that of the glucocorticoids, a class of steroid hormones known to play a role in stress and arousal. A rise in the levels of cortisol in the blood has been shown to correlate with the end of the socialisation period. In tame-line foxes, with their extended socialisation period, this rise occurs later in development (Trut et al., 2009). Glucocorticoid levels are also implicated in the developmental changes leading to piebald colouration (Trut et al., 2009). Comparative studies of the hypothalamic-pituitary-adrenal axis (HPA)—a major part of the neuroendocrine system, involved in stress and emotional control Gulevich et al., 2004)—found that by the 10th generation (the first for which data was collected) levels of glucocorticoids were significantly reduced in tame foxes (Gulgevich et al., 2004), a shift that mirrors the behavioural changes discussed above. By the 45th generation basal levels of glucocorticoids were three-to-five times lower in tame foxes than controls (Trut et al., 2009). Furthermore, levels of the same hormones have also found to be decreased in tame foxes during pregnancy and lactation (Trut et al., 2000). In other words, the entire developmental process of a tame fox kit proceeds against the backdrop of lower levels of glucocorticoid hormones.

Turning now to the role of neurotransmitters, tame foxes exhibit higher levels of serotonin in a variety of different brain regions, together with increased levels of various enzymes and other molecules involved in the synthesis of serotonin (Trut et al., 2009). Serotonin is known to play a role in the inhibition of aggression in many animals, including the fox, (Popova, 2006), and to be involved in the regulation of gene expression during development (Côté et al., 2007).

The most recent developments concern the identification of genes associated with domesticated behaviour in foxes (e.g. Lindberg et al., 2007), together with the mapping of the entire fox genome (Kukekova et al., 2007; Spady & Ostrander, 2007). Using the PCA approach to behavioural classification described above, Kukekova et al. (2011) have identified a genetic locus that seem to be associated with the differences between tame and aggressive foxes, and is orthologous—is identical by descent—to a genomic region implicated in the domestication of the dog (vonHoldt et al., 2010). This work is, of course, in its early stages, but it provides another piece of evidence that the changes observed in domesticated foxes may really parallel those seen in dogs.

This brief survey of the physical basis underlying the changes seen in domesticated foxes serves three useful purposes. Firstly, it puts some flesh on Belyaev's hypothesis of destabilizing selection, by showing what it is that is destabilized: previously adapted and integrated neuroendocrine systems. Secondly, it shows how selection against aggression can come to have such wide-ranging effects: because the neural and hormonal systems that form the biological basis of aggression also influence a wide variety of other developmental and physiological systems. Finally, it goes some way to explaining why similar changes are found across such a broad spectrum of domesticated species (see **4.2**). The neuroendocrine systems just discussed are evolutionarily ancient, and are highly conserved across species (Bidau, 2009). They provide, then, a shared physiological mechanism to account for the shared phenotypic changes.

It is notable, therefore, that a similar reduction in levels of stress hormone has also been observed in the Bengalese finch, as compared with the wild munia (see **2.4.10**). In chapter five (section **5.2.3.4**), a similar difference will be described between bonobos and chimpanzees, as part of a wider discussion as to whether bonobos, like humans, might represent an instance of self-domestication. These kind of regulatory changes to the neuroendocrine system appear to be a major mechanism in bringing about typical domesticated outcomes.

3.4.6 – Discussion

It seems, then, that the results of the farm-fox experiment provide a very powerful insight not just into the domestication of the dog but into domestication more generally. In particular, that many of the traits comprising the domestic phenotype may not have been directly selected-for themselves, but actually be the result of a correlated cascade of effects following selection against aggression, which itself is mediated by only a small number of genetic changes that influence neuroendocrine regulatory systems. However, despite the strength of this case there are, I think, reasons to suspect that it does not provide a full account of the evolutionary effects of domestication. Chief among these is that the farm-fox experiment says very little about the concept of *buffering*: the way that humans, and in particular the human-made environments in which domesticated species live, change the selection pressures those species face (Price, 1999, 2002; see also chapters two **2.4.10**, four **4.5.1.3** and five **5.1**)

One reason the role of buffering may have been neglected in discussions surrounding the farm-fox experiment is that, cats aside, dogs (and now foxes) are the only large carnivore to have ever been domesticated (Diamond, 1997). All other successfully domesticated species have been herbivores. The significance of this is that one of the major selective pressures against which human-made environments act as a buffer is predation, something of much less concern to a large carnivorous species. Even so, a careful reading of the literature on the farm-fox experiment provides some hints that the concept of buffering is not entirely irrelevant.

For example, it has been repeatedly noted that many of the phenotypic changes seen in the tame line of domesticated foxes have also been observed in the unselected, control foxes (Trut, 1999; Trut et al., 2004; Kukekova et al., 2012), although at a frequency lower by an order of magnitude (Trut et al., 2009). It may well be, then, that a regime of strong artificial selection against aggression is not necessary to bring about the relevant phenotypic changes per se, but rather is necessary to cause those changes to sweep across the population as a whole in just over fifty years. Of course it could be pointed out here, with some justification, that the control foxes are likely to have been subject to a certain amount of indirect or unconscious artificial selection against aggression, and there may be some truth in this point. However, it will be a recurring theme of the next two chapters, where I begin to explicitly consider the idea of human self-domestication, that many aspects of the domestic phenotype can be directly attributed to evolution and development occurring in a human-made environment.

3.5 – Conclusion

This chapter dealt with the second of the preconditions identified in chapter one: the emergence of the sensitivity to communicative intent. Following much the same approach as in chapter two, the possible origins of this precondition were investigated by means of a comparative example, the domestic dog. The evidence suggests that this capacity emerged in dogs as a consequence of the domestication process. Furthermore, as a result of the farm-fox experiment, we also have a strong hypothesis concerning how and why the domestication process might produce this outcome. Much like many aspects of the domestic phenotype (see **4.2**), it seems that the sensitivity to communicative intent in canids has emerged during domestication as a result of a correlated cascade of effects following selection against aggression. It is clear, however, from studies with other, non-domesticated species that domestication does not constitute a *necessary* condition for the emergence of this capacity. Rather, it seems that domestication may have 'primed' dogs such that they are able, from a very young age, to comprehend the communicative nature of cues, at a level that other species—including their ancestor, the grey wolf—only begin to approach following significant training and exposure to humans.

There are, then, two significant points to be taken forward from this chapter and the last. The first is that there is good comparative evidence that shows both the preconditions identified in chapter one—an increased role for traditional transmission, and the sensitivity to communicative intent—emerging in the context of *domestication*. The second is that each chapter identified an important factor in accounting for the outcomes of domestication. In chapter two this was the role of *environmental buffering*, in which the environment of domestication caused a range of selective pressures to be relaxed. In the present chapter a strong case was made that many of the outcomes of domestication can be related to selection on temperament, in particular to a correlated cascade of effects following *selection against aggression*. In the next two chapters the focus turns explicitly to humans and the idea that we might represent an example of self-domestication. This discussion will be informed by both the points identified above. Firstly, if both preconditions could emerge in the context of domestication in other species, might that same context not explain their emergence in humans? Secondly, the two factors identified above—relaxed selection in a buffered environment, and selection against aggression—will both be considered as possible mechanisms that might account for exactly *how* such self-domestication might possibly have happened at all.

Chapter 4

Humans as Domesticates: The Very Idea

In chapter one it was argued that cultural accounts of language structure, such as the ILM, implicitly assume certain preconditions that themselves stand in need of explanation. The first of these preconditions concerned an increased role for *traditional transmission*, with the cultural dynamic this make possible. The second related to aspects of social cognition, in particular the *sensitivity to communicative intent*, with its capacity to support the acquisition of large numbers of signal-meaning pairs. Chapters two and three each focused on one of these preconditions and explored a comparative example in which an analogous capacity or trait could be seen emerging in another species. In both cases the analogous precondition appeared in the context of *domestication*. On first sight, however, this leaves us with something of a problem. The power of evolutionary analogies lies in their providing separate data points, which can then serve to illuminate the selective environment in which traits of a certain kind are likely to emerge. But the task of this thesis is to think about how those preconditions could have emerged *in humans*. In what sense, then, is the context of *domestication* relevant to human evolution?

Fringe elements of the UFO community aside, nobody thinks that humans are being 'farmed' or 'controlled' by another species. If domestication is relevant to human evolution then it must be a kind of *self*-domestication, in which the circumstances of that evolution—some of them likely the result of humans' own actions (Odling-Smee et al., 2003)—have resulted in similar outcomes to those seen in domesticated species. Just to be clear, the idea under discussion here is not the possibility of making vague, metaphorical links between humans and other domesticates, but rather that similarities in the traits seen in domesticated species and humans reflect evolution occurring in similar contexts, with similar selective pressures. In other words, that it makes *literal* sense to say that humans are domesticated, in the same way that you might describe dogs or cows as domesticated. If something like this is the case, then the parallels drawn in the previous two chapters, regarding the preconditions for the ILM, would have considerably more force in terms of explaining how they might have emerged in humans.

In this chapter and the next, the question of human self-domestication will be dealt with in considerable detail. This discussion will be highly exploratory in nature and will have two main aims. The first aim, which forms the focus of this chapter, will be to consider the *coherence* of the notion of human self-domestication. This will entail a look at the typical outcomes of domestication, and how many of these outcomes can also be seen in humans, together with a review of the various selective processes that contribute to those typical outcomes It will also require an examination of what the term 'domestication' means, together with a brief review of the history of the idea of self-domestication in humans. The second aim, dealt with in chapter five, will be to try make the notion of self-domestication more *concrete.* In particular, through a critical discussion of three accounts of *how* self-domestication might have actually happened.

4.1 – A brief history of 'self-domestication'

The idea that humans are in some sense self-domesticated is one with a very long intellectual pedigree. One feature of this history has been the regrettable blending of scientific hypotheses regarding the emergence of 'humanness' with unfortunate political or ideological agendas regarding the supposed superiority of one human group over another. The aim of this section is to acknowledge the former while dispensing with the latter.

Two main contradictory threads run through the historical misuse of the concept of self-domestication. The first is the idea that the more domesticated, and therefore 'civilized', groups or races were somehow more 'advanced' or 'evolved' than other so-called wild groups. The second is the view that the domesticated state represented a 'weakening' or 'moral degeneration' brought on by the trappings of civilization, in contrast to the virtuous state-of-nature exhibited by wild-living human. Both views can be found in the writings of the ancient Greeks, who had a single term—*hemeros*—to refer to domesticated animals and civilized people (by which they meant, unsurprisingly, *Greeks*); and another term—*agrios*—to describe both wild animals and 'savages' who failed to till the land (Peck, 1965; Powell, 1938, both cited in Leach, 2007). In contrast, other writers in antiquity can be found lamenting the 'softening' effects of civilization (Lovejoy & Boas, 1935, cited in Leach, 2007).

More recently, of course, the notion of the 'noble savage' and the corruption linked to civilized living has been associated with Rousseau (1755). Similar contradictions can also be seen in the various eugenics movements in the late nineteenth and early twentieth centuries, for which the effects of self-domestication were explicitly invoked as a rationale (Brüne, 2007)[22]—most notoriously, of course, in Nazi Germany, but also in the preceding Weimar period (Weindling, 1985), Great Britain and the United States (Allen, 1997). Although brief, this survey should serve to make the point that the idea of human self-domestication has picked up some pretty unpleasant political, ideological and pseudo-scientific associations.

This thesis is not a political document. Fortunately, the kinds of ideas just described can be dispensed with on purely scientific grounds. All these views share a common error: the assumption that there is some kind of 'evolutionary hierarchy', atop of

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[22] For example, writing in 1914, Eugen Fischer—who would go on to become a leading Nazi eugenicist—listed blond hair and blue eyes amongst the domestication-induced variants that should be eliminated. Of course, during the Nazi period itself, these same characteristics came to embody the strong, healthy, natural Aryan 'master race'.

which sit species or groups that are 'more advanced' or 'more evolved'. This way of thinking goes back to the ancient Greek, and later mediaeval, concept of the Great Chain of Being—or *Scala naturae*—progressing from stones and minerals at the bottom, up through various plants and animals, and capped off with God and the angels (see Mayr, 1982 for a historical perspective). Humans sat just below these immortal beings, with, one presumes, more domesticated, 'civilized' humans being somewhat closer to the angels, and less domesticated, 'wild' humans somewhat closer to the beasts, or vice versa depending on your viewpoint.

From the perspective of modern evolutionary biology—in which species are the result of a shared history of common descent and subsequent adaptation to various environmental niches—this whole way of thinking is complete nonsense. One can reasonably ask whether species *X* or *Y* is better adapted to life *in a particular environment*, but to ask which species or population is 'better' per se—let alone 'more evolved'—is nonsensical. More fundamentally, evolution is blind and directionless, in multiple senses. Natural selection can be characterised as a mindless, foresightless 'algorithm' searching a design-space for solutions (Dennett, 1995). These solutions, which are often far from optimal (Marcus, 2008), have been likened to the work of a 'tinkerer' (Monod, 1977) cobbling together pre-existing resources in novel ways. Finally, the overall trajectory of evolution has itself been shaped by such a range of contingent influences and events that if the 'tape of life' were re-run there is little reason to assume the outcome would be the same as we see today (Gould, 1989). Evolution has no goal, no direction, no ladder or hierarchy along which species and groups could be placed as being more or less 'evolved'. It should be clear, then, that anyone suggesting that a particular trait or collection of traits represents some 'higher' or 'more evolved' stage is imposing an external value judgement that has no connection with the evolutionary biology itself. Such value judgements, needless to say, have no role to play in the present discussion, the focus of which is whether the human species—*Homo sapiens sapiens*—as a result of its own adaptive history, shows signs of similar evolutionary changes to species more conventionally thought of as domesticated.

Others, however, have approached the question of human self-domestication in a genuinely scientific fashion, exploring it as a hypothesis that might explain some aspects of human biology and behaviour. Charles Darwin's views on the possibility of human domestication are somewhat inconclusive. At times he appears to accept the idea, albeit expressed in a way that shows not even Darwin could entirely escape his own time:

> We might, therefore, expect that civilized men, who in one sense are highly domesticated, would be more prolific than wild men. It is also probable that the *increased fertility* of civilised nations would become, as with our domestic animals, an inherited character...
> (Darwin, 1871: pp. 45-46, emphasis in original)

Elsewhere, however, Darwin seems to cast doubt on the whole idea:

> It is, nevertheless, an error to speak of man, even if we look only to the conditions to which he has been exposed, as 'far more domesticated' (Blumenbach 1865) than any other animal. ... In another and much more important respect, man differs widely from any strictly domesticated animal; for *his breeding has never long been controlled*, either by methodical or unconscious selection. No race or body of men has been so completely subjugated by other men, as that certain individuals should be preserved, and thus unconsciously selected, from somehow excelling in utility to their masters. *Nor have certain male and female individuals been intentionally picked out and matched...*
> (Darwin, 1871: 29, emphasis in original)

Darwin's central objection here, it would seem, is that humans cannot be domesticated because they have not had a domesticat*or*, who controlled and intentionally directed their breeding. This, then, is a form of the 'human mastery' model of domestication discussed below (section **4.4**).

Darwin's views can be contrasted with those of the anthropologist Franz Boas, whose work, although sometimes couched in terms that would be unacceptable today, shares with Darwin an overriding interest in the potential explanatory significance of domestication in understanding the development of the human species as a whole, rather than a desire to exult his own particular group or denigrate others.

Boas (1938) cited a range of parallels between humans and domesticated species, including de-pigmentation, the shortening of the face, excessive length of the hair, and the loss of reproductive periodicity. He also discussed the kinds of conditions that are likely to produce these effects, ascribing the changes following domestication to three causes: *changes in environment and diet*; processes of *selection*; and *crossing*. I shall consider the first two of these in more detail here, because many of the themes raised by Boas will be important in the next chapter, where I consider possible accounts of *how* humans may have come to share some domesticated traits.

In relation to dietary and environmental changes, Boas suggested that both domesticates and humans had experienced a dietary shift to more softened, processed food, citing the “artificial change of foodstuffs by means of fire” as particularly important (cf. chapter five, section **5.2**). Boas also discussed the impact of the built environment and its role in providing protection from both climactic extremes and potential predators, in terms which are reminiscent of the discussion of the Bengalese finch in chapter two:

> ...artificial means of protection against climate and enemies are important features in the process of domestication because they modify the essential conditions of propagation and the course of individual development. Under protecting influences the chances of survival of varying forms and hence the composition of the population may be materially altered.
> (Boas, 1938: 81)

With regard to what he terms 'conscious selection' Boas admitted it was unlikely to have had that great an influence on human evolution. Intriguingly, however, he suggests that various 'social laws' and customs, such as those regulating marriage and the various prohibitions and prescriptions surrounding infanticide may have had an *unconscious* selective effect. This is an idea that will be returned to in the next chapter, particularly section **5.3**.

By invoking an important role for the environmental conditions under domestication, Boas can be seen as advocating a somewhat different model of domestication than Darwin. The tension between these two models will be discussed in much greater detail in section **4.4**, below. For now, however, it is important to realise that what motivated Boas to consider the idea that humans might be grouped with other domesticated species was the range of traits typically seen in other domesticates that could also be seen in humans.

4.2 – The domestic phenotype

It has long been known that many phenotypic similarities can be seen across a wide range of domesticated species (Darwin, 1868; Price & King 1968). This suite of phenotypic changes has come to be known as the *domestic phenotype*, defined as:

> ...that cadre of phenotypic traits that facilitates the adaptation of captive animals to their environment.
> (Price, 1999: 247)

As shown by the tables below, it is possible to split aspects of the domestic phenotype into two broad categories: those that involve hard tissue, and those that involve soft tissue and behaviour. These tables should be read in terms of how domesticated species typically differ from their wild equivalents, and are based on overviews by Leach (2003), Price (1984; 1999; 2002), Clutton-Brock (1999) and Trut et al. (2009).

Hard Tissue	
Skeletal	**Cranial**
Reduction in body size	Reduced cranial robusticity
Decreased skeletal robusticity	Reduced brain size
Reduced sexual dimorphism	Shortened facial region
	Greater diversity size/shape horns
	Reduced tooth size
	Tooth crowding/malocclusion
	Juvenile shape retained in adulthood

Table 4.1: Hard tissue changes under domestication

Soft Tissue and Behaviour		
Physiological	**Sexual and Life History**	**Environmental Responsiveness**
Increased variation in coat colour	Earlier sexual maturation	Reduced motor activity
Increased variation in hair structure	Extended breeding seasons	Reduction in information acquisition systems
Enhanced physiological performance	Increased sexual stimulation	Reduced intra-specific aggression
	Greater/more varied litter sizes	Increased docility
	More multiple births	
	Juvenile behaviours retained into adulthood	

Table 4.2: Soft tissue and behavioural changes under domestication

Of course, not all of these characteristics are found in all domesticates, but nearly all domesticated species exhibit a significant subset of these characteristics (Price, 2002). Indeed, some of the hard tissue characteristics are actually used by archaeologists as diagnostic of domestication having occurred (Zeder et al., 2006).

4.3 – The domestic phenotype in humans

As noted above, it was the observation that humans also shared many of these typical characteristics that motivated Boas' suggestion that humans might also be thought of as domesticated. More recently, this theme has been taken up by Leach (2003), who provides an extended discussion of the parallel changes in skeletal robusticity, cranial thickness and dentition that can be seen in humans and their domesticated species.

This section begins with an overview of the arguments made in Leach (2003), and references therein, regarding changes to the skeleton, cranium and teeth. I then build on the template provided by Leach and extend it to several of the other aspects of the domestic phenotype, as listed in tables 4.1 and 4.2, above.

The approach taken here has, however, one major problem. In chapter two the domesticated Bengalese finch was compared with its wild ancestor, the white-rumped munia. In chapter three the domestic dog was compared with its ancestor, the grey wolf. In discussions of the domestic phenotype more generally the comparison is usually drawn between domesticated strains and either their direct wild-living ancestor or close relatives if the ancestor is no longer extant. In the human case, however, there is only one present-day species, *Homo sapiens sapiens*, and there is no 'wild' comparator available. The solution to this problem taken here —and in other similar discussions (e.g. Leach, 2003; Bednarik, 2011a)—is either to compare trends over the course of human evolution, where this is possible, such as can be done for changes in hard tissue. Or, where this is not possible, to compare humans with their closest living relatives, the great apes.

4.3.1 – Reduced skeletal and cranial robusticity

In skeletal terms, robusticity is usually identified with thickness of long bones, such as the femur, and the degree of development shown in areas for muscle attachment. In cranial terms, too, robusticity relates to bone thickness, but also to the size and prominence of ridges, like those across the brow of the eyes, known as *tori* (singular *torus*) (Lahr & Wright, 1996). Skeletal and cranial robusticity have both consistently declined over the course of human evolution. Skeletal robusticity, as measured by changes in the thickness of the midshaft of the femur, has shown a long-term, exponential reduction over the course of the last one million years of human evolution (Ruff et al., 1993). This decline has followed a log-linear pattern, such that the overwhelming majority of the reduction has occurred in the last 100,000 years. Cranial robusticity has also shown a marked decline. In Europe, the continent with the most available data, cranial robusticity has been declining by an average of 10% every 10,000 years for the last 50,000 years (Bednarik, 2011a). The available evidence also suggests that a similar decline has occurred in most other regions of the world.

The explanations for this decline in robusticity have included the effects of increased sedentism and reduced activity due to changes in lifestyle and the impact of technology (Ruff et al., 1993), changes in climate (Pearson, 2000), and changes and stressors on diet (Cohen & Armelagos, 1984). In particular, shifting to a softer, more processed diet has been shown to significantly reduce the thickness of the cranial vault (Lieberman, 1996). As Leach (2003) has argued—and this point is relevant to many of the phenotypic characteristics discussed in this section—many of these same explanations have been invoked to explain similar changes in other species, where they are seen as linked to the wider phenomenon of domestication. In humans, however, this link is not made, possibly because of too narrow an adherence to the 'human-mastery' model of domestication, discussed below.

4.3.2 – Changes in dentition

Domestication is usually associated with a reduction in tooth size, often combined with an increase in the prevalence of malocclusions and tooth crowding. Here, too, a similar pattern can be observed over the course of human evolution. For the last 100,000 years human tooth size has been continually reducing. Between 100,000 and 10,000 years ago this reduction proceeded at a rate of 1% every 2000 years; since 10,000 years ago the rate has doubled to 1% every 1000 years (Brace et al., 1987). It should be noted that tooth-*size* is under greater genetic control than bone thickness (Larsen, 1995), suggesting that these reductions have likely proceeded through cumulative genetic changes in favour of smaller teeth, rather than changes in diet or lifestyle. In contrast, malocclusion and tooth-crowding have been shown to follow from switching to a softer, more processed diet in both humans and other species (Larsson et al., 2005; Leach, 2003). The explanations for the parallel changes seen in both humans and domesticated species have been fairly similar, including sedentism, dietary changes, and the effects of food processing techniques; and, again, only in the case of other species has this been seen as indicative of domestication (Leach, 2003).

4.3.3 – Retention of juvenile characteristics

A common theme of many instances of domestication is that physical and behavioural traits that once characterised juvenile individuals come to be retained into adulthood (Trut et al., 2009), a phenomenon known as *paedomorphosis* (Shea, 1989). Indeed, many of the characteristics listed in tables 4.1 and 4.2, above—such as the shortening of the face and reduced levels of aggression—can be linked to this wider phenomenon of juvenilization. This was seen very clearly in the discussion of the farm-fox experiment in chapter three, where various traits such as floppy ears, extended socialisation periods, piebald coat colouration and changes to the shape of the skull seem to be the result of retaining a juvenile stage into adulthood. As indicated in tables 4.1 and 4.2, this is also a pattern seen amongst domesticated species more widely. There have long been suggestions that humans present a similar instance of juvenilization.

In discussions dating from the early to mid- twentieth century (Bolk, 1926, 1929; de Beer 1958, Ashley Montagu, 1955, 1960) this phenomenon was variously discussed under the headings of, 'paedogenesis', 'foetalization', 'neoteny' and a range of other terms (see de Beer, 1958: 63 for an overview). Differences in terminology aside, however, all these authors agreed that humans, and in particular their anatomy, represented the retention of typically juvenile ape characteristics into adulthood. There was also relatively broad agreement amongst these authors about which human traits represented such juvenile retentions, as indicated in table 4.3, below.

Juvenile Characteristics Retained in Adult Humans (according to authorities in the early to mid- twentieth century)	
Retention of cranial flexure	Absence of brow ridges
Long slender neck	Absence of cranial crests
Forward position of foramen magnum	Thinness of skull bones
Orbits under cranial cavity	Globular form of skull
Flatness of face	Hairlessness of body
Retarded closure of cranial sutures	Lack of pigment in some groups
Large volume of brain (relative to body)	Thin nails
Small face and large braincase	Non-rotation of big toe
Roundheadedness	Incomplete rotation of thumb
Small teeth	Prolonged dependency period
Late eruption of teeth	Prolonged growth period

Table 4.3: Juvenile characteristics retained into adulthood
(Based largely on Ashley Montagu, 1960)

The contemporary discussion of paedomorphosis in humans begins with Stephen Jay Gould's (1977) book *Ontogeny and Phylogeny*. Gould made three key points regarding the role of paedomorphosis in human evolution. The first was that the data of those working on this question in the early twentieth century (as listed in table 4.3) could be divorced from their specific theories of evolution. In particular, some, such as Bolk (1926), insisted that humans were characterised by a *global* paedomorphosis, a position owing to his adherence to a view of evolution emphasising 'internal consistency' and his rejection of adaptation and natural selection. From a modern perspective, as Gould notes, the idea that instead we might see a *mosaic* pattern—with some features being juvenile retentions and others not—is entirely unremarkable. Gould's second point was that distinction needs to be made between two different aspects of the argument. The first is the fact that humans have a relatively retarded developmental trajectory—with a long interval between birth and maturation, a very late adolescent growth spurt and an extended post-reproductive lifespan—a pattern which has been described as distinctive a human trait as a large brain or language (Leigh, 2001). The second aspect is the paedomorphic characteristics themselves, for which this retarded developmental trajectory acts, in Gould's phrase, as an 'enabling condition'. Finally, Gould argued that the relevant comparator in seeking to establish human paedomorphosis is not other apes, who after all are not our ancestors, but *human foetuses* (as the ape foetus most likely to resemble the foetal condition of our ancestors), with the relevant question being 'how far do humans depart from their foetal condition in comparison with other primates from theirs?'. Gould's answer was that humans are “essentially” neotenous, a conclusion based largely on the retarded human developmental trajectory.

This conclusion has since been challenged on a number of grounds (see Shea, 1989 for an overview). One objection is that discussions of paedomorphosis have conflated various different process, these include: *neoteny*, the dissociation between size and shape; *rate hypomorphosis*, the slowing of growth rates with no change in the duration of growth; and *time hypomorphosis*, the reduction in the duration of the growth period with no change in rates of growth (Shea, 1989). While important, this objection need not concern us further here because the focus of the present section is simply the fact that paedomorphic traits are typically seen following domestication and the extent to which humans might also exhibit such paedomorphic characteristics. As such, I shall remain agnostic regarding the underlying processes that produced those traits.

Another major objection focuses on the fact that many human characteristics, in particular the size of the brain, are actually the result of an *extension* of growth, or *hypermorphosis*, beyond its ancestral endpoint—a process known as *peramorphosis* —rather than a retardation-based 'juvenilization' (McKinney, 1998). More recently, however, it has come to be seen that these objections are the result of conflating two different processes: slow *development* and fast *growth* (Zollikofer & Ponce de León, 2010), which together account for the paedomorphic appearance of the modern human skull. The combined effect of these two processes produces a skull that is both large (as a result of an extended period of growth) and has a juvenilized shape (as a result of slowed development). Data are now available on the ontogeny of cranial shape across various species during human evolution, as illustrated in figure 4.1 below:

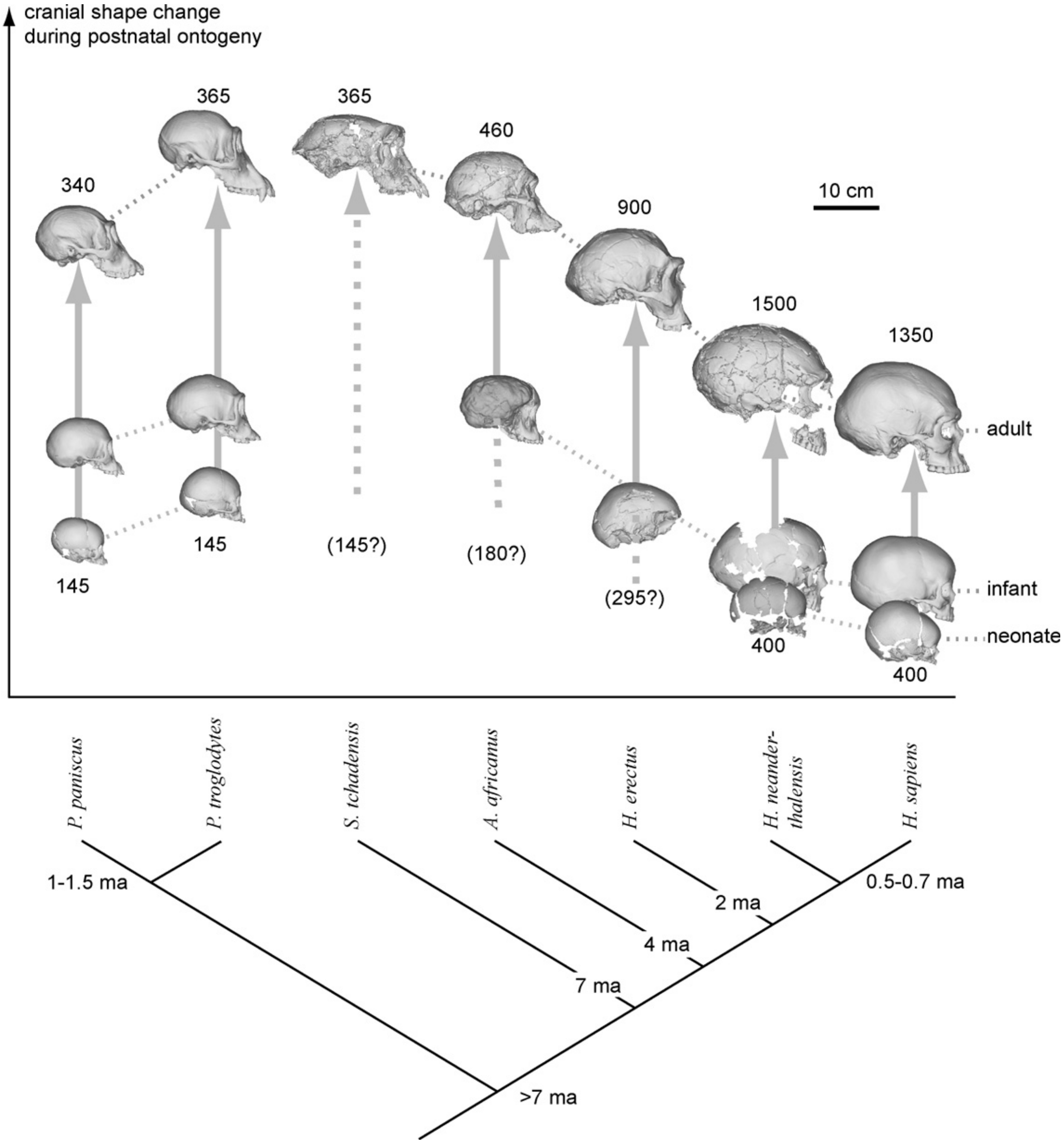

Figure 4.1: Cranial shape-change during development of human ancestors
(Taken from Zollikofer & Ponce de León, 2010)

The data in figure 4.1 should be viewed in light of Gould's argument that the relevant comparison is the extent of change seen in human adults as compared with human foetuses, relative to the extent of change over ontogeny in other, related species. As can be seen, the overall trend in human evolution has been towards adult crania that more closely resemble the shape of their foetal state (Zollikofer & Ponce de León, 2010). It should be noted, however, that this overall picture is complicated by species-specific aspects of morphology that are unrelated to heterochronic processes. For example, the comparison between modern humans and Neanderthals seems to involve prenatal changes related to differential patterns of bone-growth activation, followed by a shared post-natal pattern of developmental (Zollikofer & Ponce de León, 2010).

In making his case for humans' essential neoteny Gould (1977) argued that this paedomorphic condition was also *adaptive*. Gould's claim, echoing several earlier authors (e.g. Cohen, 1947; Jacobson, 1969; Lorenz, 1971), was that the process of retarded development, by projecting juvenile flexibility into adulthood, interacted synergistically with increasing brain size and the hyper-socialisation and dependence on learning seen in humans. This has much in common with perspectives on human life history that view the long human developmental trajectory as relating to the time needed to acquire the full set of cultural skills necessary to function in human societies (Bogin, 1999); and to the 'embodied capital' which can be built-up during the long developmental period and subsequently 'cashed in' during adulthood, including the post-reproductive period (Kaplan et al., 2000). Of course, there are also a variety of other views on the significance of human life-history (see Leigh, 2001 for a review). However, in recent years a range of evidence has emerged suggesting that the physical basis of humans' extreme behavioural flexibility may lie in the paedomorphic retention of juvenile neural plasticity.

Somel et al. (2009) compared the developmental timing of gene expression in the human and chimpanzee prefrontal cortex. While there was a mosaic pattern overall, the dominant trend, as seen in two areas of the cortex, was a neotenic shift in humans, such that the gene expression profiles of adult humans resembled those of juvenile chimpanzees. In terms of brain tissues, the human neotenic genes were significantly more likely to be expressed in areas associated with grey matter. Functionally, they were also more likely to be associated with processes of growth and development. Somel et al. argue that this delay in grey matter maturation relates to an extension of juvenile plasticity, thus providing humans with a longer period during which to acquire knowledge and skills.

Similar findings have been reported regarding the major period of synaptogenesis—the creation of synaptic connections between neurons, which are known to underlie the formation of memories and thus learning (Bufill et al., 2011). Liu et al. (2012) found that the majority of gene-expression profiles in the human, macaque and chimpanzee prefrontal cortex followed similar overall trajectories, but in humans those trajectories were significantly delayed. Many genes that reached peak expression levels during the first year in chimpanzees and macaques didn't reach peak expression until around five years in humans. This extension of synaptic plasticity may partially account for the great metabolic cost of human brains, which use 20-25% of total metabolic energy while at rest, in comparison to the 11-13% in apes and 2-8% in mammals (Bogin, 2006; Mink et al., 1981). Such heightened metabolic costs, combined with greater plasticity they enable, are both typical of the juvenile period during which most learning and neuronal remodelling takes place (Bufill et al., 2011). Again, the pattern observed in adult humans resembles that seen in juvenile chimpanzees (Bufill et al., 2011; Somel et al., 2012). It seems, then, that there is good evidence that humans are paedomorphic in terms of both many aspects of their anatomy and morphology, and in terms of the development of neural systems thought to underlie behavioural flexibility.

4.3.4 – Changes in temperament

Many of the behavioural aspects of the domestic phenotype relate to a reduction in aggression and a concomitant set of changes in temperament that alter how domesticated species engage with their environments (Price, 2002). Réale et al. (2007) suggest that temperament can be usefully broken down into five major trait categories: (1) shyness-boldness, (2) exploration-avoidance, (3) activity, (4) sociability, and (5) aggressiveness. Domesticated species typically show reduced levels of exploration and activity, together with reduced levels of aggression (Künzl et al., 2003).

Herrmann et al., (2011) compared the first two of Réale et al.'s dimensions in humans, chimpanzees, bonobos and orangutans. They found that human infants avoided novel items, whereas other apes, particularly chimpanzees and orangutans, were attracted towards novel items. Bonobos were intermediate between humans and other apes, showing a largely indifferent response. This is especially intriguing given the discussion of bonobos in the next chapter. To anticipate, evidence seems to be accumulating that bonobos, but not chimpanzees, might also share aspects of the domestic phenotype. In particular, that selection against aggression might have resulted in commonalities between bonobos and domestic dogs (discussed in chapter three) on the one hand and bonobos and humans on the other (Hare et al., 2012). These parallels include the similarities in temperament—increased shyness in the face of novelty and reduced exploration—investigated by Herrmann et al. Work comparing human temperament with that of other apes has really only just begun, but early indications suggest that at least some aspects of human temperament may also be in line with that found in the domestic phenotype.

4.3.5 – Sexual changes

Sexual dimorphism is often reduced in domesticated species compared to their wild ancestors. The evidence suggests that modern humans, too, are less sexually dimorphic than both present-day apes and our hominin ancestors. It should be understood that sexual dimorphism is not a single characteristic, but rather refers to a variety of comparators between males and females. Compared to present-day apes, humans have relatively low sexual dimorphism across a range of these characteristics. For example, tooth-size is typically around 10% greater in males than females, placing humans at the lower end of the primate range (Plavcan, 2012). In terms of overall body size, humans are also towards the low end of the primate range (Plavcan, 2012). This point is tempered by the fact that humans appear to exhibit a dimorphism in body-fat accumulation not seen in other primates, with females having much more body-fat proportionally than males (Puts, 2010). Our knowledge of the relative muscle and fat compositions of other primates is, however, relatively poor (Plavcan, 2012). Nevertheless, once body-fat is taken into account, humans fall squarely in the middle of the primate range. Humans also show relatively low levels of dimorphism in their cranial and skeletal dimensions, with both these placed somewhat intermediate between the figures for overall size and size adjusted for body fat (Plavcan, 2012). Overall, then, humans are very much at the low end of the range of sexual dimorphism seen in present-day apes.

Sexual dimorphism can also be compared between modern humans and their now-extinct hominin ancestors. These comparisons are, of course, restricted to dimorphism in hard tissue. There is also the problem of the small number of specimens, and determining whether those specimens represent two distinct species or a male and female difference within a species (Plavcan, 2001). The available evidence indicates, however, that there has been an overall trend towards reduced sexual dimorphism over the course of human evolution. A reduction in canine tooth-size dimorphism can be seen from early in the evolution of hominins, with species such as *Australopithecus afarensis* and *Australopithecus anamensis*—dating from

4.2-2.9 Mya (Ackermann & Smith, 2007)—showing little sign of substantial canine dimorphism (Plavcan, 2012). However, analyses of some of these same early species indicate substantial skeletal dimorphism (Harmon, 2006; Gordon et al., 2008; Kimbel & Delezene, 2009), which approaches that seen in gorillas today (Plavcan, 2012). These findings have, however, been contested (e.g. Nelson et al., 2011). The data for other species of the genus *Australopithecus* and for early *Homo* (e.g. *Homo habilis*, 3-2 Mya, Ackermann & Smith, 2007) are too limited to make any clear judgement (Plavcan, 2012). Although also limited and uncertain, the available data for *Homo erectus* (from c1.8 Mya, Rightmire, 2008) suggest a greater degree of dimorphism than seen in modern humans, while that for more recent species of *Homo*, including *Homo heidelbergensis*, the Neanderthals and early *Homo sapiens* suggests dimorphism broadly in line with present-day humans (Plavcan, 2012).

Sexual dimorphism is a particularly interesting trait from the perspective of this thesis because not only does it fossilise (at least in terms of hard tissue), but it is also reliably correlated with *aggression*. More precisely, it is correlated with mating systems in which there is substantial intra-male competition for access to females (Plavcan, 2012). As discussed at length in chapter three, many aspects of the domestic phenotype seem to follow as the result of a correlated cascade of effects following selection against aggression. In the next chapter, we will discuss the case of the bonobo, which represents a possible parallel example to the human one discussed here, where selection against aggression may have changed both the mating system and reduced sexual dimorphism. For now, however, it should also be noted that changes in sexual dimorphism have also been associated with a range of non mating-related factors (Plavcan, 2001), and that while high levels of dimorphism are reliably associated with a particular kind of mating system, low levels of dimorphism are not (Plavcan, 2012).

One further sexual change often found in domesticates is the extension, or complete loss, of seasonal patterns of breeding. For many years it was thought that humans, too, had lost all traces of seasonality of breeding (e.g. Symons, 1979). In particular, that human females lacked a distinct 'fertile' phase in their reproductive cycles, known as *oestrus*. This parallel between humans and other domesticates has been noted (e.g. Bednarik, 2011a), together with the possibility that both might be explained in similar terms. In recent years, however, studies of how female preferences and behaviour change across the cycle have found that human females actually do have a distinct, fertile phase that corresponds to oestrus (Gangestad & Thornhill, 2008). It still remains the case, however, that human females exhibit what has been termed *extended sexuality* (Rodríguez-Gironés & Enquist, 2001), in which they remain sexually receptive across their entire cycle.

This is something seen across a variety of bird and mammal species, where the best supported explanation seems to relate to the material benefits females can obtain from males through this strategy (Rodríguez-Gironés & Enquist, 2001). Firstly, through females being able to both control paternity, but also sow sufficient confusion over paternity to mitigate against dangers such as infanticide. And, secondly, through more immediate benefits that might accrue through the granting of sexual access (Gangestead & Thornhill, 2008). This, then, seems a more likely account of the evolution of extended sexuality in human females than one rooted in the nature of the domesticated environment, where it is accounted for by a combination of better nutrition, artificial selection for early maturation and relaxed selection on male mate-competition (Price, 1985).

4.3.6 – Brain size: The glaring exception?

Domestication is typically associated with a reduction in brain size. The long-term trajectory of human evolution, however, has been one of *increasing* brain size (Rightmire, 2004), with hominin brains tripling in size over the last four to five million years (Henneberg, 1998). This increase is reflected in the high encephalization quotient (EQ)—the relationship between body size and brain size—seen in humans (Jerison, 1973). By this measure, humans have a brain about seven times as large as would be expected for a mammal of our size. It is important to note, however, that this size increase has not been uniform across all brain areas. In particular, the neocortex—part of the telencephalon, or forebrain—is enlarged to a far greater extent than other sub-cortical areas, such as the striatum (Deacon, 1990, 1997). This point will be important later.

The evolution of the human brain has not, however, been one long uninterrupted increase in size. The last 50,000 years has actually seen a *decrease* in brain size (Henneberg, 1998), from a peak cranial volume of about 1500cc to the present-day volume of around 1350cc. Interestingly, this decrease occurred at the same time as the reductions in robusticity and teeth-size discussed above. Could it also be an indicator of domestication, as some (e.g. Allman, 2000) have suggested? It is tempting, too, to suggest that this reduction was enabled as a result of the support provided by complex cultural productions (Tobias, 1971), the creation of which have been argued to extend and enhance human cognition beyond what is possible with the brain alone (e.g. Clark, 1997). Might this have enabled the emergence of individuals who had to rely less on their own brains, and could thus afford smaller ones? In short, could the buffering provided by the human-made environment have relaxed selection on human brain size, in a similar way seen in other domesticates? Tempting as this line of reasoning is, there are three arguments that make it unlikely to be true.

The first is that brain-size variation in present-day populations is no greater, and perhaps smaller, than the variation seen in fossil hominins (Henneberg, 1998). This is not what would be expected if brain size had reduced in response to a relaxation of selection, as the resulting drift should produce an increase in variation. The second is that virtually all the reduction in brain size seen over the last 50,000 years can be explained in relation to a concomitant reduction in body size (Ruff et al., 1997). The parallel reductions in robusticity and brain size may not, then, be two signs of the same trend—human self-domestication—but rather one (reduced robusticity) may actually account for the other (reduced brain size), at least if a Jerison-like analysis of

EQ is accepted[23]. The final objection concerns the scale and pattern of brain-size reduction under domestication. The scale of brain-size reduction seen amongst domesticates typically reflects the degree of encephalization in the wild ancestor (Kruska, 2005), with more encephalized species such as pigs showing greater reductions (34%) than less encephalized species such as mice (no change). Humans are significantly more encephalized than pigs, and yet the recent reduction seen in humans is significantly *less* than that seen in pigs. The *pattern* of brain-size reduction under domestication is also not uniform, with the greatest reductions seen in the telencephalon (or cerebrum) and the diencephalon, which together constitute the mammalian forebrain (Kruska, 2005). Recall, however, that is just these areas that have shown the greatest increase over the course of human evolution.

It seems, then, that a reduction in brain size is one aspect of the domestic phenotype that humans do not share. Although recent human evolution does involve a reduction in brain size, it seems likely that this can be attributed to a parallel reduction in body size. But even in the absence of a body-size link, the details of brain-size reduction under domestication simply do not fit the human case. It may be that this is one trait where the fact that domestication, in this instance, is *self*-domestication is actually important, with humans, as both constructors and inhabitants of their environment, not subject to the same reduction in stimulation and opportunities for sensory exploration (Price, 2002) experienced by other species living in that environment (Leach, 2003).

4.3.7 – Build-up of deleterious alleles

The main focus of this section so far has been on the typical *phenotypic* effects of domestication. However, one further outcome seen in many domesticated species is the build-up of deleterious alleles[24], something that has been described as the 'cost of

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[23] It should be noted that Jerison's measure of brain size is now considered somewhat simplistic (see Deacon, 1997 for a wide-ranging discussion of the topic). However, for present purposes these complications can be ignored.

[24] Some mutations have their effects *conditionally*, such that a given allele might be neutral in one

domestication' (Lu et al., 2006). This build-up has been documented across a wide range of domesticated species, from dogs (Björnerfeldt et al., 2006; Cruz et al., 2008) to domesticated strains of Yak (Wang et al., 2011). I will explore this topic in more detail in chapter five (section **5.1.1.7**), for now, however, the key point is that similar observations have long been made for humans.

From the middle of the twentieth century onwards, there have been a range of warnings about the damaging accumulation of deleterious alleles in human populations (Haldane, 1939; Muller, 1950; Mayr, 1963), as a result of those alleles no longer being eliminated by natural selection, at least in industrialized societies. Post (1971) presented data showing higher rates of colour blindness, myopia, deformities of the nasal septum, and other conditions with a known genetic cause in industrialized populations than in 'primitive' peoples. There have continued to be periodic warnings of the dangers of this mutational accumulation for the future of human health (e.g. Crow, 1997; Lynch, 2010). In the case of both humans (Crow, 1997) and domesticated species (Lu et al., 2006; chapter five, **5.1.1.7**), the build-up of deleterious alleles has been linked to the 'buffering' provided by the nature of the human-made environment. Again, much as with many of the phenotypic characteristics, a parallel can be drawn between humans and domesticates not simply on the presence of similar changes but in terms of the explanations invoked to account for those changes.

4.3.8 – Summary

There are, then, a range of parallels that can be drawn between humans and domesticated species, as regards a number of the features of the domestic phenotype. This section started with the arguments made by Leach (2003) that humans and domesticates show similar changes in skeletal, cranial and dental morphology. This

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environment, deleterious in another and beneficial in a third. Other mutations, however, are described as *unconditionally* deleterious, because they negatively impact the functioning of an important biological system, such as respiration, which is deleterious regardless of the environmental situation (Elena & de Visser, 2003). Throughout this thesis the phrases 'deleterious allele' or 'deleterious mutation' should be read as being *unconditionally* deleterious.

approach was then extended to other aspects of the domestic phenotype, where a range of further similarities were also found. It is important to note, however, that there are some clear exceptions. The most obvious of these relates to the changes in brain size, which in humans fit neither the direction or pattern of that seen in other domesticated species. This may reflect one area where *self*-domestication might differ from domestication as normally understood, because the former may not involve the loss of opportunities for mental stimulation and activity often associated with the latter.

Nevertheless, in many of those traits that do show a parallel, two points made by Leach can be seen to hold. The first is simply that humans exhibit many aspects of the domestic phenotype. The second is that many of the explanations for why those characteristics might have appeared in both cases—human and domesticate—are often of a similar kind, relating to changes in climate or diet, or to the effects of selection on temperament. Despite this latter similarity, these changes are only usually viewed as indicative of domestication when seen in other species. Leach argues that this is a result of how the process of domestication has often been conceived. If domestication is *defined* as a process that is driven and controlled by conscious selective control over breeding and living conditions, then it would seem impossible for it to apply to humans. The possibility that humans might in some sense be self-domesticated requires, therefore, that we examine the concept of domestication itself.

4.4 – What do we mean by 'domestication'?

The various conceptions of domestication fall along what we might call the *exploitation-mutualism continuum*. As an example of the exploitation end of this continuum, consider the following two definitions:

> [a domestic animal is] bred in captivity for the *purposes* of subsistence or profit, in a human community that *controls* its breeding, its organisation of territory and its food supply.
> (Clutton-Brock, 1992: 41, my emphasis)

> The essence of domestication is the *capture* and taming by man of animals of a species with particular behavioural characteristics, their *removal* from their natural living area and breeding community, and their maintenance under *controlled* breeding conditions...
> (Bökönyi, 1989: 22, my emphasis)

As the added emphasis makes clear, these definitions very much focus on domestication as the human 'mastery' of nature, through the capture, removal and control of other species, by humans, for our own conscious purposes.

It should be noted, however, that these definitions can be given two readings. On the first reading they describe the *conditions* of many present-day domesticated species. To some degree at least, this reading is clearly correct: for example, domesticated cattle and dogs *are* kept in controlled territories, with regulated breeding, and to serve human needs, whether those needs be food, companionship or something else. On the second reading, however, the definitions might be taken to describe the *process* whereby wild-living species came to take on their current domesticated form. As such, this second reading might be taken to suggest that the typical characteristics of domesticated animals—the domestic phenotype—are predominately, or even entirely, the result of the choices and purposes of their human domesticators, the result, that is, of artificial selection and selective breeding.

The difference between these two readings also raises a further question: should domestication be defined in terms of its *conditions*—being kept in captivity by humans—or by its *outcomes*, the emergence of that constellation of phenotypic traits known as the domestic phenotype? Furthermore, while there is something to be said for both definitions, it is worth asking to what extent they can be divorced. For example, while a tiger cub raised in captivity might well be *tame*, it wouldn't necessarily be considered a *domesticated* animal (Driscoll et al., 2009), despite qualifying under a purely conditions model. Conversely, the presence of certain aspects of the domestic phenotype is often used by archaeologists as part of their assessment as to whether domestication had occurred at a particular point in time (Zeder et al., 2006). Of course, these two approaches to domestication are not necessarily mutually exclusive; however, the tension between them lies behind much of the discussion in the rest of this thesis. Those who entirely reject an outcomes-based view of domestication are unlikely to accept humans as being domesticated.

To return to the current discussion, however, it is far from universally agreed that this 'human mastery' model provides a full account of the process of domestication. In such a model, other species are relegated to the role of passive 'victims' of human exploitation; or, to put it another way, views on the exploitation end of the continuum conceive of domestication largely as a human cultural activity (Zeder, 2006). Others who have considered the nature of domestication, particularly those coming from the perspective of evolutionary biology, have argued that it is best viewed as an example of a mutualism (O'Connor, 1997; Morey, 1994), in which two species engage in co-operative behaviour that is evolutionarily beneficial to both parties (West et al., 2007). For the domesticated species the evolutionary benefit can be measured in terms of its dramatically increased biomass, and the occupation of geographical ranges far in excess of what would be possible in the absence of human involvement (Budiansky, 1994). This mutualistic perspective is well captured by the following quotation, which stands in contrast to the two above:

> People did not take sheep into domestication: rather people and sheep entered into a particular interaction by behavioural adaptation on the part of both species...The benefits of domestication need to be examined explicitly from the sheep's point of view. (O'Connor, 1997: 152)

There is a case, then, for domestication to be seen as a form of evolutionary mutualism. However, to assess the strength of this case, it is useful to compare the domestications undertaken by humans with similar examples in other species. Perhaps the most illuminating available comparisons concern the 'agricultural' practices that have evolved in three different orders of insects: ants, termites and beetles (Schultz & Brady, 2008). These examples of insect agriculture show striking parallels with the practice of domestication and agriculture in humans. Ants, for example, 'capture' an area of the environment, which is then transformed through the selective tending of favoured fungal species into a something of a monoculture (Mueller et al., 2005). Much like the monocultures created by humans, these ant-made monocultures are prone to devastating outbreaks of disease, which the cultivating insects control through the management of a range of microbes (Mueller et al., 2005). This agricultural arrangement also clearly benefits both parties. For example, the fungal species tended by leaf-cutter ants benefit from the ants exclusion of other species, while the ants benefit from the actions of the fungus in degrading their harvested plant material (Kooij et al., 2011).

In light of these parallels it is tempting to view human agriculture and domestication as another example of such a mutualism—as an instance of a natural evolutionary process, rather than the exploitation of other species by human beings who are somehow 'outside' the natural world. There is, however, a limit to how far the parallels between ant and human agriculture and domestication can be taken. In particular, there is a fundamental equality in the ant example that is missing in the human case. In the ant-fungus mutualism both parties adapt to one another *genetically* (Mueller et al., 2005). In the human-domesticate case, however, one party to the mutualism—the humans—can also adapt *culturally* through the transmission of learned behaviours, a process that typically operates much faster than genetic adaptation (Mueller et al., 2005; Mesoudi, et al., 2004). In addition, humans are able to plan ahead, operating with foresight, which is also not possible in the realm of genetic adaptation. This is not to deny the fact that humans *have* adapted genetically to the presence of domesticated species. For example, lactose tolerance is found mainly in those populations with a history of dairy farming (Bersaglieri et al., 2004). Rather, the point is that while domesticated species have *only* been able to adapt to humans genetically, humans have had other, faster means to adapt themselves to the presence of domesticated species. As a result, although the link between humans and their domesticates is an evolutionary mutualism, it is an atypical and unbalanced mutualism, in which one partner, the human, is able to adapt, direct and respond to the relationship to a much greater extent that the other.

Some of the tension between the mutualistic and 'human mastery' views of domestication can be resolved by the realisation that the two models apply to different stages of the same historical process, rather than as competing characterisations of one stage. Conventionally, the single term 'domestication' is applied to the entire process, spread over tens of thousands of years, which has resulted in the domestic species we know today. This hides a much more complex reality, however, because many of the phenomenon that we associate with domestication today, such as the goal-directed breeding of 'pure' varieties or 'types' are of relatively recent origin, and played little to no role in most of the history of domestication. Leach (2007) argues that domestication is better seen as a multi-stage process, which began with humans and other species adapting to each other and to the human-made environment, and today includes the direct manipulation of the genome. Leach's four stages are set out below:

1. *Adaptation to the human-made environment*—beginning with the very first associations between humans and other species.

2. *Adaptation to human agricultural or farming operations*—beginning c.10,000 years ago, this includes all such activity and carries no implication that those operations are carried out with the purpose of bringing about desired changes in the other species, although some may have been directed at the general preservation of 'good' lineages.

3. *Methodical selection by humans*—the deliberate attempt to improve or 'fix' particular breeds, based on the increasing understanding of hereditary in the eighteenth century.

4. *Genetic engineering*—favoured traits are manipulated at the level of the genotype rather than the phenotype, and even the barrier of cross-species mating is removed as genes can be transferred directly between highly unrelated species.

It is important to realise, of course, that each stage does not replace the previous one, but rather introduces a new process that operates alongside the earlier processes. Despite living in the age of genetic engineering, methodical selection is still very much in operation, as is the pressure to adapt to both human actions and to the human-made environment. Historically, too, the traits characteristic of the domestic phenotype have emerged in response to all four of Leach's stages, with the first two having been in operation for by much the longest period. Finally, while all four stages have the potential to influence human evolution, the first two would seem to be the most likely to have had a significant impact.

Related to Leach's multi-stage model of domestication is Zeder's (2012) account of their being multiple 'pathways' to domestication, in terms of how domesticates might have ended up in close association with humans. One possibility is what Zeder terms the *commensal pathway*, in which the association begins with the would-be domesticate coming to frequent or exploit human settlements and habitations. The domestic dog (Morey, 1994) and cat (Driscoll et al., 2007) are both thought to have originated via this kind of process. The second potential route is the *prey pathway*, in which species originally hunted for food, such as sheep, goats and cattle, slowly come under human management, eventually becoming bred and farmed by humans. The third route is termed the *directed pathway*, in which animals are intentionally brought under human control for specific purposes, perhaps following the model set by earlier 'prey pathway' domesticates. The horse and donkey are thought to represent examples of this kind of domestication (Zeder, 2012).

This notion of different pathways is useful because it illustrates that there is not one uniform process of domestication that must have been undergone by every species exhibiting some aspect of the domestic phenotype. For example, domestications proceeding along the commensal pathway would involve long periods in the first two of Leach's stages of domestication. In contrast, those following the directed pathway would enter stage three much earlier in the domestication process, putting them on what Zeder terms the 'fast track' to domestication. Zeder's pathways, then, can be seen as describing different 'entry points' into the stages of domestication outlined by Leach. It is tempting to ask at which of these stages a species can be said to be 'really domesticated'. The trouble with this question, of course, is that we are dealing with a continuum, so that any answer will be somewhat arbitrary. It is more fruitful, as Zeder (2012) argues, to talk about the various distance along the road of domestication travelled by different species, with some travelling further and faster than others. I shall return to these considerations in the next chapter. To anticipate that discussion, however, humans—together with some other examples—might represent instances of domestication having progressed along the first two of the stages outlined by Leach.

Domestication is, then, a biological phenomenon—a mutualism, grounded in evolution—*and* a human cultural activity (Clutton-Brock, 1999; Zeder, 2006). The two kinds of definitions considered above each emphasise one of these two facets of domestication, with those on the exploitation end of the continuum emphasising the cultural aspect, and those on the mutualism end emphasising the biological aspect. It is also more fruitful to view domestication as a multi-stage process along which different species might progress at different rates, rather than a single process undergone identically by all. The key point for present purposes, however, is that it is inadequate to characterise domestication as solely a human cultural activity, in which our conscious choices exploit and alter other species. As a result, it is important to consider the different ways in which domestication can have evolutionary effects, aside from conscious selective breeding on the part of the domesticator.

4.5 – The evolutionary processes involved in domestication

Evolutionary processes can be divided into those that produce random changes in gene frequencies, such as inbreeding and genetic drift, and those that produce non-random changes, such as selection (Price, 2002; Griffiths et al., 2004). As my concern here is with the *typical* outcomes of domestication, the domestic phenotype, I am only going to focus on those evolutionary processes that are non-random. This is not to say that inbreeding and genetic drift are not operative; indeed the small, 'founder-like' populations often seen in relation to domestication (Price, 2002) provide optimal conditions for both inbreeding and genetic drift to have the greatest evolutionary impact (Griffiths et al., 2004). However, the similarities seen across a wide range of domesticated species cannot, by definition, be accounted for by a random process. As a result, I will focus on the various *selective* processes that have contributed to the domestic phenotype. I will also discuss the role that developmental plasticity might play in the creation of the domestic phenotype—through what has been termed *ecophenotypic responses* (Leach, 2003)—in which similar phenotypic traits appear in every generation as a result of development occurring in a similar environment (West-Eberhard, 2003).

4.5.1 – Selective processes

There are three selective processes that play a role in the production of the domestic phenotype (Price & King, 1968):

(a) Artificial selection
(b) Natural selection in the domesticated environment
(c) Relaxation of selection

It should be noted, of course, that, strictly speaking, (c) is really a component of (b): the fact that certain selective pressures are relaxed under domestication—such as the risk of predation—is simply one aspect of the environment in which natural selection operates following domestication. However, the inclusion of relaxed selection as a separate process here serves to emphasise that the evolutionary impact of domestication comes not only from the novel things it *adds* to an organism's environment, such as human-controlled artificial selection, but also what it *removes*, in the form of various selective pressures that were important in the wild but not in captivity. In the remainder of this section I will discuss each of these three processes in turn.

4.5.1.1 – Artificial selection

At its broadest, artificial selection refers to the human intervention in plant and animal reproduction in order to ensure the spread and maintenance of desirable traits—desirable *to humans*, that is. It has been suggested (e.g. Price, 2002) that artificial selection differs from natural selection in that it is applied prior to reproduction, rather than measured after reproduction, by an individual's contribution to the next generation. However, while this may be true for the paradigmatic example of artificial selection—selective breeding—artificial selection can operate in a variety of other ways too. This is reflected in the two major distinctions that have been made in relation to artificial selection.

The first distinction is between what has been termed *strong* and *weak* forms of artificial selection (Driscoll et al., 2009). In the strong form the selection is pre-zygotic—it is applied before breeding has occurred—and consists in the pairing together of individuals that exhibit favoured traits. This is probably what Price had in mind, and is also what accounts for the close identification of artificial selection with selective breeding. In the weak form the selection is post-zygotic, and involves the elimination of individuals who fail to exhibit favoured traits. Of course, such post-zygotic selection also has pre-zygotic consequences, in the obvious sense that all future matings will only involve those allowed to survive. However, this effect is considerably less precise than true pre-zygotic selection as it doesn't involve the pairing together of *specific* individuals, hence the designation *weak*.

The second distinction, which traces back to Darwin (1868), is between human-initiated selection that is inadvertent (unconscious) and that which is intentional (conscious). Unconscious selection occurs when humans, for whatever reason and however subtly, favour certain individuals over others, without any knowledge or intent regarding the long-term effects of their actions (Ryan, 2009). By contrast, conscious selection occurs when humans intentionally set out to produce change in a particular trait. Artificial selection can, therefore, take four possible forms:

	Pre-zygotic	**Post-zygotic**
Conscious	Belgian Blue cattle	Culling herd
Unconscious	*????*	Coonstripe shrimp

Table 4.4: Forms of artificial selection

Moving clockwise through table 4.4, a startling example of conscious pre-zygotic selection can be seen in cattle, most famously the Belgian blue. Since the 1950s breeders have been selecting for the 'double-muscled' phenotype, which had previously been an infrequent aberration in the breed (Arthur, 1995). Such cattle are not only strikingly large, with multiple ripples of inflated muscle tissue, but are also virtually incapable of giving birth unaided, generally requiring Caesarean section (Vandenheede et al., 2001). Conscious post-zygotic selection might be exemplified by the culling of disfavoured animals from a herd. An example of unconscious post-zygotic selection comes from experimental work on the coonstripe shrimp, and the nature of its escape responses. Frequent handling by experimenters meant that individuals with violent escape responses were often injured—an *inadvertent* culling of the herd—resulting in a population with much reduced escape responses (Marliave et al., 1993). Finally, I am unaware of any example of the unconscious mate-pairing of specific individuals that resulted in a directional evolutionary trend, although such an effect seems logically possible. All four forms are capable of bringing about evolutionary change, although conscious pre-zygotic selection probably has the greatest potential to produce powerful, rapid effects (Driscoll et al., 2009); of course, in recent decades these selective processes have also been augmented by the techniques of IVF and genetic engineering.

The four-way distinction made in table 4.4 is important when considering human self-domestication. While all four processes are theoretically possible, they have very different implications. Conscious pre-zygotic selection in humans might require something like a systematic program of eugenics (Leach, 2003); whereas conscious post-zygotic selection could occur through a process of selective infanticide. I am unaware of any evidence that either of these kind of phenomena have played a major role in human evolution. The situation is very different when considering the two unconscious forms of artificial selection. Such unconscious selection might proceed, much like in the coonstripe shrimp, from the circumstances in which an organism lives and the manner in which it is treated. This should recall Leach's first two stages of domestication. The possibility that something like this might have played a role in human self-domestication will be explored in the next chapter.

4.5.1.2 – Natural selection in the environment of domestication

Any selection faced by organisms under domestication that is not ascribable to one form or other of artificial selection, must be *natural* selection (Price & King, 1968; Price, 1999). Like natural selection in any environment, natural selection under domestication reflects differential reproductive success (Griffiths et al., 2004)—or, more correctly, differential contributions to the gene pool of subsequent generations, in terms of inclusive fitness (Hamilton, 1964; Dawkins, 1976; Grafen, 2009)—in this instance, differential reproductive success in the environment of domestication (Price, 1999).

Natural selection does not cease once a population is in a domesticated environment. Indeed, even if artificial selection is in operation there is no reason to assume that the traits selected by humans will be those with the greatest potential to survive and reproduce in a domesticated setting, as such natural selection always has an important explanatory role (Price, 2002). This point can be vividly illustrated by long-term experimental work carried out on the prairie deermouse (Price, 1967). When an initial, wild-caught population of deermice was placed in captivity only 60% of females managed to produce a litter. However, after seventeen years of captive breeding, 90% of the females in the 25th generation successfully produced a litter. This change occurred in the absence of any conscious selection for fertility or any other reproductively related traits, and represents an adaptation by the deermice to the conditions of the domesticated environment itself, something that has been seen in a wide variety of other species (Price, 2002). Of course, this raises the question of the nature of the domesticated environment, and in particular how it typically differs from wild environments.

The environment of domestication

The first point to note is that wild and domesticated environments are really two poles on a continuum, ranging from completely free-living, through semi-wild but managed, and on to captive environments, which themselves may range from safari parks to laboratory cages (Carlstead, 1996). Nevertheless it is possible to point to a number of dimensions along which the environment of domestication typically differs from wild environments. The following list is taken from Price and King (1968) and Price (1999; 2002).

(a) Shelter
(b) Space
(c) Type and availability of food
(d) Predation risk
(e) Social environment

It should be readily apparent that many of these dimensions are closely interrelated. For example, the space required by an individual animal in the wild is in large part determined by the availability of food and shelter, combined with the nature of their species' social interaction. The famously solitary lifestyle of the orangutan, for example, is likely a result of the scarcity of ecological resources in its habitat (Whiten & van Schaik, 2007), and can be seen to change in the presence of abundant food supplies (Sugardjito et al., 1987). In contrast, animals in a domesticated setting, in which food and shelter are provided, are usually kept in conditions in which both the quantity and quality of space is reduced (Hediger, 1964; Price, 2002). This change in the availability of space can also have implications for the social environment of the species. Population densities are often higher than would be found under natural conditions (Dawkins, 1980), and the age and sex structure of domesticated populations is often more uniform than seen in the wild (Zohary et al., 1998), as it becomes inconvenient to have a large number of potentially aggressive males, say, in a relatively small space.

Predation under domestication is vastly reduced—and sometimes eliminated entirely—as a result of animals living in enclosures, shelters and other aspects of the built environment (Price, 2002). In the wild, rates of predation can be very high; for example, in some years predation from wolves can account for up to 60% of all deaths amongst European red deer (Jedrzejewski et al., 2000), and thus constitutes an extremely strong selective pressure. The kinds of food available in captivity may also differ significantly. In the wild a great deal of time may be required to obtain food and that food may vary seasonally. Under domestication food and water is usually provided, often at a fixed location, with little effort needed to acquire it, and no seasonal variation (Price, 2002). The type of food available may vary, too, with animals often fed softer foods than in the wild (Lieberman et al., 2004).

4.5.1.3 – Relaxation of selection

The concept of selection being 'relaxed' has already been encountered in chapter two, as part of Deacon's (2009) account of the differences between the Bengalese finch and its wild ancestor, the white-rumped munia. In order to prevent confusion, however, it will be useful to pause here and consider what exactly is meant by the term *relaxation of selection*, because it can be interpreted in two different ways, which we might call *radical* and *conservative*.

On the radical interpretation, the term might refer to a situation in which it was *selection itself* that was being relaxed, in the sense of selection no longer playing a major evolutionary role. An argument of this sort is sometimes seen in relation to humans, in particular that the products of culture, technology and especially medicine have, in effect, stopped or massively reduced the action of natural selection in our species, causing us to be 'buffered' against the action of natural selection per se (e.g. Varki et al., 2008). There are, however, two reasons why I will not be using the radical interpretation in the discussion that follows (see also chapter 5, section **5.3** for further discussion of this issue). The first is that this position, which in relation to humans has been dubbed the *human evolutionary stasis argument*, is both doubtful theoretically (Powell, 2011) and seemingly contradicted by the evidence of recent selective sweeps in the human genome (Nielsen et al., 2007). The second is simply that this radical interpretation constitutes a far bolder and more sweeping claim than is required for present purposes.

On the conservative interpretation, what is relaxed are particular selective *pressures*, rather than selection in general. For example, the greatly reduced risk of predation in domesticated environments might mean that, relative to the wild, the selective pressure *from predation* could be said to be relaxed. Of course, this in no way requires that selection itself has been relaxed or somehow ceased to be an important evolutionary force. Indeed, the previous section described some of the ways in which the environment of domestication typically differs from the wild environment, differences which can introduce new selection pressures. As we shall see, these new pressures may themselves contribute to the production of the domestication phenotype. It is in this conservative sense that the term *relaxation of selection* should be understood here.

It should be clear, then, that natural selection continues once a species enters the domesticated setting. This continuation occurs in relation to a changed pattern of selective pressures, part of which is explained by some previously important selective pressures coming to be relaxed. Many of the selective pressures faced under domestication stem from the systematic differences between domestic and wild environments. These include the effects of living in a built environment, changes to the nature and availability of food and alterations to the social systems that follow from aspects of the domesticated environment. In the next chapter (section **5.1**) I present an extended discussion of the role that continued natural selection, and the relaxation of selection play in creating the domestic phenotype. For now, however, it is enough to note that natural selection is clearly a process that is also applicable to the human case.

4.5.1.4 – What about sexual selection?

There has, of course, been one very obvious omission from the above discussion of selective processes, *sexual selection*. The authoritative modern survey of sexual selection by Malte Andersson, in agreement with Darwin's (1871) original formulation, describes sexual selection as:

> ...a shorthand phrase for differences in reproductive success, caused by competition over mates, and related to the expression of the trait.
> (Andersson, 1994: 7)

I will say very little about sexual selection specifically, an omission for which there are two interrelated reasons. The first is that sexual selection is actually a subset of natural selection (Andersson, 1994: 8). It is true, of course, that sexual selection can result in traits that, from the point of view of *survival*, appear to be maladaptive, with the peacock's tail being the classic example. However, as discussed above (**4.5.1.2**), the ultimate currency of natural selection is not survival per se, but *differential reproductive success*, a point echoed in Andersson's definition above. Survival only matters because the dead tend not to reproduce. Equally, the possession of traits that attract mates only matters because, in sexually reproducing species, those who fail to attract mates tend not to reproduce. Sexual selection is not, then, a different *evolutionary process* to natural selection that I need to consider on its own.

The second reason relates to the notion of sexual selection as a shorthand. There are certainly some traits such as ornate plumage and intricate displays that only make sense as the result of selective pressure arising from competition for mates. As such, sexual selection picks out an interesting subset of natural selection. However, the picking out of this subset is of limited utility in the present discussion (although see **5.3** for one proposal relating self-domestication to aspects of mate choice). The literature on the domestic phenotype makes little reference to sexual selection. Indeed, when I do refer to sexual selection it is usually in the context of selective pressure on mate competition having been relaxed in the domesticated environment, and requires no difference in approach to any other instance of relaxed selection.

These observations regarding sexual selection have implications for how we should think about selection in general. In particular, it is important to distinguish between the overall concept of *selection* per se—the evolutionary process, or 'design algorithm' (Dennett, 1995), in which randomly generated, heritable variation is 'sifted' with respect to fitness consequences—and terms which pick out a subset of that process relating to specific aspects of the selective environment, such as '*sexual* selection' or '*social* selection'. These last two do not designate different *evolutionary processes*, rather they serve as a shorthand for selection occurring in response to pressures stemming from mate-choice or the need to function in social groups, respectively. We might just as easily refer to 'climatic selection' or 'geological selection', if we thought that shorthand terms picking out instances of selection related to, say, changes in temperature or volcanic activity might serve a similarly useful purpose.

It will be noted that in this section I have not referred to '*natural* selection'. This is because I believe that a similar analysis can be made regarding the difference between 'natural' and 'artificial' selection: both pick out a subset of selective pressures. *Natural* selection, considered broadly, designates selection occurring in response to selective pressures with a *non-human* origin. *Artificial* selection refers to selection relating to pressures stemming from human actions, whether they be conscious or unconscious. Humans are part of the natural world. If the balance of selective pressures faced by another species is changed by our actions, this is no different—in principle at least—to that balance being changed by the behaviour of some other species. Of course, in practice the outcomes may be very different to those expected under any other kind of selective backdrop: double-muscled cows that are unable to give birth unaided are unthinkable outside a selective context profoundly influenced by humans. But this does not mean that artificial selection constitutes a different *process* to natural selection, any more than the impossibility of the peacocks' tail outside the context of mate-competition renders sexual selection a different process[25]. As was the case with sexual selection, these arguments do not deny the frequent *utility* of the distinction between natural and artificial selection. Indeed, this distinction is repeatedly called upon in the current thesis. The point here is simply that we shouldn't confuse the *evolutionary process* of selection with the nature and origin of the background conditions under which selection happens to be operating in any given instance. I shall return to this point in chapter five (**5.1.4**), when I compare one view regarding how self-domestication might have occurred to the perspective that has come to be known as *niche construction*.

4.5.2 – Ecophenotypic responses: development under domestication

The domesticated environment is not just the context in which selection occurs, it is also the context of *development*. Once domesticated, each generation undergoes development in an environment of the kind described above: free from predation, within a species-atypical social structure, with the available food determined by humans, etc. The power of developmental plasticity to respond to environmental and other changes is only recently coming to be appreciated (West-Eberhard, 2005). This raises the possibility that some aspects of the domestic phenotype are found in each generation as a result of similar plastic responses to the domesticated environment, which both lacks certain 'key stimuli' found in the wild (Price, 1999), and introduces new stimuli the species would not normally encounter (Price, 2002).

This developmental perspective on the influence of the domesticated environment is yet another process that is equally applicable to the human case. Humans and other domesticates both develop in a human-made environment, which buffers them from

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[25] It makes no difference to this point that artificial selection can be 'intentional' or 'directed'. The capacity to engage in such foresight-driven action is a characteristic of our species. If the selective environment of another species is altered by humans engaging that particular capacity, this is no different—at least considered abstractly *as a process*—than it being altered by some other species engaging its own peculiar capacities. Nothing is changed either by invoking the techniques of genetic engineering, as this is not a *selective* process at all, but rather involves the directed production and alteration of *variation* itself, thus bypassing the selective process entirely.

some selective pressures and exposes them to others. It should perhaps not be surprising, then, if the protection from climatic extremes or eating of softer foods had some similar developmental effects on humans as it does in other species.

4.6 – Discussion

The aim of this chapter was to investigate the coherence of applying the concept of 'domestication' to humans; and, furthermore, to explore reasons why we might be motivated to do so. Across species, domestication is associated with a range of typical outcomes, which have come to be known as the domestic phenotype. Many of these same changes, from the reduction in skeletal and cranial robusticity, through an overall neotenous shift in development, to the domestication-associated accumulation of deleterious alleles can also be seen in humans. It is these similarities that have led many to argue that humans, too, should be considered a domesticated species. The arguments of chapters two and three can be seen as adding two further parallels between humans and domesticated species, in the form of the two preconditions identified in chapter one. Of course, the parallels discussed in those chapters have not been seen in domesticated species as a whole. Furthermore, the key point in humans is that both these preconditions appeared *together*. Both these points need to be addressed, and I shall return to them in chapter six, where I consider some potential questions thrown up by the argument of this thesis.

The argument regarding parallel changes has often been hampered, however, by a 'conditions' view of domestication, as something that, by definition, is consciously done *by* humans *to* another species living under our control. This view can be contrasted with the 'outcomes' view of domestication, in which a species is considered domesticated to the extent that it exhibits aspects of the domestic phenotype. The degree to which one accepts the possibility of human self-domestication will likely be governed by the weights one places on these two different views of domestication. Under a conditions view, the similarities between humans and domesticates cannot possibly indicate that both have been domesticated, as this simply cannot apply in the human case. Under an outcomes view, these similarities, together with similarities in the more precise explanations of how specific changes occurred, indicate that a parallel process is likely to have been in operation (see also chapter five, particularly **5.1.2** and **5.1.3**). A great deal of the tension between the conditions and outcomes views of domestication can be relieved, however, once we realise that domestication is best characterised as a multi-stage process, along which different species proceed at different speeds via differing pathways, rather than a single uniform process.

Related to the conditions view of domestication is the idea that changes under domestication can be identified with the operation of artificial selection. There are, however, a range of processes involved in the emergence of the domestic phenotype. Some of these, such as artificial selection, would seem to have limited scope for operation in humans (although see chapter five, section **5.3**, for a possible counter-example). Others, such as natural selection, the relaxation of selection and ecophenotypic responses during development, are clearly process that could easily produce similar outcomes in humans. It is important to note, too, that the first two of Leach's stages of domestication and the commensal pathway identified by Zeder, only require these processes to explain the changes associated with domestication. If this is the case, then the conceptual barriers to viewing humans as domesticates may well be considerably lowered. The idea, then, that humans are self-domesticated does not require that human life and breeding have been controlled by some external domesticat*or*. Instead, taking a sufficiently outcomes-based view of domestication, it is simply the suggestion that human evolution has occurred in sufficiently similar contexts to domesticated species, via sufficiently similar processes, such that similar evolutionary outcomes have occurred. With its coherence as a concept now in place, the next chapter turns to the question of *how* self-domestication might have happened, through an investigation of three different, possibly complementary, evolutionary scenarios.

Chapter 5

Humans as Domesticates: How Might it have Happened?

The conclusion of the last chapter was that the concept of domestication can be coherently applied to humans. This possibility depends on the extent to which one accepts an outcomes-based view of domestication—in terms of the domestic phenotype, much of which is shared by humans—as distinct from a conditions-based view, with its focus on external control by a domesticator. This still leaves us, however, with the question of *concreteness*: what are we saying actually happened when we claim humans are self-domesticated? One might object, after all, that it is the *conditions* of domestication—with evolution occurring in an environment controlled by humans—that are responsible for the *outcomes* typically seen in domesticated species. If similar outcomes in humans are also to be seen as a sign of domestication, then they would require a somewhat different explanation, given that humans have not been controlled by some outside agency. The focus of this chapter, then, is to critically assess a number of the possible accounts of *how* humans might have become self-domesticated.

Three such accounts will be discussed below. Each of these relate directly to the selective processes involved in domestication discussed in chapter four (**4.5.1**) and to aspects of one or both the case studies discussed in chapters two and three. The first account links self-domestication to a process of *adaptation to the human-made environment*. Crucially, this is an environment in which *humans* have lived longer than any other species. The second account links self-domestication to humans having undergone *selection against aggression*. This relates to the discussion of the domestic dog and the farm-fox experiment in chapter three, where many features of the domestic phenotype appeared as part of a correlated cascade of effects following selection on temperament. Finally, I will consider the possibility that a process with effects analogous to artificial selection may have also been in operation in humans. In particular, the idea that *culturally mediated constructs of mate-choice* may have resulted in humans applying something akin to artificial selection to themselves.

5.1 – Adaptation to the human-made environment

In this section I will review a range of evidence suggesting that many aspects of the domestic phenotype can be explained as the result of organisms adapting to the nature of the human-made environment. As discussed in chapter four (**4.5**), there are three ways in which aspects of this environment can contribute to the typical outcomes of domestication:

- Continuing *natural selection*
- The *relaxation* of previously important selection pressures
- *Development* occurring in the human-made environment

All three of these processes are equally applicable to the human case. Indeed, as argued above, may be *particularly* applicable to humans, given that they are the species that has lived in the human-made environment longest of all. Given this, the fact that humans might exhibit some of the evolutionary consequences of living in such an environment should not really be all that surprising. The first aim of this section, then, is to examine a range of evidence linking the domestic phenotype to the effects of the human-made environment, rather than necessarily as a result of consciously applied artificial selection. The second aim is to explore some parallel cases, not typically thought of as domestications, that also show a link between the domestic phenotype and the human-made environment. Finally, I will briefly compare this account of self-domestication with *niche construction* theory (Odling-Smee et al., 2003), as they appear, superficially at least, to share some similarities.

5.1.1 – The domestic phenotype as an adaptation to the human-made environment

In this section I will discuss a number of the aspects of the domestic phenotype—as listed in chapter four, figures 4.1 and 4.2—with an eye to the role played by the adaptation to the human-made environment in explaining their emergence. This section is inspired by, and constitutes an expansion of, arguments put forward by Leach (2003) and references therein.

5.1.1.1 – Reduced body size

A reduction in overall body size is a very common consequence of domestication, as is the concomitant reduction in robusticity (Price, 2002). Some of the explanations for these anatomical changes have focused on the active role of the human domesticator. For example, Grigson (1969, cited in Leach, 2003) suggested that the reduction of body-size in cattle was a result of selective breeding to facilitate handling. More recently, however, there has been a shift towards explanations that emphasise the role of the environment of domestication itself, following a similar move in attempts to understand plant domestication (e. g. Heiser, 1988).

Tchernov and Horwitz (1991) argue that body-size reduction constitutes an adaptive response to the novel, human-created environment, and can be conceptualized in terms of a shift from *K*- to *r*-selection. *K*- and *r*-selection represent two different evolutionary reproductive strategies. In simple terms, *K*-selection involves the direction of energy and resources into a small number of offspring, thus ensuring the maximal fitness of those offspring. This strategy is typical of organisms with a large body size, slower growth and lower fecundity. In contrast, an *r*-selection strategy involves the production of larger numbers of offspring, but with less energy invested in each individual. This strategy is usually associated with species with greater fecundity, faster growth and smaller body size.

Of course, these two strategies really sit on a continuum, along which it is possible to shift given changing ecological conditions. Tchernov and Horwitz argue that just such a shift was encouraged by the ecological circumstances following domestication. The key components of which include: the reduction in predation risk; the decrease in inter-specific competition; the change in the type and predictability of food availability; the unpredictable patterns of culling; and the fact that mate-choice was partially taken over by humans. This set of new, unpredictable conditions, combined with increased intra-specific competition encouraged a shift towards an r-selection strategy, together with a concomitant reduction in body size. It is worth noting that many of the sexual changes discussed below—for example, increased litter sizes and extended breeding seasons—fit nicely into this picture.

Zohary et al. (1998), in a discussion of domesticated sheep and goats, have argued that the breakdown of ancestral patterns of alpha-male dominance has reduced pressure for larger male body and horn size. And, furthermore, that both male and female skeletal robusticity was reduced as a result of no longer needing to navigate precipitous terrain. In a similar vein, Tchernov and Valla (1997), in relation to early domesticated dogs, found not only a reduction in overall body size, but a particular reduction in certain limb dimensions, which they attribute to the reduced mobility required of those dogs living with humans.

5.1.1.2 – Reduced sexual dimorphism

Reductions in the size differences between the sexes is also a frequent outcome of domestication (Price, 2002). Polák and Frynta (2009) examined sexual dimorphism, as measured by overall body mass, in domesticated sheep and goats. They found that domesticated breeds exhibited significantly reduced sexual dimorphism as compared with their wild relatives. Polák and Frynta attribute this difference to the relaxation of sexual selection under domestication. However, a similar study of domesticated cattle breeds found no such reduction in sexual dimorphism (Polák & Frynta, 2010). Interestingly, when Polák and Frynta substituted shoulder-height for body mass as their measure of sexual dimorphism, domestic cattle came out as significantly less dimorphic than their wild counterparts. This might possibly represent something of a trade-off between the reduced sexual selection typical of the domesticated environment and the artificial selection for increased size.

5.1.1.3 – Reduced cranial robusticity and dental changes

Changes in cranial robusticity and dentition are also common following domestication. Some explanations for these changes emphasise their genetic, heritable nature. for example, the deliberate selection of hornless cattle—a trait associated with reduced cranial thickness—in order to make them easier to handle (Zeuner, 1963), or the reduction of horn size and cranial thickness as a result of the breakdown of dominance patterns amongst males in the domesticated environment (Zohary et al., 1998).

Cranial thickness, face size and the crowding and malocclusion of teeth have all also been related to *development* occurring within the domesticated environment (see **4.5.2**), in particular to the reduced scope for physical activity and changes in diet. Lieberman (1996) reports experimental findings from a study on pig siblings raised in high- and low-exercise conditions. Those raised in the high-exercise condition had cranial vaults nearly 30% thicker than those raised in the low-exercise condition. Lieberman argues that this difference is likely mediated by higher levels of growth hormone being released in the high-exercise pigs.

A similar developmental account can be given in the case of changes to facial shape and the crowding and malocclusion of teeth. Studies on rats (Yamada & Kimmel, 1991) and squirrel monkeys (Courruccini & Beecher, 1982) have shown that both facial shape and problems relating to dentition are deeply influenced by the kinds of available food. In particular, diets of soft food are associated with thinner and shorter jawbones, and teeth that are displaced, rotated, crowded and maloccluded. Similar results have also been found in minipigs (Ciochon et al., 1997), in which those fed on a soft diet also showed shorter jawbones and malocclusions; and in (non-mini) pigs (Larsson et al., 2005), with those fed on soft-diets also having more malocclusions. Most of these studies compared hard food with near-liquid food, however Lieberman et al. (2004) found a similar result in hyraxes fed either raw (hard) or cooked (soft) food, with those fed a cooked diet exhibiting shorter and narrower faces than those fed on a raw diet.

5.1.1.4 – Reduced brain size

As noted in chapter four, domestication has been associated with a decrease in brain size across a wide variety of species (Price, 2002). These reductions are not uniform across all areas of the brain, with the greatest size reductions generally found in the *telencephalon* (or cerebrum) and *diencephalon*, which together constitute the mammalian forebrain, the seat of 'higher' processing functions (Kruska, 2005). Domestication is also often associated with a marked decrease in the size of brain areas related to sensory functions, especially those involved in stimulus processing (Kruska, 2005). In addition, domesticates also exhibit size-reduction of the cerebellum, which is involved in the integration of motor and sensory inputs, and in parts of the limbic system, which has a role in emotion and motivation (Kruska, 2005). Finally, there is evidence that the sense organs of domesticated species show a reduction in size and cell count that broadly parallels those reductions seen in sensory brain areas (Kruska, 2005).

The mammalian brain has, then, responded to domestication by reducing in total size, with particular size-reductions in those areas related to 'higher' cognitive processes, motor and sensory processing and integration, and emotional and motivational control. What might explain this pattern of brain-size reduction? One possibility is that they relate to the reduced 'environmental reactivity' (**5.1.1.7**) seen in many domesticates, and may well have been actively favoured by humans during the domestication process (Kruska, 2005), perhaps with a view to making animals easier to handle. An alternative is that these same changes reflect something about the nature of the domesticated environment itself, which is often associated with very much reduced sensory, motor and cognitive demands, as relates to finding food, avoiding predators, competing with rival species, etc. (Price, 2002).

Reductions in brain-size following domestication are not, however, restricted to mammals. Hatchery reared salmon also have significantly smaller brains than their wild counterparts (Marchetti & Nevitt, 2003). Intriguingly, the most reduced areas—the telencephalon and sensory regions—closely parallel those in mammals (Marchetti & Nevitt, 2003). These brain regions relate to traits, such as predator avoidance, that are known to become deficient under domestication even without any direct artificial selection (Gross, 1998). The mammalian pattern of brain-size reduction under domestication is also paralleled in domesticated birds, which also show brain-size reductions proportional to the encephalization of their wild ancestors (Price, 2002).

5.1.1.5 – Increased variation

The greater variability of domesticated species as compared to their wild counterparts is something that has been noted from Darwin (1868) onwards. In this section I will primarily focus on the variability observed in coat colour, while also briefly discussing variation in hair structure and skull shape, particularly in dogs.

Fang et al. (2009) compared the variation in coat colour between wild and domesticated pigs, finding that domesticated strains exhibited significantly greater variation. The differing pattern of mutations in domesticated and wild pigs suggests that this difference is likely down to artificial selection, as it doesn't fit the pattern expected for relaxed selection. In line with this conclusion, Ludwig et al. (2009) present data from horses suggesting that the coat-colour variations typical of domestic horses appeared in the last five thousand years, and are likely the result of selective breeding. A recent review of the coat colour under domestication (Cieslak et al., 2011) presents broad agreement with these two studies. Coat colour is a highly visible trait and so easy to selectively breed, even in the earlier, less advanced stages of domestication. Patterned, visible coat colour is also, as Fang et al. note, prized both aesthetically and as making stock easier to manage than the less visible, camouflaged coats typically found in the wild.

Turning now to hair structure, Cadieu et al. (2009) conducted a genetic study of eighty breeds of domestic dog to identify the genes associated with different coat types. The vast majority of the variation could be accounted for as a result of mutations in just three genes, shared by many breeds of long-haired dog. None of these mutations were observed in grey wolves or in short-haired breeds, suggesting that these two groups carry the ancestral form. For present purposes, however, the key point is that most breeds are of very recent origin (Cadieu et al., 2009), and thus this wide variety of hair types is, like the variation in coat colour, probably the result of artificial selection.

One further interesting point is the apparent relationship between genes associated with coat colour or hair consistency and a wide variety of other characteristics. In any given case this association might be the result of *linkage*—different genes being close together on the same chromosome, and thus tending to be inherited together—or the result of *pleiotropy*, a single gene having multiple effects (Cieslak et al., 2011). The best known example of this phenomenon is the farm-fox experiment (Trut, 1999; this thesis, chapter 3), in which changes in both coat colour and hair-form appeared following selection for tame behaviour. Changes in pigmentation has also been found in Norway rats that were selected for tameness in a similar way (Gulevich et al., 2010).

Turning finally to skull shape, Drake and Klingbergen (2010) compared the diversity of skull shapes amongst domestic dog breeds with that found in grey wolves, coyotes and golden jackals, (see also Wayne, 1986). They divided dogs into companion and working groups and found that diversity of skull shape was highest for companion dogs, with working dogs intermediate between companion dogs and the wild species. The authors point to the reduced need to process hard or tough foods under domestication and, more recently, to the active creation of breeds partly marked by their head shape as the two likely interacting causes of this great diversity.

5.1.1.6 – Sexual changes

Some of the changes relating to sexual behaviour, such as the decrease in sexual dimorphism, have already been discussed. However, domestication is also associated with a range of changes affecting reproductive efficiency. These changes including accelerated sexual maturation, the breakdown of seasonal breeding patterns, and an increase in litter sizes (Setchell, 1992).

The accelerated sexual maturation associated with domestication is seen in a wide variety of domesticated birds and canids (Price, 2002), in many agricultural species (Price, 1999), and in rats (Clark & Price, 1981). Several explanations have been advanced for this acceleration. It may be related to ecophenotypic factors such as improvements in diet (Price, 1985), or a response to changes in photoperiodicity (Andersson et al., 1998). Of course, it might be related to artificial selection directed towards maximising the return from stock (Price, 1985). It has also been suggested that accelerated maturation might relate somewhat more indirectly to the human control of breeding and population structure (Zohary et al., 1998; Price, 1985), which creates a situation in which dominance hierarchies breakdown, and so selective pressure for competitive, aggressive behaviour between males is relaxed. Under such conditions, young males no longer have to compete for females with older, more dominant males, but can potentially begin to reproduce as soon as they are able to copulate (Price, 2002).

The breakdown of seasonal breeding patterns could in some cases also be the result of selective breeding for year-round production of young (Price, 1985). However, Price also argues that this breakdown should be seen in the context of why such patterns were adaptive in the wild. In particular, that seasonality in breeding makes sense as an adaptation to a harsh environment in which it is advantageous to produce young at the time of year that food is most abundant and the climate most favourable. Given this, it's reasonable to suggest that the breakdown may in some cases relate to the more favourable conditions under domestication (Price, 1999). Domesticated species tend to have larger litter sizes than their wild relatives. Again, this shift is seen across a wide variety of species (Price, 2002; Clark & Price, 1981). It, too, might be related to differences in nutrition, selective breeding (Clark & Price, 1981), or adaptation to the domesticated environment (Price, 1999; Tchernov & Horwitz, 1991).

One notable point about all three of these changes in sexual behaviour is that they tie very neatly into the shift from *K*- to *r*-selection discussed above. Recall that this shift is essentially the move from a strategy based on producing a small number of heavily invested-in offspring, to producing a larger number of less invested-in offspring, and was argued to have occurred as a response to the nature of the domesticated environment (Tchernov & Horwitz, 1991). These three sexual changes —earlier puberty, year-round breeding and larger litter sizes—all fit logically into this shift, enabling as they do the production of a larger number of offspring (Tchernov & Horwitz, 1991).

5.1.1.7 – Changes in temperament and environmental reactivity

Populations of captive-reared fish differ markedly from their wild counterparts in a range of physiological and behavioural traits (Gross, 1998). Farmed fish show a reduced wariness in the face of novel objects and diminished anti-predator responses (Huntingford, 2004). Hybrids produced between farmed and wild fish exhibit anti-predator responses intermediate between the two, indicating this difference has some heritable component (Houde et al., 2010). These differences can, however, be reduced during development by the use predator-like stimuli in hatcheries

(Huntingford, 2004; Brown et al., 2003). Similar findings have been reported in the Chilean scallop, which is reared in hatcheries and also shows reduced anti-predator responses (Brokordt et al., 2006). In neither case have these reduced responses been selected by humans. Rather, they are the result of adaptation to the predator-free conditions of captivity, and the impact of developmental experience (Gross, 1998; Huntingford, 2004).

Similar kinds of temperamental changes have also been observed in birds and mammals. Domesticated White Leghorn chickens show significantly reduced levels of fear on exposure to novel spaces and objects, aerial predators and humans, compared to their wild ancestor the red junglefowl (Campler et al., 2009). The domesticated birds also exhibited reduced levels of activity, less intense social behaviour and reduced exploratory behaviour (Jensen, 2006). Again, this attenuation has been shown experimentally to follow simply from breeding multiple generation of red junglefowl in captive conditions, *explicitly* without any attempt at artificial selection (Håkansson & Jensen, 2008). The authors' suggest that a combination of genetic drift, following the relaxation of selection, and possible unintentional selection on stress-coping systems could explain their results.

Predator vigilance in cattle is also known to decline under domestication, with freely ranging domesticated cattle exhibiting significantly lower levels of vigilance than wild ungulates (Kluever et al., 2008). It is interesting to note that the few studies that have attempted to examine the adaptive significance of temperament in wild populations have found significant links between levels of fearfulness and the risk of predation (Dingemanse & Réale, 2005; Archard & Braithwaite, 2010), suggesting a link between declining vigilance and the predator-free nature of the domesticated environment.

Domestication is also associated with reductions in aggression. Domesticated Norway rats exhibit an attenuation of aggression both to humans and conspecifics (Blanchard et al., 1986 ; Price, 1999), with their thresholds for defensive aggression seemingly raised. One explanation is that aggression has reduced as a result of selection for ease of handling (Blanchard et al., 1986; Plyusnina et al., 2011). However, there is also evidence that the impact of the domesticated environment on dominance relationships can also affect the level of intraspecific aggression. In particular, that rats raised in cages have reduced dominance hierarchies, higher thresholds for defensive behaviour, and continue juvenile-like play-fighting longer into adulthood than do rats living in more open conditions (Adams & Boise, 1989). These differences possibly relate to the frequencies with which the two populations encountered unknown intruders. Similar findings have also been reported for domesticated mice (Blanchard et al., 1998).

The influence that development under domestication can have on aggression is well illustrated by work on salmon and other farmed fish. The intensity of that aggression can be heavily influenced by altering feeding regimes (Ruzzante, 1994). If food is delivered in such a way as to maximise competition then domesticated fish can actually end up being *more* aggressive than their wild counterparts (Huntingford, 2004); whereas other feeding regimes can lower aggression levels. A similar argument has been made in relation to reductions in aggression among domesticated sheep and goats, with the breakdown of normal population structure following domestication resulting in reduced competition, particularly male-to-male competition for females, and so less aggressive behaviour overall (Zohary et al., 1998).

It has been argued that this general attenuation of reactivity, responsiveness and aggression constitutes the single most important effect of domestication (Price, 2002). More broadly, this reduction in 'reactivity' also involves reduced levels of motor activity (Price, 1999) and a diminution of the sensory apparatus (Kruska, 2005). Price (2002) points to four factors about domestication likely linked to the reduction in reactivity: (1) It being biologically 'safe' with few predators; (2) The limited opportunities for perceptual or locomotor stimulation; (3) The reduced personal space, with limited ability to escape from conspecifics; and (4) Artificial selection for more tractable individuals. It should be clear from the above discussion that even if artificial selection were minimal or absent—as indeed it is in the experimental work with red junglefowl—that we should still expect many of these same kinds of changes under domestication, as a result of Price's first three points.

5.1.1.8 – Build-up of deleterious alleles

There are two major proposals for how domestication can result in the build-up of deleterious alleles (Lu et al., 2006). The first involves the relaxation of certain selective pressures that were present in the wild environment, meaning that those alleles are no longer eliminated under domestication. The second involves the interaction between artificial and natural selection and is an example of the Hill-Robertson effect (Hill & Robertson, 1966), which shows that selection is most effective (at eliminating deleterious alleles) when the various alleles involved can freely recombine (Lu et al., 2006)—that is, when there is no genetic *linkage* (Slatkin, 2008). However, when strong artificial selection is applied to a selected variant other associated alleles can also increase in frequency through the phenomenon of genetic hitchhiking (Barton, 2000). Of course, such hitchhiking is possible under wild conditions as well, but as artificial selection is often so extremely strong the scope for such linkage greatly increases, as does the number and magnitude of the deleterious mutations that are able to hitchhike upon it (Lu et al., 2006).

There is emerging evidence from a range of species that domestication is very often associated with a build-up of deleterious alleles, in the sense discussed in **4.3.7**. Cruz et al. (2008) found a higher frequency of non-synonymous substitutions—mutations that alter the amino acid sequence of a given protein—in the nuclear DNA of domesticated dogs than in their ancestors, the grey wolf. The authors consider both of the mechanisms described above as likely to have contributed to this difference. Björnerfeldt et al. (2006) describe a similar result following a comparison of the mitochondrial DNA of domestic dogs and wolves.

Wang et al. (2011) compared the mitochondrial DNA of wild and domesticated yaks, and also found a higher frequency of non-synonymous substitutions in the domesticated strain. In this case the authors explicitly argue for an explanation in terms of the relaxation of selective pressure, particularly as relates to efficiency of energy metabolism, 95% of which is carried out by mitochondria in eukaryotic cells. Wild yaks live at high altitude and often travel great distances putting a selective premium on efficient metabolism. In contrast, domesticated yaks generally live at lower altitudes and are far less mobile (Wang et al., 2011). Similar findings have been reported in comparisons of domesticated and wild rice (Lu et al., 2006), where the Hill-Robertson effect seems the most likely candidate, and in yeast (Gu et al., 2005), where the authors cite relaxed selection as the most likely cause.

5.1.2 – The domestic phenotype in inadvertent domesticates

The phenomenon of 'inadvertent domestication' among endangered species in captive breeding programs (O'Regan & Kitchener, 2005) constitutes another parallel example linking the domestic phenotype to aspects of the environment of domestication. This phenomenon is particularly interesting in terms of this first account of self-domestication, because artificial selection is not at all the aim of those involved in such programs. Indeed, the emergence of the domestic phenotype is increasingly seen as a serious problem in terms of successfully returning animals to the wild (Frankham, 2008).

Softer diets in captivity have been found to increase the rate of malocclusion in both cheetahs (Fitch & Fagan, 1982) and Asian elephants (Fagan et al., 2001). A number of cranial, skeletal and muscle-related changes have also been observed across a range of species in response to captivity (O'Regan & Kitchener, 2005). Other species show signs of inadvertent domestication in terms of changes in brain size. One such example is the Przewalski's wild horse, the population of which is now totally derived from captive-bred individuals (O'Reagan & Kitchener, 2005). These horses have been bred with every effort to maintain their genetic diversity and to prevent anything resembling selective breeding. Yet despite these efforts, the brain-weight of these captive-bred horses is now 16% lower than that of wild-born individuals, and their cranial volume has decreased by 14%, bringing them broadly into line with conventionally domesticated horses (Rohrs & Ebinger, 1998, cited in O'Regan & Kitchener, 2005).

The build-up of deleterious alleles is also coming to be recognised as a problem for captive-breeding programs (Frankham, 2008). Work with drosophila indicates that this build-up can occur surprisingly rapidly (Woodworth et al., 2002) and can be very difficult to prevent. The inter-breeding of wild and escaped domesticated members of the same species is also a problem. Kidd et al. (2009) report the growing concern for wild populations of American mink as they breed with domestic escapees and thus absorb a large body of deleterious alleles into the wild gene pool. One of the major examples of this phenomenon is that of farmed and wild salmon, the hybrids of which show reduced survival and fitness, and decreased predator avoidance in comparison to their pure-bred wild counterparts (McGinnity et al., 2003; Hutchings & Fraser, 2008).

5.1.3 – The domestic phenotype in commensal species

In chapter four (**4.4**) the concept of there being various 'pathways' to domestication was discussed. One of these was the *commensal pathway*, in which domestication began through other species coming to live in and exploit human environments. As discussed there, many species, including the domestic dog, are thought to have begun the domestication process in just this manner. There are, however, several species that have become commensal but have not then gone on to become conventionally domesticated. Intriguingly, however, these species have also come to exhibit aspects of the domestic phenotype.

The two major examples of these are the various subspecies of the house mouse and the house sparrow (Leach, 2003). In comparison to sympatrically living wild species, the house mouse has a shorter face, reduced molar row, longer tail and a possible reduction in overall size (Tchernov, 1984). Similarly, the house sparrow has seen an overall reduction in size, as compared with its wild relative, especially in relation to those parts of the body involved in food processing and terrestrial locomotion (Morales Muñiz et al., 1995; Leach, 2003).

Commensal species represent an intriguing middle ground, because although they live *with us* they are not controlled *by us*. This relates to the two different approaches to thinking about domestication discussed in chapter four. If we take a 'human mastery' approach to domestication and define it in terms of certain *conditions*—i.e. being kept in captivity and managed by human beings—then commensals cannot be understood as domesticated in any way. Indeed, some who have taken this approach have ruled them out on just this basis (e.g. Hemmer, 1990). On the other hand, if we take an *outcomes* view of domestication—emphasising the domestic phenotype—then it is no great leap to also include commensals (Leach, 2003). This is especially true given the more nuanced understanding of the domestication process, with its various stages and pathways, outlined in chapter four.

5.1.4 – How does this account relate to niche construction?

The account of self-domestication being explored in this section suggests that humans may have come to share aspects of the domestic phenotype because the environment we created *for ourselves* shares much in common with that we created for our domesticated species. As such, this account seems very similar to the body of theoretical work known as *niche construction* (Odling-Smee et al., 2003). On closer inspection, however, this similarity is only superficial. Indeed, the approach taken to self-domestication in this section (**5.1**), and indeed the next (**5.2**), can actually be seen as the *inverse* of the niche construction perspective.

The key to understanding this inversion lies in the different ways of characterising the role of human action in evolution. For advocates of niche construction, the active role of organisms' own behaviour has been left out of evolutionary thinking, and constitutes a 'neglected' *evolutionary process* (Odling-Smee et al., 2003). This view derives from the idea that the fit between organism and environment, conventionally ascribed to the process of natural selection, is actually better explained as a result of *two* processes: *natural selection*, in which organisms adapt to better 'fit' their environments; and *niche construction* in which organisms modify their environments so as to better fit them (see Lewontin, 1983).

This two-process view is associated with the concept of 'reciprocal causation' (Laland et al., 2011), in which niche constructing behaviour and natural selection interact in a cyclical fashion. An oft-cited example of this kind of causation in humans concerns the spread of alleles for the continued production of the enzyme lactase in adults—and thus the capacity to digest dairy products throughout life—in populations engaged in dairy farming (Bersaglieri et al., 2004). The evolutionary conditions favouring lactase persistence were set up by a cultural practice (dairy farming), which in turn was further supported by selection for lactase persistence. A key component of the niche construction view, therefore, is the claim that changes in selective pressures deriving from an organism's own actions, rather than from some abiotic source such as change in the climate, require a different theoretical approach, because they represent a distinct evolutionary process, i.e. niche construction.

In the account of self-domestication just considered, however, the argument is that the *origin* of the environment of domestication is *not*, in itself, particularly important. It doesn't matter whether the environment was made *by* the organism in question (as in the case of humans), *for* the organism (as in the case of other domesticates) or simply *adopted* as a habitat, like any other might have been (as in the case of commensals). What matters, rather, is that because all three of these groups shared, to a greater or lesser extent, the same kind of environment, they also faced similar selective conditions, and thus came to exhibit similar responses, as reflected in the domestic phenotype. Indeed, the argument would remain the same even if the domesticated environment had sprung forth from the earth entirely through physical processes. This is important because niche construction has been criticised on exactly this point of difference.

It is helpful to view these criticisms in light of arguments made in the previous chapter (**4.5.1.4**), regarding the distinction between the *process* of selection—in which heritable variation is 'sifted' with respect to fitness consequences—and shorthand terms, such as 'sexual selection', that pick out a subset of this process in relation to particular aspects of the selective environment. In a similar vein, critics of niche construction have argued that it, too, simply picks out a particular subset of the selective process. In this case, that subset relating to aspects of the selective environment previously influenced by an organism's behaviour (Dickins & Dickins, 2008). As such, it no more warrants the title of a distinct *evolutionary process*[26] than does sexual selection, social selection, or the hypothetical 'climatic selection' discussed in **4.5.1.4**.

Following this parallel, the dairy farming case might better be described as an example of ‘own-action selection’, in which selection occurs in response to pressures deriving from an organism’s own behaviour. The evolutionary process responsible for the adaptive phenotype—continued lactase production in adulthood—is natural selection, acting on variation in the population in response to certain aspects of the selective environment. The fact that this instance of selection occurred in response to selective pressures deriving from the organism’s own behaviour in no way changes the nature of this process (Scott-Phillips et al., 2011), any more than the peacocks’ tail requires a new process to explain its emergence because the relevant selective pressure derived from competition for mates.

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[26] The term *evolutionary process* has a precise meaning. Biological evolution *is* change in gene frequencies. For something to qualify as a process of evolution, thus conceived, requires therefore that it be a process whereby *gene frequencies change*. This can either be through the introduction of new variants or by changing the relative frequency of existing variants. In this sense there are four evolutionary processes: mutation, gene flow, drift and selection. Of course, many other factors can influence the course of evolution, but they do so at one remove, through the effect they have on one or more of these four processes. For example, a change in the climate can have profound evolutionary consequences, but it does so because it alters the circumstances under which selection and other processes operate.

It is interesting to note what *would* be required for niche construction to constitute a novel evolutionary process. To return once more to the example of dairy farming. If niche construction, in the form of dairy farming behaviour, really were to constitute a distinct evolutionary process then it would have to do something like the following: *directly* cause the emergence of alleles underlying lactase persistence, thus bypassing the standard neo-Darwinian account whereby randomly generated mutations and standing variation are sifted by selection (Dickins & Dickins, 2008; **2.4.4**, this thesis)[27]. Instead, dairy farming simply introduced a new source of nutrition into the environment—dairy products such as milk and cheese—thereby altering selective conditions, such that variation underlying lactase persistence, and thus lifelong access to this new nutritional resource, came to be favoured through the process of selection (Scott-Phillips et al., 2013).

Much more could and has been said regarding the niche construction perspective (Laland et al., 2001; Laland & Sterelny, 2006; Scott-Phillips et al., 2013). For present purposes, however, what matters is that the account of self-domestication just discussed avoids the criticisms that have been levelled at niche construction. In particular, it avoids having to make the claim that there is something ‘special’ about selection in response to pressures stemming from an organism’s own actions. Special, that is, in comparison to those *same* pressures stemming from some other source. This problem arises as a result of conflating *evolutionary processes*, like selection, with the nature and origin of the pressures that characterise the selective environment in any given case.

Changes in the climate, the need to compete for mates, and alterations brought about by an organism’s own behaviour are not evolutionary processes in themselves, but aspects of the adaptive landscape against which process such as selection occur (Scott-Phillips et al., 2013). Thus in order to sustain the *theoretical* claims made for niche construction, it is not enough simply to point to examples of 'reciprocal causation', like the impact of dairy farming. Such examples, although fascinating—

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[27] Niche construction would thereby cause an alteration in gene frequencies, through the generation of new variation, *independently* of the four processes identified in footnote 18.

and real—from the viewpoint of *descriptive* natural history, are, from a theoretical perspective, something of a red herring, because they entail the additional, and unsupportable, claim that selection pressure stemming from an organism's own actions constitutes a novel evolutionary process[28]. This claim is a fundamental category error, which the present account of self-domestication manages to avoid. Indeed, as argued above, it is premised on the opposite position: similarities in environmental circumstances will have similar evolutionary effects regardless of how those environmental circumstances came into being.

5.1.5 – Summary and criticisms

This first account relates human self-domestication to similarities in the environments of humans and their domesticated species. Despite the obvious power of artificial selection, much of the domestic phenotype can be attributed to evolution and development occurring in a particular human-made environment, which relaxes and alters selective pressure across a range of domains. The key point here is that humans and other domesticates have long shared this environment, with humans living in it longest of all. As such, it should really be no surprise that similar changes might have occurred both in humans and domesticates. This also allows sense to be made of the parallel changes seen in commensal species and in captive breeding programs in which huge effort is put into *avoiding* domestication. This account of self-domestication has, therefore, much to recommend it, not least the range of convergent examples illustrating that aspects of the domestic phenotype can emerge as a result of evolution and development occurring in a human-made environment.

There are, however, some important problems with this account. The first concerns the time-frame over which it might possibly have been in operation. Leach's (2003) discussion of the parallel physical changes in humans and their domesticates focused on the last 20,000 years or so of human evolution. Yet the evidence discussed in

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[28] It is also necessary to explain why *this* kind of change in selection pressures constitutes an evolutionary process, while alterations in selective pressure from other sources, such as climatic shifts, do not.

chapter four (**4.3.1**) suggests that the domestic phenotype has likely been emerging in humans over a much longer time-scale. The focus placed on the role of sedentism and the human-made environment is also problematic, because of the relatively recent origin of herd management and more formal agricultural practices (Zeder, 2011) that make this kind of sedentism a possibility. Finally, it remains an open question whether the very possibility of permanent settlements in human-made environments, and other such complex cultural activities actually *presupposes* the very changes in temperament, co-operative behaviour and communication—and even language (e.g. Gil, 2008)—that self-domestication itself is being invoked to explain.

These problems do not rule out some kind of role for the parallel adaptation of humans and their domesticates to the human-made environment. They do, however, show that if humans are to be seen as self-domesticated—particularly if that self-domestication is to be linked to major changes in temperament or the role of cultural transmission—then the kind of account described in this section cannot be the whole story. In order for self-domestication to have served that kind of role it must have had a much greater time-depth in human evolution. The next section will examine a second account of self-domestication that meets just these criteria.

5.2 – Natural selection against aggression

In chapter three we discussed the case of the domestic dog, as illuminated by the farm-fox experiment, and saw how many aspects of the domestic phenotype resulted simply from selecting against aggression. In that example, the selection involved was artificial: the source of the selective pressure was the decisions of human breeders. However, as discussed in chapter four (**4.5.1.4**) and above (**5.1.4**), there is nothing inherently special about the *origins* of selection pressures that changes either the processes involved or the likely outcomes. It should be expected, therefore, that selective pressure for reduced aggression from *any* source should result in similar phenotypic changes. To the extent that selection against aggression is likely to play a role in human self-domestication, it seems unlikely to be the result of artificial selection. After all, humans are not being bred by some external agency (although see **5.3** for the claim that we might be doing it *to ourselves*). Rather, changes to temperament would have to occur through *natural* selection.

One example where something like this may have occurred is the bonobo, which may also share many aspects of the domestic phenotype (Hare et al., 2012). Natural selection is thought to have acted against aggression in bonobos as a consequence of aspects of their feeding ecology, which in turn have influenced bonobo social structures (Hare et al., 2012). The bonobo, then, has the potential to act as a 'bridge' between the artificial selection in dogs and foxes and the natural selection required for a similar argument to be made in relation to humans. Once the bonobo example has been sketched in some detail, I will turn to the question of how a parallel process might have occurred in humans.

5.2.1 – The self-domesticated bonobo: a model for humans?

Humans have two equally close relatives among living primates: the well-known chimpanzee (*Pan troglodytes*) and its less famous cousin the bonobo (*Pan paniscus*). Both *Pan* species share a common ancestor with humans around 5-7 Ma (Ruvolo, 1997), and diverged from each other some 1-2 Ma (Won & Hey, 2005). Bonobos, originally known as 'pygmy chimpanzees' (Coolridge, 1933), were only recognised as a separate species in the 1930s, while chimpanzees have been known to science for hundreds of years. In the wild, bonobos are only found south of the Congo river —in what is today the Democratic Republic of Congo—whereas chimpanzees are found in a range of habitats across central and western Africa. This relative isolation has contributed to their continuing status as the 'forgotten ape' (de Waal & Lanting, 1997). Such a status is unfortunate because bonobos and chimpanzees differ from each other in their anatomy, social organisation and even cognitive skills.

It has long been argued that bonobos, particularly in terms of the size and shape of their crania, are paedomorphic with respect to chimpanzees (Shea, 1983, 1989; Lieberman et al., 2007), although see Mitteroecker et al. 2005 for a dissenting view. As discussed in chapters three and four, such paedomorphism is typical of domestication, with many aspects of the domestic phenotype being correlated expressions of this underlying developmental shift. More recently, a strong argument has been put forward that as well as exhibiting cranial paedomorphism bonobos also display a range of other aspects of the domestic phenotype (Hare et al., 2012). These include smaller crania (Coolridge, 1933; Cramer, 1977), reduced teeth size (Zihlman and Cramer, 1978; Pilbrow, 2006) and reduced sexual dimorphism (Cramer, 1977).

The physical differences between the two *Pan* species mirror the differences between wild and domesticated dogs (as discussed in chapter three) and wild and domesticated species more generally (as discussed in chapter four and **5.1**). Furthermore, the discussion in chapter three shows that they form part of a correlated cluster of changes that follow from selection against aggression. In what follows, I will sketch the outline of how natural selection has been argued to have acted against aggression in bonobos. With that in place, I will then discuss some of the behavioural, cognitive and hormonal differences seen between chimpanzees and bonobos, many of which mirror those seen in dogs and domesticated species more generally.

5.2.2 – Why are bonobos less aggressive than chimpanzees?

The differing temperaments of bonobos and chimpanzees have been linked to differences in their social organisation, which in turn reflects differences in their feeding ecology. In brief, bonobo societies are structured such that there is simply less 'reward' for aggression, and this structuring is, in turn, a consequence of aspects of their feeding ecology that reduce the requirement for intense competition for food. In the rest of this section I will unpack both the social and ecological aspects of this explanation.

5.2.2.1 – Bonobo social organisation

In proximate terms, the temperamental differences between bonobos and chimpanzees have been related to differences in their social organisation. One key difference concerns the composition of foraging parties. Bonobo parties are more stable, usually formed of a greater proportion of the whole community (25-51%) than in chimpanzees (9-30%), and contain a higher proportion of females (Furuichi, 2011). The role of females in bonobo society also differs markedly from that seen in chimpanzees. Bonobo females are much more gregarious, and form more close social associations (Furuichi, 2011), than do chimpanzee females (Muroyama & Sugiyama, 1994). Female bonobos also have very high social status, and appear to be dominant over males in certain situations, particularly in the context of food competition (Furuichi, 2011), while the reverse appears true in chimpanzees (Boesch & Boesch, 1989). Bonobo females also play an important role in determining their sons' social status. In chimpanzees, males usually achieve high social status during prime adult age, whereas male bonobos typically achieve the same status during late adolescence or early adulthood, at precisely the time their *mothers* are of prime adult age (Furuichi, 1997). Finally, female bonobos exhibit a prolonged period of pseudo-oestrus (Kano, 1992), in which they are sexually receptive but not fertile, something not seen in chimpanzees (Furuichi, 2011).

These aspects of bonobo social organisation form a nexus in which male aggression is less beneficial. The high status of females, frequency of female-female coalitions, high proportion of females in foraging parties, and the influence of mothers on the social status of males combine to create a situation in which male harassment of females and male aggression more generally is reduced (Furuichi, 2011). The period of pseudo-oestrus also reduces the need for males to compete for access to females, by rendering it harder for high-ranking males to monopolise females. With greater numbers of receptive females available, the challenge for males is not so much winning access in fights with other males, but gaining the preference of females (Furuichi, 2011). In other words, non-aggressive strategies such as forming affiliative bonds with females or exploiting ties to high-ranking mothers become much more important (Kano, 1992, Surbeck et al., 2012a).

5.2.2.2 – Bonobo feeding ecology

In ultimate terms, the contrasting social organisations of chimpanzees and bonobos have been related to differences in the feeding ecology of the two species. Bonobos, recall, are entirely restricted to an area south of the Congo River, this habitat has been argued to differ from that of chimpanzees in three systematic ways. Firstly, the size of available food patches is much greater. Secondly, those food patches include a much greater proportion of terrestrial plants (White & Wrangham, 1988). These two differences reduce the cost of travel between patches and of competition for food at any given patch (Furuichi, 2011), both of which costs are often higher for females than males. These reduced costs may be what permits higher proportions of females to join foraging parties, together with the range of other differences this leads to. Finally, gorillas are completely absent from the territorial range of bonobos (Malenky & Wrangham, 1994), thereby eliminating another potential feeding competitor, particularly in relation to terrestrial plants. The relationships between aspects of social organisation and feeding ecology are illustrated in figure 5.1:

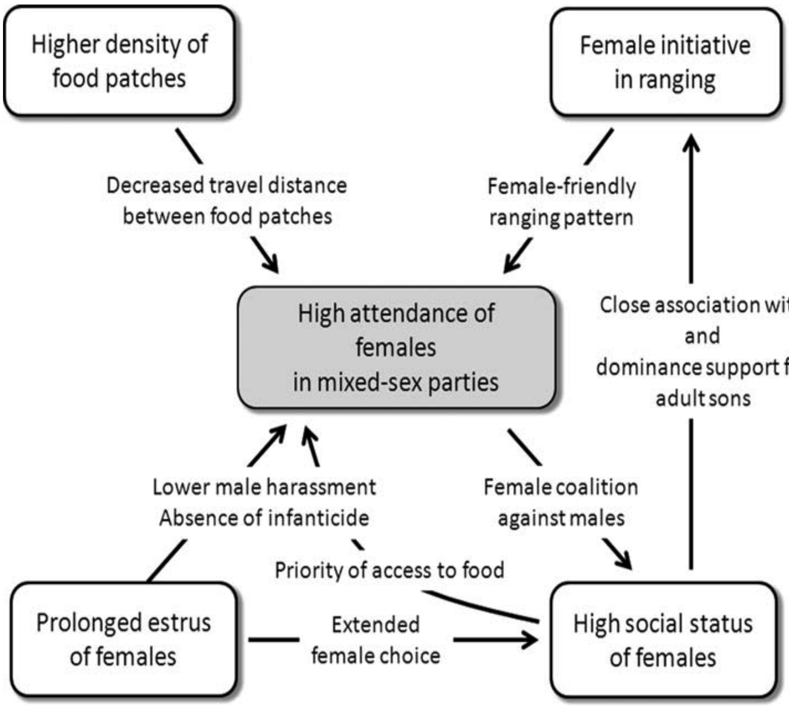

Figure 5.1: Relationships between bonobo feeding ecology and social organisation (Taken from Furuichi, 2011)

5.2.3 – Behavioural, cognitive and physiological differences

In this section I will consider four interrelated ways in which bonobos and chimpanzees have been found to differ, in addition to the hard-tissue differences already referred to above. The first is evidence showing higher levels of social tolerance and co-operation in bonobos than in chimpanzees. The second concerns differences in their social cognition. The third relates both these cognitive and behavioural differences to shifts in developmental timing. Finally, I will consider some of the neural, hormonal and genetic underpinnings of these differences.

5.2.3.1 – Differences in social tolerance and co-operation

In recent years a range of studies have compared chimpanzees and bonobos on their ability to engage in co-operative behaviour and their levels of social tolerance. On one view—the *hunting hypothesis*—chimpanzees should have an advantage as a result of their engaging in co-operative hunting (Boesch, 2002, 2005). On another view—the *emotional reactivity hypothesis* (Hare & Tomasello, 2005)—bonobos should have an advantage because, like dogs, they have experienced selection for reduced levels of aggression.

Hare et al. (2007) compared the willingness of chimpanzees and bonobos to co-operate on various feeding tasks. When the task required the retrieval of food that was difficult to monopolise there was no significant difference between the two species. However, when the task involved food that could easily be monopolised, bonobo dyads were more willing to co-operate than chimpanzee dyads. Hare and Kwetuenda (2010) examined the conditions under which bonobos were willing to voluntarily share their own food. They presented bonobos with a situation in which they could either eat a food pile by themselves or open a door to another bonobo, and therefore share the food. Bonobos exhibited a significant preference for opening the door, even though this meant missing out on some food they could have had themselves. This result stands in marked contrast to findings with chimpanzees in the wild (Gilby, 2006) and under experimental conditions (Jensen et al., 2006), in which their choices seem to be entirely self-focused, and where they display little regard to the welfare of unrelated individuals (Silk et al., 2005).

The bonobos in Hare and Kwetuenda's study could, of course, have been motivated by selfish considerations, such as a desire to engage in social interaction. Tan and Hare (2013) conducted a series of follow-up experiments, which produced four key findings that together illuminate the question of motivation. Firstly, they found that bonobos, when presented with a choice of two doors, preferred to open the door for a *stranger*, with whom they then shared the food, rather than a co-group member. Secondly, they also found that the remaining, unopened door, which would allow the admittance of the original subject's co-group member, was then usually opened *by the stranger*, rather than the original subject. The strangers were, therefore, willingly permitting themselves to be outnumbered by members of another group, something to which chimpanzees are known to be particularly averse (Wilson et al., 2001). Thirdly, they found that bonobos were willing to pull a rope to release another individual—whether a stranger or a group-mate—to allow them access to food that they themselves could not access. This willingness to make an effort on behalf of another individual with no obvious self-reward is something not seen in chimpanzees (Jensen et al., 2006). Finally, they found that bonobos were *unwilling* to help another individual when a lack of social interaction was combined with having to forfeit some food of their own.

It seems, then, that not only do bonobos exhibit greater levels of social tolerance and co-operation than chimpanzees, particularly in relation to co-feeding, but that they also show a much higher willingness to be actively pro-social, especially with regard to unknown individuals. Bonobos seem to not only be more tolerant and co-operative but also less xenophobic than chimpanzees, a difference also reflected in the nature of the two species' inter-group encounters in the wild (Furuichi, 2011). These differences resemble those seen between dogs and wolves, and provide further evidence that selection has acted on temperament in bonobos.

5.2.3.2 – Differences in social cognition

The differences between the two species as regards social tolerance also seem related to differences in social cognition. In comparisons across a range of tasks, bonobos have been found to outperform chimpanzees on theory of mind-related tasks, while chimpanzees outperformed bonobos on tool-use tasks (Herrmann et al., 2010). No significant differences were found on other tasks, such as the understanding of physical causality. These findings relate to work discussed in chapter four (**4.3.4**) concerning temperamental differences between humans and the great ape species, which found bonobos to be intermediate between humans (who were more wary) and other apes (who were less wary) in terms of their reactions of novelty. Research with human children has shown that temperament at age three—particularly the exhibition of a shy-withdrawn stance to the world—together with perceptual sensitivity to faces and other stimuli, predicts performance on theory of mind tasks at age five (Wellman et al., 2011). Wellman et al.'s (2011) interpretation of shy-withdrawn temperament in this study is not one of fearfulness but of a watchful, observant 'standing back', much like the aversion to novelty seen more in bonobos than chimpanzees.

The influence of perceptual sensitivity also parallels findings with dogs, whose willingness to look back at human faces plays a role in their outperforming wolves in the object choice task (see **3.1.2.1**). Such tasks do not assess theory of mind itself, but do investigate the related, if simpler, sensitivity to communicative intent. It is interesting, then, that work with dogs, bonobos and human children is all pointing to a similar kind of relationship between temperament and aspects of social cognition relating to intention reading. It should be noted, of course, that Wellman et al.'s work examines the relationship between temperament and theory of mind during *ontogeny*, whereas in the bonobo-chimpanzee case the relationship is a *phylogenetic* one, but the parallel remains intriguing nevertheless.

5.2.3.3 – These differences are related to shifts in developmental timing

In chapter three we saw how selection against aggression in a population of foxes resulted in the emergence of many aspects of the domestic phenotype, and that it did so as a result of changes in hormonal and other systems that regulate the rate and timing of development. In this section I will explore some parallels to this in the bonobo.

Wobber et al. (2010a) tested adult and juvenile bonobos and chimpanzees on various tasks to compare the two species over the course of development. Juvenile chimpanzees were found to co-feed significantly more than adult chimpanzees. In contrast, bonobos exhibited no difference between juveniles and adults. In a social inhibition task, chimpanzees were able to successfully inhibit their response in order to gain food at a much younger age than bonobos, who only achieved parity with the chimpanzees when significantly older. Finally, the two species were tested on a reversal-learning task, in which they first learnt which of two experimenters would provide food, and then had to adapt when the experimenters switched roles. Again the same pattern emerged, with younger chimpanzees outperforming bonobos, and bonobos only coming to match chimpanzee performance when older. Rosati and Hare (2012) also found similar evidence of developmental delays in relation to aspects of bonobo spatial cognition.

These findings of developmental differences are particularly interesting in the present context, because they suggest a mechanism that might account for the differences in temperament and social cognition, discussed above: bonobos and chimpanzees start out as juveniles with similar temperaments, but bonobos retain that temperamental disposition into adulthood (Wobber et al., 2010b; Brosnan, 2010).

5.2.3.4 – Hormonal, neural and genetic foundations of chimpanzee-bonobo differences

The behavioural differences between bonobos and chimpanzees are underpinned by differences in their hormonal responses. Wobber et al. (2010c) presented bonobo and chimpanzee dyads with a competitive food task. Males of both species exhibited a hormonal surge before the task began, but this surge took the form of a *different hormone* in each species. Bonobo males experienced an increase in the stress hormone cortisol; whereas chimpanzee males experienced a surge in testosterone. The authors argue that this difference relates to how the two species responded to competitive situations, with bonobos viewing them as social stressors and chimpanzees viewing them as contests to determine status.

These experimental results have also been mirrored by work with wild-living bonobos. In the majority of vertebrate species, including chimpanzees (Muller & Wrangham, 2004), mate-competition between males is related to heightened levels of testosterone, with the highest ranking, and therefore most successful, males showing the greatest increases (Hirschenhauser & Oliveira, 2006). The relationship between mate-competition, testosterone levels and dominance has been termed the 'challenge hypothesis' (Wingfield et al., 1990). This hypothesis does not seem to hold in bonobos (Surbeck et al., 2012a). While bonobo males do show increased aggression in the presence of fertile females, it is *inversely* correlated with rank. Furthermore, the rate of grooming between males and unrelated females is also negatively correlated with their level and rate of increase of testosterone, with high ranking males grooming unrelated females most often. In many species, cortisol levels are also related to dominance, particularly if rank is maintained through aggressive behaviour (Goymann & Wingfield, 2004). Surbeck et al. (2012b) found that cortisol levels in bonobo males did not generally correlate with rank. The hormonal responses in bonobo males seem to be determined, then, more by the need to maintain friendly relationships between the sexes rather than by aggressive interactions between males (Surbeck et al., 2012a, 2012b). These hormonal changes should recall those seen in both the Bengalese finch (**2.4.10**) and domesticated foxes (**3.4.5**), both of which show reductions in levels of stress hormone relative to their wild ancestors.

In addition to these hormonal differences there is work suggesting that the brains of bonobos and chimpanzees differ, with bonobos having more grey matter in brain systems associated with both the control of aggression and empathetic responses to others (Rilling et al., 2012). Finally, there is also some early indications that many of these changes in bonobos may be underpinned by some of the same genes that are typically associated with domestication (Pennisi, 2011). These neural and genetic findings are, of course, quite preliminary and await further confirmation. However, given the striking hormonal parallels between bonobos and all the cases of domestication discussed in this thesis, it is possible that the mechanisms underlying self-domestication in the bonobo are very much the same as underlie more conventional domestications.

5.2.4 – Summary

The bonobo presents an example, then, where natural selection against aggression has possibly resulted in a similar set of outcomes to those described for domesticated dogs and foxes in chapter three. This relates to arguments made above (**5.1.4**) and in the last chapter (**4.1.5.4**) that it is not where the selective pressure *originates* that matters, but what that selective pressure *actually is*. If there is selection against aggression, then it doesn't matter whether that takes the form of artificial selection stemming from human breeders or natural selection stemming from environmental conditions. This is an important expansion of the argument made in chapter three, because if the dogs and foxes were considered alone it might be possible to object that the outcome was the result of 'strong, directional artificial selection', and therefore irrelevant to humans. The bonobo example, together with the theoretical arguments, should indicate that this objection is premature. If selection against aggression can produce the outcomes it has in dogs—and seems to have in bonobos—then it can also produce those outcomes in humans.

5.2.5 – Selection against aggression in humans

In this section I will consider some hypotheses concerning how a similar process of selection against aggression might also have occurred in humans. The main focus of this section will be on one hypothesis that links selection on temperament in humans to aspects of their feeding ecology, particularly the role of *cooking* in human evolution.

5.2.5.1 – The cooking hypothesis

In focusing on feeding ecology, the cooking hypothesis has much in common with the account of self-domestication in bonobos. The logic of the cooking hypothesis, as set out in Wrangham (2009), can be summarised as follows:

i. Humans are biologically adapted to eating cooked food; we are *obligate* cooks

ii. This shift to obligate cooking is reflected in many aspects of our physiology

iii. This same shift fundamentally alters the social challenges associated with feeding, with significant implications for selection on temperament

iv. This shift in feeding ecology created a situation in which more co-operative individuals were favoured over aggressive or competitive individuals

For present purposes, one final point can be added to this summary.

v. Such selection against aggression would have produced a similar correlated cascade of effect in humans to those seen in dogs and foxes (chapter three) and bonobos (above), resulting in humans coming to exhibit many of the same aspects of the domestic phenotype

This fifth point is not, strictly speaking, part of the cooking hypothesis itself—although it is sometimes hinted at by its proponents (e.g. Wrangham, 2009: 184-185)—it does, however, follow directly from many of the arguments presented in this thesis, especially chapter three, and so will not be further discussed in this section. Points i-iv, however, require a more detailed examination.

I will deal with points i and ii in combination, as together they represent the basic foundation of the cooking hypothesis, and form the prime reason it deserves to be taken seriously. The evidence supporting these two points can be summarised as follows (taken from Wrangham et al., 1999; Wrangham & Conklin-Brittain, 2003; Wrangham, 2009; Organ et al., 2011):

- There are no current or past examples of human populations or individuals surviving for an extended period of time on raw food alone, this includes all recorded hunter-gatherer groups, including the Inuit.

- Members of modern 'raw-foodist' movements experience very high rates of energy deficiency (30%) and female raw-foodists also have a very high incidence of amenorrhea (50%) and disordered menstrual cycles. This is despite their access to the nutritionally enriched products of modern agriculture.

- Humans are the *only* species known to be unable to survive on raw food. Although other species typically *prefer* cooked food when presented with a choice, only humans seem to consistently suffer ill health on raw-only diets.

- The human digestive system is small compared to many other primate species. Humans have a smaller gut volume, caecum and colon, together with a much faster passage of material through the system. Together, these features suggest an adaptation to a diet of very high caloric density.

- Human teeth are much smaller than would be expected given a primate of our size, furthermore this difference cannot be accounted for solely in terms of correlated changes in body-size.

- Humans spend a much smaller portion of their day chewing (4.7%) than would be predicted (48%) for a primate of our size, and yet manage to consume sufficient calories to power a large body.

- Cooking and other non-thermal processing techniques enhance the palatability of food, make chewing much easier and increase the energy provided by both plant matter and meat.

There is, then, a strong argument that modern humans are adapted to eating cooked food. Firstly, humans are large-bodied mammals, with the high caloric requirements that entails, whose digestive systems and teeth seem ill-equipped to deal with processing large amounts of food and who spend a tiny fraction of the expected time actually chewing and consuming that food. Secondly, human health fares badly on uncooked diets, with no population—outside some modern, urban subcultures—ever being known to survive entirely on raw food. And, finally, cooking greatly increases the calories that can be extracted from food. Cooking, therefore, renders food into the calorically dense, more chewable form to which human guts seem adapted and which small human teeth can easily chew in a relatively short period of time.

These considerations give rise to two further questions, that relate to points **iii** and **iv**, above. Firstly, what effect has this unusual dietary niche had on other aspects of human evolution, such as social organisation and reproductive behaviour? If you grant that humans are obligate eaters of cooked food, then you must also grant that this is likely to have had other far-reaching implications. The second question concerns *when* this shift to obligate cooking might have occurred. If eating cooked food is a relatively recent phenomenon then many aspects of human physiology and social organisation are likely to pre-date it. If, however, reliance on cooking had a more distant origin, then it becomes much more plausible to ascribe it a powerful shaping role in human evolution.

5.2.5.2 – Evolutionary effects of eating cooked food

The arguments relating cooking to human social evolution proceed from the observation that when food has to be cooked, as opposed to eaten raw when found, it becomes far more vulnerable to *theft* (Wrangham et al., 1999). The act of cooking requires that food collected from a wide area be brought to a single point for processing, where heating and other techniques are applied. Such a processing point is, therefore, a highly vulnerable target for raiders or scavengers. In the literature on the cooking hypothesis, two inferences have been drawn from this observation. In many discussions these two inferences are blended together. For present purposes, however, it is important to tease them apart.

The first inference relates to the implications of cooking, and particularly the vulnerability of cooked food to theft, for *temperament*:

> If the first cooks were temperamentally like chimpanzees, life would have been absurdly difficult for females or low-status males trying to cook a meal. Cooked food would have been intensely valuable. Even the act of gathering creates value merely by assembling raw foods into a pile. Cooking only increases its attraction. Subordinate individuals cooking their own meals would have been vulnerable to petty theft or worse. (Wrangham, 2009: 158)

The argument here, then, is that a typically ape-like temperament is simply untenable in a species that had become an obligate eater of cooked food. Under this view, a shift in human feeding ecology precipitated a shift in the selective pressures surrounding temperament, much like in the bonobo. This inference is also supported by the strong aversion to anything like competition surrounding cooking and feeding in modern hunter-gatherer societies (Wrangham, 2009).

The second inference relates cooking to the typical human pattern of *female-male bonding*. This phenomenon has been addressed by two major theoretical perspectives. The *male-provisioning hypothesis* (e.g. Lovejoy, 1981), which relates bonding to the benefits females gain from being provisioned by males; and *bodyguard*-type hypotheses (e.g. Mesnick, 1997) in which males protect females from violence, sexual or otherwise, from other males. The logic of the cooking hypothesis combines aspects of both these approaches to produce what might be termed the *food guarding hypothesis*:

> Our proposal is that females formed bonds with males to protect themselves from food thieves, with the result that to a large extent females provisioned males. Pressure on females to form effective bonds then selected for extended and intensified female sexual attractiveness.
> (Wrangham et al., 1999: 575)

This inference can be seen as a more specific subset of the temperament inference. Females, being physically weaker than males, would be the primary targets of food theft and so would benefit from forming bonds with males to protect stores of food, or food in the process of being cooked. Such bonds would be cemented by females provisioning males with food and becoming sexually receptive for longer periods of the year. It is notable, however, that while the first inference follows fairly directly if you grant the 'theft premise', this second inference makes a raft of further assumptions.

The distinction between these two inferences becomes very important when we come to consider some of the criticisms of the cooking hypothesis. One major criticism focuses on the assumption that tubers and other underground storage organs served as major sources of nutrition over human evolution (see Wrangham et al., 1999). In comparison to the evidence for meat, however, there is little evidence that tubers formed an important part of the diet of early hominins (Shipman, 2009). Furthermore, the archaeological remains identified as 'digging sticks' in order to support this position bear little resemblance to those used by modern hunter-gatherers (Bunn, 1999).

Considered alone, however, these objections are far from fatal. After all, there is now evidence that cooking increases the digestibility and caloric quality of meat (Carmody et al., 2011) as well as plant matter. Underground tubers also only represent one potential type of food to which cooking might have been applied (Wrangham et al., 1999). Furthermore, it is only to be expected that fewer traces remain of the processing of soft plant matter than of the readily fossilisable bones of animals. The core of the cooking hypothesis remains intact, then, even if there is little evidence for the importance of underground tubers. This is because none of the inferences relating to *temperament* require cooking to involve any specific food type. If cooking makes food easier to steal, and if humans had become obligate cooks, then the associated selection on temperament could happen regardless of whether the food involved was tubers, other vegetable matter or meat.

This 'tuber objection' becomes far stronger, however, if the cooking hypothesis has to account for the human pattern of *female-male bonding*. If females gain male protection by provisioning them with food, then this has to involve food which *females would have controlled*. But on comparative grounds with modern hunter-gatherers, this rules out meat. As Wrangham et al. (1999: 576) concede, 'It is likely that females never controlled meat and therefore it could not be stolen from them.' It is important to note, therefore, that the temperament inference and the female-male bonding inference are separable, despite the fact that they are often run together in many of the published discussions of the cooking hypothesis. Of course, for the purposes of the present thesis there is no need to account for the emergence of female-male bonding in humans. Rather, the cooking hypothesis is presented as a plausible explanation as to why selection on *temperament* may have occurred during human evolution.

5.2.5.3 – When did cooking begin?

Even if we accept the basic premises of the cooking hypothesis, there still remains the question of *when* the shift to obligate cooking might have occurred. Is cooking an evolutionarily ancient enough behaviour to plausibly account for the many effects ascribed to it? The answer to this question depends on which way it is approached.

The advocates of the cooking hypothesis take what might be termed a 'physical inference' approach. This begins with the observation, detailed above, that many aspects of human biology and physiology reflect our status as obligate eaters of cooked food. The next stage is to ask at what point in human evolution these tell-tale signs of obligate cooking first become apparent. The answer, based on the anatomy of the digestive system, the size of the teeth and the estimated chewing time required if earlier hominin species *didn't* cook their food, is that *Homo erectus/ergaster* must have had a diet that included cooked food (Organ et al., 2011; Gowlett & Wrangham, 2013). This dates the origins of cooking to c1.8 Mya, judging by remains showing a broadly modern pattern of physiology from Africa (Finlayson, 2005) and Eurasia (Pontzer et al., 2010).

However, to argue that humans ate cooked food is to argue that humans, opportunistically or systematically, used or controlled *fire*. This is a problem for the cooking hypothesis, because there is little archaeological evidence, in Europe at least, for the control of fire prior to 400 Kya (Roebroeks & Villa, 2011). This lack of evidence is especially troubling because, in archaeological terms, Europe is by far the most thoroughly explored region of the world. Referring to sites dating prior to 400 Kya, Roebroeks and Villa (2011: 5212) conclude that the 'number and quality of these early sites are significant, and this absence of evidence cannot be ignored'. The archaeological evidence points, therefore, to a significantly later date for the control of fire than is required by the cooking hypothesis.

There have, however, been numerous claims for evidence of much earlier control of fire at various Asian and African sites, some dating from 1.6 Mya or older (e.g. Bellomo & Keen, 1997; Rowlett, 1999, 2000; see Gowlett & Wrangham, 2013 for broader survey). The problem with interpreting many of these early sites, especially if open-air, is that evidence of prehistoric fire is not necessarily evidence that *humans* controlled it. Other explanations such as wildfires can never be ruled out. This is especially true given that these early sites lack the hearths or other 'combustion structures' that appear in many of the more recent sites (Roebroeks & Villa, 2011) and which serve to confirm that the fire was under human control. As a result, the archaeological consensus has tended to view the control of fire as a relatively recent phenomenon in human evolution, restricted to *Homo sapiens*, the Neanderthals and perhaps their shared ancestor *Homo heidelbergensis* (Shipman, 2009; Roeboecks & Villa, 2011).

This consensus is, however, being challenged by a range of recent discoveries, particularly from Wondewerk Cave in South Africa (Beaumont, 2011; Berna et al., 2012), which provide the strongest evidence yet for a much earlier date for the control of fire. Berna et al. (2012) conducted a micromorphological analysis of sediment, stone and organic remains found deep within the cave site. Their findings provide strong evidence that bones and plant matter were burned at the site around 1.0 Mya, in close association to evidence of human occupation. They also note that wildfires or lightening strikes are unlikely given the deep (30m) cave location, and that other possible sources of naturally combustible material, such as guano, are largely absent. These findings strongly link the control of fire to *Homo erectus* for the first time, although not at the very earliest dates suggested by the physical inference approach. They also support the need to supplement archaeological evidence, which by its very nature becomes sparser and less representative the further back in time we go, with other approaches such as the physical inference approach (Gowlett & Wrangham, 2013), together with work in genetics, primatology and broader evolutionary theory (Dunbar, 2009).

5.2.6 – Summary and criticisms

It is important to remember that the account of self-domestication discussed in this section is not dependent on the eventual empirical fate of the cooking hypothesis. The cooking hypothesis is simply one possible account of why selection may have acted against aggression in humans. Others have proposed that selection on temperament could be related to the fact that humans engage in co-operative breeding (Burkart et al., 2009; Burkart & van Schaik, 2010), or to the phenomenon of cultural group selection (Richerson & Boyd, 2005). There will not, however, be space in the present thesis to discuss these alternative accounts.

This second account of human self-domestication has a range of strengths and weaknesses. On the positive side, an account of self-domestication rooted in selection against aggression has significantly more evolutionary time-depth than one rooted in the nature of the human-made environment. This makes this second account a more plausible explanation for how self-domestication could have come to have far-reaching effects on humans evolution. In the bonobo, there is a well-evidenced example of natural selection against aggression resulting in many of the same outcomes as was seen in the dogs and foxes, discussed in chapter three. Together with some theoretical considerations, this removes the concern that the findings with dogs and foxes cannot be applicable to humans because they involved directional, artificial selection.

The weakness of this selection-against-aggression account, however, lies in the evidential support for how and why something similar to that seen in bonobos could have occurred in humans. The cooking hypothesis represents the most fully worked-out scenario of how selection may have come to act on temperament in humans. It presents a very strong case that humans are obligate cooks, and that a reliance on cooked food has contributed to the shaping of human biology and physiology. Where it is less strong, however, is in terms of the evidence that cooking *necessarily* has the social, and therefore temperamental, implications imputed to it, and evidence that humans have been cooking for long enough for it to have had as wide an evolutionary effect as claimed.

5.3 – Culturally mediated mate-choice as an analogue of artificial selection

Throughout this chapter and the last there has been something of a tacit assumption that artificial selection is not relevant to humans, and therefore cannot account for human self-domestication. This assumption was based on the idea that humans have not been bred or controlled by any external species, that while humans may be domesticated, they certainly don't have a domesticator. There is a possibility, however, that this rejection of artificial selection has been too hasty. Humans have obviously not been selected by some external agency, but perhaps we have been artificially *selecting ourselves*. More precisely, there remains the possibility that human breeding practices have come to be directed in a way that presents a much closer analogue to artificial selection than we might normally assume. If this is the case, then human self-domestication may have taken a much more directed (although still unconscious) form.

5.3.1 – Bednarik's hypothesis

In terms reminiscent of arguments made by Franz Boas (see **4.1**), Bednarik (2011a, 2011b) has suggested that self-domestication proceeded through a process somewhat analogous to selective breeding, with mate-choice becoming increasingly driven by cultural determinants, particularly a preference for neotenic features:

> It is suggested that around 40 ka ago, cultural practice had become such a determining force in human society that breeding mate selection became increasingly moderated by cultural factors, *i.e.*, by factors attributable to learned behavior. These could have included the application of a variety of cultural constructs in such choices, such as social standing, communication skills, body decoration (which becomes notably prominent 40 ka ago, although existing earlier), and most especially *culturally negotiated constructs of physical attractiveness*.
> (Bednarik, 2011b: pp. 20-21, emphasis in original)

According to Bednarik, it is this culturally mediated preference that accounts for humans having becoming increasing gracile and neotenous over the course of their evolution, and especially over the last 50,000 years. Bednarik (2011a) considers three possible explanations for this pattern of evolution:

1) *Replacement hypothesis*: in which more robust populations of hominids on all continents were replaced by more gracile, modern humans in a second 'Out of Africa' event

2) *Gene-flow hypothesis*: in which gene flow and introgression cause the spread of more gracile phenotypes, but without any mass movement of population.

3) *Cultural moderation of breeding patterns*: in which human mate-choice becomes increasingly moderated by culturally derived norms and preferences favouring more gracile and neotenous forms.

The first two hypotheses represent two sides of an ongoing debate in archaeology and other disciplines concerned with human origins (e.g. Stringer & Gamble, 1993; Templeton, 2002). There is no space in the present thesis to evaluate the merits of each side in this complex debate; nor is there any need, as my aim is simply to assess Bednarik's proposed account of self-domestication[29]. I will focus, therefore, on the third of these hypotheses. To bring this hypothesis into focus, however, it is necessary to briefly consider Bednarik's reasons for rejecting the first two.

Bednarik (2011a) presents a survey of the skeletal, archaeological and genetic

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[29] Indeed, it is somewhat puzzling why Bednarik chose to contrast these three hypotheses. The first two *assume* the emergence of gracility, and then provide differing accounts of how that gracility might spread. In contrast, the third represents an attempt to account for *why* that gracility itself might have emerged.

evidence, concluding that there is no evidence for the replacement hypothesis, thus placing himself at odds with the archaeological consensus of the last few decades (e.g. Stewart & Singer, 2012). He concedes, however, that the evidence is much more supportive of the gene-flow hypothesis. If he stopped here, Bednarik would place himself within a minority, but nevertheless significant, group of scholars on human evolution (e.g. Templeton, 2013). Why, then, does he go on to reject this hypothesis, and endorse an account of domestication driven by culturally mediated constructs of mate-choice? The answer lies in the nature of the changes seen in recent human evolution:

> ...the changes that did occur *contradict all canons of Darwinian evolution*. Without a significant change in their environmental mega-niche, these humans experienced numerous deleterious physiological changes to become gracile. The thickness of their skulls decreased radically, as did the general robusticity of their skeletons. The traces of muscle attachments indicate that physical strength declined markedly, perhaps by as much as 50%. On top of that, their brain shrank by around 200 cc (~13%), and that occurred during a time when the demands on their mental abilities are thought to have increased exponentially.
> (Bednarik, 2011b: 18, emphasis in original)

Hyperbolic talk of 'contradicted canons' aside, it is clear that Bednarik invokes hypothesis three—in which culturally mediated mate-choice sees humans selectively breeding themselves—because he considers the observed changes to be *maladaptive*, and therefore inexplicable in terms of natural selection.

5.3.2 – Initial problems with Bednarik's hypothesis

This way of framing the hypothesis immediately brings out some problems. Firstly, traits are not adaptive or maladaptive per se, but rather *in relation to a particular environment.* The claim, therefore, that something like reduced cranial thickness is *definitionally* maladaptive is difficult to accept. Secondly, the claim that these changes occurred in the absence of any alteration to the 'environmental mega-niche' ignores the possibility, discussed at length in this thesis, that such changes might represent adaptive responses to much more subtle environmental shifts, such as aspects of the human-made environment or changes in feeding ecology. Finally, as argued in chapter four (**4.3.6**), the reduction in brain size cited by Bednarik can be explained entirely as a correlated effect of reductions in body size. These considerations alone should cast doubt on Bednarik's hypothesis. Even if we ignore these initial concerns, however, there are other problems that affect not just Bednarik's account, but any account of a similar type.

5.3.3 – Bednarik's proposal as sexual selection

Bednarik's proposal, in its claim that cultural constructs came to direct *mate-choice*, is clearly appealing to sexual selection. What is less clear, however, is the mechanism Bednarik has in mind in making that appeal, in particular whether he is appealing to a condition-dependent or condition-independent model of sexual selection (Jones & Ratterman, 2009; Kokko et al., 2003). This distinction matters.

On occasion, Bednarik appears to be making a condition-dependent argument, in which the criteria of mate-choice function as indicators for some aspect of mate quality. In terms of the discussion in chapter two **(2.3.3** and **2.3.4)**, this represents a three-factor mechanism, with a *preference*, a favoured *trait* and some difference in *viability* of which the trait serves as an indicator. In comparing humans to other species, Bednarik claims:

> Other primates (indeed, all other animals) exhibit no preferences in mate selection of youth or specific body ratios, facial features, skin tone or hair; *yet in present humans these are deeply entrenched, perhaps "hardwired". Facial symmetry, seen to imply high immunocompetence*, is also of importance, and in female humans neotenous facial and other features are strongly preferred by males.
> (Bednarik, 2011b: 20, my emphasis)

The implication here is clearly that the criteria of mate choice—such as facial symmetry—reflect mate quality. This is difficult to square, however, with the more radical idea that mate-choice had come to be *directed* by cultural constructs. If those constructs merely reflect indicators of mate-quality, then this is just another instance of standard sexual selection, which as we saw in **4.5.1.4** is simply a subset of natural selection. Alternatively, they might represent examples of 'evoked culture', in which cultural mating preferences and strategies co-vary with ecological conditions (Gangestad et al., 2006). Here, too, there is no sign of the radical argument Bednarik sometimes appears to be putting forward, as such 'evoked' constructs simply reflect current adaptive circumstances. The condition-dependent reading of Bednarik's argument, therefore, renders it fairly trivial. Rather than cultural constructs coming independently to drive human evolution in a manner akin to artificial selection, we simply have cultural constructs that are reflective of mate quality and ecological conditions.

At other times, however, Bednarik appears to be arguing for a condition-independent, two-factor mechanism, in which culturally constructed *preferences* and biological *traits*, such as more gracile crania and other aspects of neotenous appearance, interact with no link to viability:

> When breeding mate selection becomes moderated by cultural factors (such as cultural constructs of attractiveness, along with perhaps social position, communication ability, body adornment), the laws of evolutionary theory become suspended, and are supplanted by Mendelian laws of inheritance, the basis of the discipline of genetics: evolution by natural selection is replaced by breeding, or artificial selection, resulting in *domestication*.
> (Bednarik, 2011b: 18, emphasis in original)

This condition-independent reading chimes much more clearly with the earlier talk of 'suspended evolutionary canons', it would also, if shown to be correct, provide a genuine explanation as to how humans might have domesticated themselves in a way analogous to artificial selection. Unfortunately, this more radical reading of Bednarik's position has two major problems. The first concerns its partial resemblance to the concept of a *Fisherian runaway* (see **2.3.3**). The second concerns the supposed suspension of natural selection.

5.3.4 – Culturally constructed mate-choice as Fisherian runaway

The first thing to note, of course, is that the process proposed by Bednarik is not completely identical with Fisher's runaway process. The major difference is that in the Fisherian case both preference and trait are genetically encoded, whereas in Bednarik's hypothesis—at least on the condition-independent reading—only the resulting traits have a genetic basis, with the preferences being culturally constructed. However, both processes share a certain similarity of structure, in positing only *two* factors—preference and trait—with no link to any aspect of viability. As many of the problems with Fisher's process stem from the limitations surrounding when this two-factor account is feasible (Andersson, 1994), it seems likely that they may also apply in the present case.

The principle problem is that all the conditions under which a pure Fisherian runaway can work involve the assumption that there is no *cost* involved in the choice-making process (Maynard Smith, 1991)[30]. This problem is further exacerbated if we assume, as Bednarik appears to do, that the favoured trait is detrimental to fitness. A system which combines a detrimental trait with costly choice can only be stable when that detrimental trait also functions as an *indicator* of some other aspect of mate quality (Maynard Smith, 1991), in the sense of a Zahavian handicap (Zahavi, 1975). Of course, in this situation we have moved away from the kind of two-factor model proposed by both Fisher and Bednarik towards a three-factor model of trait, preference and viability differences.

The conditions under which a purely two-factor model of mate-choice can work are, therefore, very limited. Although Fisher's and Bednarik's proposals are not identical,

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[30] Fisherian runaways can function given a cost to mate-choice, if we assume a mutational bias in relation to the favoured trait. That is, if we assume that mutations have a greater chance of reducing the overall functioning of a trait than enhancing it. In these situations it may pay females to choose males with an exaggerated form of the trait, even if that exaggerated form is detrimental. However, this only functions to *maintain* an already existing trait and doesn't account for how such a cycle might initially get started (Maynard Smith, 1991).

they both take a two-factor form. The common theme connecting the limitations on that kind of two-factor account is that it is untenable in situations where there is a *selective cost* to that trait-preference link, whether that be in terms of choice itself being costly, or in terms of the favoured trait being detrimental but without it also functioning as an indicator of broader mate-quality. These objections might ease, however, in a situation in which natural selection was no longer in operation. As indicated in the above quotes, Bednarik appears to be proposing that just such a situation is in operation in humans.

5.3.5 – Culturally constructed mate-choice as 'natural selection is over for humans'

The idea that natural selection has ceased to be of importance in human evolution is one that is often in the news and has received discussion in a number of prominent publications (Balter, 2005; Stock, 2008; Ward, 2009). The following quote, from the geneticist Steve Jones, nicely illustrates this line of thinking:

> The central issue is what one means by 'evolving,'...Most people when they think of evolution mean natural selection, a change to a different or better adapted state. In that sense, in the developed world, human evolution has stopped.
> (quoted in Balter, 2005)

The intuition driving this idea is that humans are 'buffered' from natural selection, through a combination of our extreme behavioural plasticity, our ability to modify the environment, and our capacity to adapt culturally, and then transmit those cultural adaptations to subsequent generations (Varki et al., 2008; Crabtree, 2013a, 2013b). There has been much talk of buffering in this thesis, so it is important here to revisit a point made in the previous chapter. This is the distinction between the claim that a given culturally transmitted practice or environmental modification might buffer humans from a *particular selective pressure*, and the claim that the cumulative effect of human culture and environmental modifications have buffered humans from the action of *natural selection per se*, rendering it irrelevant as an evolutionary force. Given the range and scope of changes under consideration, Bednarik's argument clearly requires some form of this second claim. Furthermore, his proposal requires that this not only be the case today, but across *tens of thousands* of years. Regardless of the time scale in question, however, this kind of position is both empirically and theoretically unsupportable.

Turning first to the empirical evidence, there are a range of reasons to reject Jones's claim that 'human evolution has stopped'. Firstly, there is increasing evidence of recent selective sweeps in the human genome (Voight et al., 2006; Sabeti et al., 2007; Barreiro et al., 2008), a strong sign of positive natural selection. Secondly, many of the supposed 'buffering' factors, such as the human capacity to adapt through cultural means, actually *introduce new selection pressures* (Powell, 2011; cf. Deacon, 2009). The link between dairy farming and selection for lactose tolerance discussed above (**5.1.4**) is just one such example. There are also arguments to suggest a much broader link between phenotypic plasticity—of which cultural behaviour forms a part (see **2.4.6**)—and the introduction of new selection pressures (West-Eberhard, 2003, 2005). Furthermore, many of the outcomes of domestication, as discussed in **5.1**, also relate to the human-made environment introducing new selective pressures. Of course, the exact balance between buffering old pressures and introducing new ones remains an open question (Powell, 2011), which the discussion of deleterious alleles (see **4.3.7** and **5.1.1.8**) forms one approach to addressing. It should be clear, however, that simply pointing to potential buffering processes does not settle this question.

On the theoretical side, the problems arise from Jones's conflation of 'evolution' with 'natural selection', and 'natural selection' with 'change to a different or better adapted state'. Taking the second conflation first, it is simply not the case that selection always, or even mostly, acts to produce 'directional' change to some 'better state'. Selection can, of course, act like this, but it can also work in a variety of different 'modes', including *stabilising selection*, which acts to reduce the genetic diversity of a population, through favouring intermediate trait values; and *purifying selection*, which eliminates deleterious alleles (Barton et al., 2007). This leads us back to the first conflation, because the absence of natural selection does not result in a situation in which evolution per se no longer occurs—a kind of *stasis*—but instead a situation in which evolution is characterised by *genetic drift*, with its associated build-up of (usually) deleterious mutations. As a result, the only way to prevent currently adaptive structures and behaviours from being eroded through the process of genetic drift, is for selection—specifically purifying selection—to eliminate deleterious mutations as they arise (Powell, 2011).

Ironically, this last point also applies to preserving the cognitive, behavioural and cultural capacities that are often cited as undermining the role of natural selection (Powell, 2011). Without the action of purifying selection, the genetic bases of these capabilities would be eroded through drift. Similar considerations also apply to the whole range of basic physiological processes and structures such as the respiratory system and vital organs (Powell, 2011). In many cases the genetic variation underpinning these basic functions is highly conserved across species (Shubin et al., 1997, 2009), indicating that it has been successfully preserved against the impact of deleterious mutations for a very long time indeed. This process continues today in humans, as in all species (Powell, 2011). The key point, then, is that once the false equivalence of 'natural selection' with 'directional change' is broken down, it becomes theoretically untenable to claim that natural selection is no longer important in humans.

5.3.6 – Summary

Bednarik's account of self-domestication is both intriguing and superficially plausible, but fails to stand up on closer inspection. In its two-factor, condition-independent form it represents a radical account of how self-domestication might have occurred. Unfortunately, this two-factor approach to sexual selection severely limits the conditions under which the process might occur. One of those conditions is that natural selection no longer be in operation in humans. This is something that can be rejected on both empirical and theoretical grounds for humans today, and these problems are only exacerbated by Bednarik's need to project this selection-free situation tens of thousands of years into the past. Taken in its three-factor form, the argument becomes more plausible, but also more prosaic, as it essentially collapses to a story of adaptation and sexual selection.

5.4 – Discussion

This chapter considered three possible accounts of how self-domestication might have occurred in humans. The first focused on the idea that similarities between humans and other domesticated species might relate to both living in similar, human-made environments. One strength of this account lies in its evolutionary logic: similarities in environments will produce similar selective pressure and therefore similar phenotypic outcomes. A second strength is the wide-range of evidence that living in the human-made environment actually *has* contributed to the emergence of the domestic phenotype in conventional domesticates, such as livestock, and more unusual instances such as commensal species and the inadvertent domestications in captive breeding programs. The weakness of this account lies in the available time-frame in which it could have occurred. If living in a human-made environment is the key to self-domestication, then this requires that such an environment already exist. This immediately restricts the discussion to the last few tens of thousands of years of human evolution. Such a restriction, together with the capacities it seems required to assume, make this account difficult to accept as the full story of self-domestication.

The second account examined the idea that selection on temperament, particularly aggression, might explain self-domestication. This approach has a much greater potential evolutionary time-depth, thereby avoiding the major problem with the first account. It also supported by the considerable evidence that such selection on temperament does indeed result in many of the typical outcomes of domestication, as seen following artificial selection in foxes and natural selection in bonobos. The weakness of this account lies in pinpointing and providing evidence for how this kind of selection on temperament could have occurred in humans. The cooking hypothesis represents the most fully worked-out candidate of this process, but not all its aspects are equally well supported by the evidence.

The third account explored the possibility that something akin to artificial selection could have occurred in humans, as a result of cultural constructs coming to direct mate-choice. This represents by far the least plausible of the three accounts, as it requires a range of assumptions that are completely unsupportable on closer examination. It is worth noting that the problems with this third account are of a different kind to those of the first two. For the first two accounts the problem is one of *whether* they actually occurred in humans. In both cases, however, there is little doubt that they *could* have occurred; and, furthermore, there is good evidence that *if* they did, they would result in humans coming to share many similarities with other domesticates. For the third account, however, there are strong reasons to think that the scenario it outlines is not possible *in principle*. We have, then, two plausible accounts of how human self-domestication could have occurred. The problem, therefore, lies not in finding an account of self-domestication, but rather in picking between those on offer. Of course, there is nothing mutually exclusive about these accounts, and every possibility that they might represent two re-enforcing stages of the same process.

Chapter 6

Summary and Discussion

The focus of this thesis has been on the relationship between two ideas. The first is that language is the product of an evolutionary process. The second is that humans are a self-domesticated species. Each of these ideas has a long intellectual history, and the present thesis is certainly not the first time they have been explicitly linked. However, the specific aim of this thesis has been to consider the potential relationship between self-domestication and *cultural* accounts of language evolution.

I have focused on one particular cultural account, the Iterated Learning Model (ILM). The ILM describes a mechanism whereby structured language emerges through a process of repeated instances of cultural transmission. However, this mechanism, unlike the entirely genetic mechanism advocated by Pinker and Bloom (1990), itself stands in need of explanation. How might this mechanism have come to be possible in the first place? The hypothesis explored in this thesis is that a process of self-domestication might have produced the necessary preconditions for that cultural mechanism. The exploration of this hypothesis over the last five chapters has surveyed a very wide range of evidence, arguments and theory. In this final chapter, I present a summary and discussion of that survey.

This summary is divided into three main sections. In the first section the focus is on *language evolution*. In particular, I summarise my discussion of the ILM, detailing how it works and identifying its necessary preconditions. In the second section, I step back somewhat to consider some implications for our understanding of the relationship between culture, biology and evolution—implications that relate directly to the discussion of the ILM. Finally, in the third section I turn to *self-domestication*, addressing its link to the identified preconditions, its coherence as a concept and some possible ways in which it might have occurred.

6.1 – Language Evolution

6.1.1 – How the ILM works: internally and externally

The examination of the ILM presented in chapter one had two broad sets of conclusions. The first concerned the *internal* functioning of the ILM. The ILM account of compositionality depends on the interplay between two pressures. The pressure to be *compressible* and the pressure to be *expressive*. Through repeated generations of transmission, language adapts itself to these two pressures. The outcome of that adaptive process—compositionality—represents a compromise between the pressures, such that language compresses in such a way as to not sacrifice expressive capacity.

However, this internal account immediately raised a second question: why does language find itself having to adapt to *those* two pressures and not other ones? This new question has an *external* focus, relating to the origin of the compressibility and expressivity pressures themselves. This question of origin has revealingly different answers for the two pressures.

The pressure to be *compressible* is inherent to cultural transmission. It simply reflects the basic tendency of culturally transmitted systems to simplify—to become more compressed—and thus easier to learn. As we have seen, this is not restricted to language, but is also true of birdsong and indeed any culturally transmitted system. It represents, in other words, a kind of *informational regularity*. It is plain, therefore, why language should find itself having to adapt to a pressure for compressibility. If language is culturally transmitted, then it will inevitably face a pressure to simplify and compress, and will do so unless that pressure is checked by some other influence.

For the ILM, that other influence is the *expressivity* pressure. Unlike the pressure to compress, the expressivity pressure does not simply arise out of the nature of cultural transmission. It requires an explanation. The bulk of the work on the ILM now traces the origin of this pressure to the communicative function for which language is used. This still leaves the question of why language should have to adapt to a pressure stemming from *communication*, rather than some other function. The clear evolutionary answer to this question is *natural selection*: language structure comes to reflect its communicative function, because that is the function under selection (see **1.4.5.1**). The pressure for expressivity faced by the language, then, is a knock-on effect of language users being under selection for communication. This bare statement is expanded in the following two sections.

6.1.2 – Structure and function: the role of natural selection in cultural accounts

It is common to see 'cultural' accounts of language structure contrasted with 'biological' accounts (e.g. Kirby et al., 2008). Often, however, the exact basis of this distinction is not entirely clear. Should biological accounts be distinguished from cultural accounts in terms of *whether* they appeal to natural selection, or in terms of the *role* they ascribe it. The conclusion of this thesis is the latter, specifically in terms of *what* is being selected. To see why, it is necessary to reflect on what it means to include natural selection as part of an explanation.

An appeal to natural selection is an appeal to *function* in order to explain *form*. This point requires two further extensions. Firstly, it is necessary to identify the *correct* function in any given case. Secondly, it is necessary to recognise that similar functions can be delivered via a range of different mechanisms. For example, species living in cold climates exhibit a range of different *mechanisms*—from blubber and fur in mammals to antifreeze-like liquid in the blood of certain fish—that all serve the same ultimate *function*, keeping the organism sufficiently warm. Both these points are important when we compare cultural and biological accounts.

First consider the biological account provided by Pinker and Bloom. The function they identify is communication. However, 'communication' is an extremely broad term, and Pinker and Bloom had a specific form of it in mind: *code-like* communication. In their words, the "communication of propositional structures over a serial channel." Turning now to the question of mechanism, Pinker and Bloom argued that the details of linguistic structure were themselves encoded into the genome. They argued, in other words, for an entirely *genetic* mechanism. As discussed in chapter one (**1.4.5.6**), it is this choice of mechanism that renders their account biological. This pairing of a code-like function with an entirely genetic mechanism is no accident, because code-like communication is heavily dependent on all involved sharing exactly the same set of encodings (see **1.4.5.3**). It is natural, therefore, to link code-like communication with a tightly controlling genetic mechanism. Indeed, the communication systems of many other species, including our primate relatives, follow just this pattern (**1.4.1**): the system is code-like and the full set of signals are present from birth, suggesting tight genetic control.

Pinker and Bloom's views are internally coherent. However, both aspects of the argument just outlined face major problems. Firstly, their identification of code-like communication as the relevant function is simply unsupportable. As argued at length in chapter one (**1.4.5.3** and **1.4.5.4**), linguistic communication is simply not well characterised by the code model, and is much better described by the ostensive-inferential model. This point is amplified further by the recognition that, far from being an isolated communicative code, language is deeply integrated into a wider, fundamentally multi-modal system of inferential communication (**1.4.5.4**). There are also reasons to question Pinker and Bloom's appeal to an entirely genetic mechanism (see **1.2.2**). There is growing evidence that cultural transmission has a powerful mediating influence on language structure, suggesting that the structure seen in language is not simply isomorphic with the underlying genetics. In addition, there is increasing evidence that universals of the sort expected under Pinker and Bloom's picture simply do not exist.

These problems with Pinker and Bloom's account provide a useful starting point for our discussion of the ILM. Consider first the question of function. For the ILM, communication is also the relevant function—it is to this function that we can trace the expressivity pressure. However, for the reasons outlined above, the form of communication in question here cannot be code-like communication. Furthermore, as we saw in chapter one (**1.4.5.3**), the adoption of the code-model sees us inexorably descending into the bootstrapping problem. The escape from these difficulties lies in the realisation that linguistic communication is *inferential* in nature, and part of a wider multi-modal system. The expressivity pressure is the pressure on language to be expressive enough to function as part of that wider system.

Turning now to mechanism, the ILM appeals directly to the mediating influence of cultural transmission. In particular, to the fact that cultural transmission is an inherently structure-creating process. Indeed, it is this that accounts for the pressure to be compressible. Given that language structure emerges through the interplay between both pressures, the complete mechanism here is a combination of inferential communication and cultural transmission. Both aspects of this mechanism have a genetic basis. Once this in place, the operation of the mechanism can deliver a structured language as described in the ILM. The question of the ILM's preconditions, then, is the question of how this mechanism might come into being.

6.1.3 – Preconditions of the ILM

The summary of the ILM just presented is crucial in understanding why it has the preconditions that it does. In chapter one (**1.3)** five such preconditions were discussed. It was argued, however, that these five really represent different aspects of two underlying preconditions. The first of these is that the communication system be *culturally transmitted*. The second is the emergence of particular skills of social cognition underlying the capacity to *infer communicative intent*. The most basic of which is the simple awareness that a behaviour was meant communicatively at all.

The first precondition brings into existence the structure-creating process of cultural transmission itself. In doing so, it creates an new kind of *informational regularity*. Once in place, this regularity should be thought of in similar terms to regularities arising from the laws of physics. It stands ripe for exploitation as a source of structure 'for free'. Any system that comes to be transmitted culturally will face this pressure to compress, to become easier to learn, and will change—will become more structured—to reflect this pressure. However, this precondition on its own is not enough, because while it *will* deliver a structured language, there is simply no reason to expect that structure to be adaptive for language users—adaptive, that is, to function effectively as part of a wider inferential system of communication. This was seen most clearly in Kirby et al.'s (2008) first experiment where the language adapted to the pressure of transmission by becoming systematically underspecified. This represented the structuring of a previously random language, but not in a way that was adaptive for its users. And, furthermore, not in a way that resembles any real human languages observable today.

The second precondition is important in two interrelated ways. The first concerns the need for the transmitted system to consist of signal-*meaning* pairs, rather than just signals as in birdsong. Furthermore, the system must consist of a large enough number of such pairings in order to generate a bottleneck. The capacity to infer communicative intent—to infer meaning—and the simple awareness of communicative intent *at all*, upon which this is built, is what enables this to be possible.

However, this very same set of skills also form the foundation for the capacity to engage in *any* kind of inferential communication whatsoever. Such communication need not be linguistic, and can involve pointing, gesture and other modifications of the shared environment. Indeed, these forms of non-linguistic inferential communication, by virtue of their non-arbitrary nature, have the capacity to ground the subsequent emergence of arbitrary learned symbols. Language serves as an enhancement of inferential communication, and it is selective pressure on this *general type* of communication—rather than on *linguistic* communication specifically—that forms the best explanation for why language has to adapt to a pressure—expressivity—relating to communication and not something else. Indeed, as noted in chapter one, the inference of communicative intent *is* the inferential half of ostensive-*inferential* communication. The same capacities of social cognition that permit the learning of signal-meaning pairs also create the functional context—inferential communication—in which the expressivity pressure arises.

What the ILM shows, then, is that compositional structure is the ineluctable outcome of a union between a culturally transmitted communication system and a pressure to be expressive in relation to inferential communication. The effect of this is not to falsify an account of genetically encoded language structure, but to render it *unnecessary*. In an organism who's capacities have given rise to the informational regularities inherent to cultural transmission, selective pressure for expressivity—that is, for expanded and enhanced ostensive-inferential communication—will automatically co-opt and exploit those regularities. The genetic encoding of the details of language structure is as unnecessary, then, as the genetic encoding of the details of the down-step in human locomotion.

Intermezzo

Implications for thinking about culture and evolution

The view of the ILM outlined above provides a worked example that has implications for how we might think about the role of culture in evolution more generally. These implications were considered in greater detail in chapter two, as part of a wider discussion of evolutionary inheritance conducted under the banner of Deacon's (2009) conception of *epigenetic parsimony*. The key to understanding how culture fits into this picture lies in maintaining a clear distinction between the process of cultural *evolution*—in which cumulative culture emerges through the differential spread, reproduction and elaboration of cultural variants—and the role played by cultural *inheritance* in organismic evolution (see **2.4.7**). Most importantly, we should not allow our increasing understanding of the power and complexity of the former to cause us to misunderstand the role played by the latter. To see why this is important, both in general and for cultural accounts of language specifically, it helps to view the arguments developed in chapter two in light of some other views of culture and evolution, many of which have been touched on in this thesis.

One common approach, particularly in the literature on evolutionary psychology, emphasises the role of so-called 'evoked' culture, in which the variants that appear constitute adaptive reflections of current ecological conditions (Tooby & Cosmides, 1992). For example, some apparently cultural differences in mate preferences have been shown to co-vary with the available sources of nutrition and extent of parasitism (Gangestead et al., 2006). This view of culture sees it as something of a 'jukebox', in which developmental experience 'selects' from a from a pre-stored set of options (Tooby & Cosmides, 1992).

Pinker and Bloom's (1990) account of language evolution can also been seen in similar terms (Sterelny, 2006). The genome stores a set of innate linguistic principles, with culture relegated to switching the relevant parameters one way or the other. Under this conception of culture, both cultural evolution and cultural inheritance are rendered irrelevant. Cultural variants are not seen as the product of an evolutionary process; rather, they reflect a given genotype's response to a particular environment. Nor is culture an additional form of inheritance, as observed cultural variation simply reflects the differential expression of genetic inheritance.

Others, however, have focused on 'epidemological' or *transmitted* culture (Richerson & Boyd, 2005). They argue, quite correctly, that while some aspects of culture may fit the evoked model, many others do not. For example, Richerson and Boyd (2005: 46) imagine a scenario in which they are dropped in a remote, semi-desert location and asked to survive:

> ...we certainly don't command any practiced hunter gatherer-skills. If such skills are needed to survive as hunter-gatherers in deserts, they had better be lying quietly, heretofore little used, in innate modules in our heads. Give us the resources to survive a few months in our new home before you take away our last steel tool and last can of beans—a little time to see what comes naturally.

Richerson and Boyd's point, of course, is that such knowledge does not simply get 'evoked' by ecological conditions. It is passed between generations, with each generation cumulatively building on the output of the last. The resulting body of tools, techniques and cultural knowledge becomes far more than any one individual could invent during their own lifetime. This process, of the differential spread of variants and their continued elaboration, is the process of cultural *evolution*. Richerson and Boyd are right to emphasise its importance, and spend a good deal of their book elaborating on models and data that reveal some of the surprising ways in which it operates. This serves as a valuable counterweight to the jukebox model of culture. However, the emphasis which they rightly place on cultural *evolution* leads them into potential confusion when they come to think about the place of cultural *inheritance* in human evolution.

This confusion is exemplified by their notion of genes and culture forming a system of 'dual-inheritance'. This term is ambiguous. Should it be read weakly, as a simple statement that both genes and culture *are* inherited; or, should it be read more strongly, as the claim that they represent similar *kinds* of inheritance, with similar evolutionary roles? The weaker claim is uncontroversial; plenty of things are inherited. The stronger claim, however, is difficult to support given the discussion of extrinsic inheritance and phenotypic plasticity in chapter two (**2.4.6** and **2.4.7**).

To recap briefly, cultural inheritance is extrinsic inheritance: it is dependent on organisms being intrinsically structured in such a way as to be able to make use of it. That intrinsic structuring takes the form of various learning capacities and biases. Together, these capacities and biases constitute an aspect of *phenotypic plasticity*. They represent, in other words, a way in which phenotypes can be tailored during development. As a result, they function statistically—on average—to deliver adaptive responses to challenges faced over the life-course. This puts cultural inheritance—as a form of extrinsically inherited, trans-generational plasticity—on an entirely different footing from genetic inheritance, which is not a mechanism of phenotypic plasticity at all, and indeed forms the heritable, intrinsic basis for all such mechanisms. To speak here, then, of a system of 'dual-inheritance', with its implication that the two forms of inheritance rest on a similar footing, is highly misleading.

If this vital distinction between the two forms of inheritance is not recognised it can bring us to some very mistaken conclusions. The general basis of these errors lies in making a contrast between adaptive outcomes that are the result of *plastic responses* and those that are the result of *natural selection*. This contrast is fallacious because the mechanisms underlying plasticity are themselves produced, maintained and adaptively adjusted by natural selection (see **2.4.6**). If we fail to recognise that cultural inheritance is an aspect of one of those mechanisms of plasticity, instead viewing it as a form of inheritance akin to the genetic, then we can easily come to believe that cultural inheritance has nothing to do with natural selection at all.

In relation to language evolution, and particularly the ILM, this kind of view only serves to compound the difficulties of accounting for the expressivity pressure. As discussed above and in chapter one (**1.4.5**), the principle problem here is accounting for why language should find itself having to adapt to a pressure, expressivity, arising from *communication* rather than some other function. Natural selection provides a clear way of addressing just this kind of problem: the structure of a trait comes to reflect the functions for which it was under selection and not other ones.

However, there are two factors that seemingly prevent the ILM from drawing on this explanatory resource. The first concerns its adoption, if only implicitly and methodologically, of the code model of linguistic communication, and has been dealt with above. The second concerns the view that cultural inheritance and natural selection should be seen as contrasting and competing explanations. If this were indeed true, then it would make it difficult to justify an appeal to natural selection to account for the expressivity pressure, on the grounds that natural selection is only relevant for genetic inheritance. However, as we have just seen, this is not the case. Like any other aspect of plasticity, cultural inheritance and cultural transmission are enabled, biased and adaptively adjusted by natural selection.

We can see, then, that a dual-inheritance view of culture and genetics has the potential to lead us astray in our thinking about language evolution. What is needed, therefore, is a way to retain the insights regarding the importance of cultural *evolution* without also committing ourselves to a picture of unsustainable equivalence between genetic and cultural *inheritance*. The account of the ILM explored in chapter one and the wider discussion of evolutionary inheritance explored in chapter two allow us to see, in broad terms, how this might be done. The key to this solution lies in Deacon's conception of epigenetic parsimony. Of which the account of the ILM presented in **6.1** serves as an example.

What we might call the 'epigenetic parsimony' view of the ILM, and of culture more generally, addresses both the potential problems identified above in relation to the culture-biology relationship. Its focus on the informational regularities of cultural transmission, together with their self-organising potential, allows us to recognise the explanatory significance of cultural *evolution*. The dynamics of the cultural evolutionary process stand as something that most definitely needs to be understood. However, this view is perfectly compatible with the fact that those regularities and dynamics are part of a complex mechanism of phenotypic plasticity. It is simply not the case that we have to adopt a dual-inheritance view of evolution—with the unsustainable equivalence between culture and genetics that it requires—in order to give the process of cultural evolution its due prominence.

Furthermore, once the informational regularities of cultural transmission are in place, they present—much like any other reliably present epigenetic regularity—as something that can be exploited by evolution. In the case of the ILM, for organisms engaged in a particular kind of communication—inferential communication—the regularities of cultural transmission can be harnessed to deliver a language structured so as to function as an enhancement of that form of communication. Of course, to the extent that cultural transmission presents such regularities, there is nothing to restrict this viewpoint solely to language. We might call this the *regularity exploitation* view of culture. Certain mechanisms of phenotypic plasticity enable cultural transmission. In doing so they bring into being a dynamical system with its own self-organising regularities. These regularities can the be exploited in order to bring about structural outcomes of various kinds.

The view outlined here allows us to see that we are not faced with a binary choice between a picture of culture as 'evoked jukebox', which totally disregards cultural evolution, and a picture of culture as an independent, parallel system of inheritance that should be seen as similar in kind to genetic inheritance and that has nothing whatsoever to do with natural selection. Finally, it also allows us to place our analysis of the preconditions of the ILM in a much wider evolutionary context, as we can now see the ILM as detailing a specific instance of the more general phenomenon of epigenetic parsimony.

6.2 – Self-domestication

6.2.1 – Importance for language evolution

The importance of self-domestication for language evolution, and in particular for cultural accounts such as the ILM, lies in the comparative evidence showing the two preconditions identified above emerging in the context of domestication. Chapter two presented a discussion of the first precondition—an increased role for traditional transmission—emerging in the Bengalese finch. The mechanisms accounting for this emergence centre on the buffering effects of the domesticated environment, in particular the absence of predators and sympatric, closely related species. It seems likely that female preference for complex song also had a role to play. Chapter three presented a discussion of aspects of the second precondition—the sensitivity to communicative intent—emerging in the domestic dog. A long-term experimental reconstruction of this domestication process, the farm-fox experiment, pinpointed a key role for selection on temperament, particularly selection against aggression, in producing not just this precondition itself, but a much wider range of the typical outcomes of domestication. The task of the rest of the thesis, at least as far as self-domestication was concerned, was to examine whether the concept of domestication could be coherently applied to humans and, if so, to make more concrete how such a process might have occurred. If this could be done, then the findings of the comparative studies could also shed light on the emergence of the preconditions in humans.

6.2.2 – Coherence of the concept

The concept of domestication can be coherently applied to humans. Domesticated species are typified by a shared set of characteristics, known as the *domestic phenotype*. As argued in chapter four (**4.3**), humans share in many of these characteristics. It is these phenotypic parallels that form the basis for the view that humans, too, might be domesticated.

The acceptance of this argument from parallel changes depends on the perspective one takes on domestication. The 'conditions' view of domestication emphasises the role of an external agency, a domesticat*or*, controlling the life-cycle and breeding of the domesticated species. In contrast, an 'outcomes' view of domestication considers the emergence of the domestic phenotype as its defining mark. This view stems from the observation that domestication is not simply the *state* of living under human control, or of living in a human-made environment, but of having become *adapted* to that environment. The domestic phenotype is the outcome of that process of adaptation.

Both views have much to recommend them. The conditions view clearly describes the existence of many present-day domesticates. It also describes the manner in which many of those species likely entered the environment to which the domestic phenotype can be seen as an adaptation. The outcomes view allows us to make sense of those cases which don't entirely fit the conditions view, but that do exhibit aspects of the domestic phenotype. These include commensal species (**5.1.2**), inadvertent domesticates (**5.1.2**) and, indeed, humans (**4.3**). These two views of domestication can be reconciled when it is realised that domestication is not a single monolithic condition, but a multi-stage process, with various entry points, along which different species will likely proceed at different rates (**4.4**). Not all those pathways and stages will necessarily be characterised in the terms of the 'conditions' conception of domestication, but aspects of the domestic phenotype would be expected to emerge in all of them.

The domestic phenotype is sometimes identified as the outcome of artificial selection. The discussion in chapter four (**4.5**), however, shows that this identification is overly simplistic. While artificial selection is undoubtedly important, the domestic phenotype is the product of a range of evolutionary processes—including continuing natural selection and the relaxation of selection—together with development consistently occurring in the domesticated environment. These processes are perfectly applicable to humans. Furthermore, the strong evidence that many aspects of the domestic phenotype are the outcome of a correlated cascade following selection on temperament (**3.4**) is also applicable to humans, at least in principle, because the selection involved does not have to be artificial in order to have this effect (see **4.5.1.4**; **5.1.4**; **5.2.1**).

6.2.3 – Making the concept more concrete: possible mechanisms

Drawing on the discussion in chapters two, three and four, chapter five presented three possible accounts of *how* humans might have come to self-domesticate. The first of these focused on the role of adaptation to the human-made environment. One major aspect of that environment, particularly stressed in chapter two in the discussion of the Bengalese finch, concerns the way in which it buffers against some selection pressures and introduces new ones. The discussion in chapter five (**5.1**) presented a range of evidence that much of the domestic phenotype emerges as a result of adaptation to this human-made environment. It was also stressed that it is humans themselves that have been living longest in this environment. This first account, then, sees self-domestication as the result of humans having to adapt to a similar set of environmental circumstances—human-made ones—that have also faced other domesticated species. The major problem with this account of self-domestication, however, concerned the relatively limited time-depth in human evolution during which it could possibly have occurred.

The second account focused on the possibility that the domestic phenotype might be explained as a result of a correlated cascade of effects following selection against aggression. This derives from the strong evidence, primarily from the farm-fox experiment (**3.4**), that many aspects of the domestic phenotype can be produced simply through selection acting on temperament.. In the case of the farmed foxes that selection was artificial. A range of theoretical arguments and fundamental evolutionary reasoning indicate that selection of *any* kind against aggression should have a similar set of outcomes (see **4.5.1.4**; **5.1.4**; **5.2.1**). This second account, then, sees self-domestication as a correlated by-product of humans also having undergone selection against aggression.

This possibility was first explored in relation to bonobos, who appear behaviourally, morphologically and physiologically to be relatively 'domesticated' in comparison with chimpanzees. These differences seem likely to derive from bonobos having undergone *natural* selection against aggression. The origin of this pressure is likely linked to bonobo social organisation, which in turn relates to aspects of their feeding ecology. The most fully worked-out account of why humans might also have undergone a similar process of selection against aggression—the cooking hypothesis—also relates to feeding ecology. This account of self-domestication has considerably more evolutionary time-depth, and thus a much greater scope to cause far-reaching evolutionary effects. However, some of the detailed support required by the cooking hypothesis, such as evidence for the early control of fire, is somewhat missing.

Finally, the third account considered the potential role of culturally constructed preferences coming to drive human mate-choice, resulting in a kind of 'selective breeding' that caused many aspects of the domestic phenotype to spread through the human population. While this account has an initial plausibility, it also has a number of pretty insurmountable weaknesses. The first concerns its resemblance to a Fisherian runaway scenario, with which it shares many of the same operational limitations. The second concerns its assumption that natural selection is no longer an important evolutionary process in humans. This assumption is untenable on empirical and theoretical grounds, and becomes even more so if it is supposed to apply across tens of thousands of years of human evolution.

6.3 – Conclusions

Work on the ILM describes a mechanism for the production of structured language. That mechanism consists of the self-organising dynamical regularities of cultural transmission, together with the boundary setting influence of a particular form of communication—inferential communication. The relationship between these two factors—the reliably present epigenetic system of self-organisation, and the genetically based boundary setting influence that exploits that self-organisation—is captured in the concept of epigenetic parsimony. The union of these two factors causes culturally transmitted language to not only become progressively more structured, but to do so in such a way as to function effectively in inferential communication. The preconditions of the ILM can be seen, then, as the emergence of these two aspects of the mechanism.

The comparative evidence shows both these preconditions emerging in the context of domestication. In the Bengalese finch we have learning, and the traditional transmission it enables, taking on a much more prominent role following domestication. In the domestic dog we see the emergence of one of the key foundations underpinning both the inference of communicative intent and inferential communication itself. These serve as vital clues to the possible origin of the two preconditions in humans. The relevance of these clues to the human case is further increased by the recognition that the evolutionary context in which they appear—domestication—is one that can be coherently applied to humans. Several possible accounts of how self-domestication might have occurred in humans are available. The eventual fate of these hypotheses depends, of course, on the empirical evidence. However, in combination with the discussion of the domestic phenotype, they present as a clear target for subsequent theoretical and empirical work.

Coda

Expanding, refining and testing the argument

I. The chain of the argument

The argument presented in this thesis can be profitably conceived of as a chain, in which links are made between previously disparate findings, theories and perspectives. In short, the argument is that the findings of those working on domestication speak directly to the questions of those working on cultural accounts of language structure. It may be helpful here to lay out the chain of the argument in its barest possible form:

1. The cultural transmission of language has important consequences for the structure of language

2. This transmission is only possible for organisms with particular capacities

3. At a minimum, those abilities include the capacity to learn new signals—thus allowing cultural transmission to influence the communication system—and the capacity to make inferences regarding communicative intent

4. In order to account fully for language structure in cultural evolutionary terms we need to also have an account of the emergence of those capacities

5. There exist comparative case studies in which both these capacities can be seen emerging in the evolutionary context of domestication

6. Making an argument from evolutionary analogy, domestication can also account for the emergence of these capacities in humans

Like any chain, each of the links in this argument represents a potential vulnerability. However, the first four links are all well-attested elsewhere and together form the starting point of this thesis. As such, I will say no more about them in this discussion. The final two links—or rather, the *connection* between the last two links and the first four—is what forms the core of this thesis. In the next two sections I will take these two points in turn, and offer a set of conceptual clarifications, together with thoughts about how these aspects of the argument might be testable and what might constitute relevant sources of evidence.

II. A tale of *two* mechanisms: buffering and selection on temperament?

Throughout this thesis two mechanisms have been discussed in relation to the emergence of the domestic phenotype. Each of these mechanisms was featured in one of the two comparative case studies. In the discussion of the Bengalese finch in chapter two, the focus was mainly on the role of buffering and relaxed selection. In the discussion of the domestic dog in chapter three, the focus was mainly on the role of selection acting on temperament. The role of environmental buffering was also explored in relation to humans (**5.1**), commensals (**5.1.3**), and endangered species in captive breeding programs (**5.1.2**). In addition, the role of selection on temperament was explored in relation to humans (**5.2.5**) and bonobos (**5.2.1**). For the most part, these two mechanisms have been discussed separately. In this section, however, I want to consider how these mechanisms might be related, together with two further issues that arise out of that discussion.

i. What is the relationship between the mechanisms?

It is helpful to begin with the role of selection on temperament, as exemplified by the work on the farm-fox experiment. The starting point of this work was Dmitry K. Belyaev's hypothesis of *destabilizing selection* (see **3.4**), in which he suggested that the typical outcomes of domestication followed from the breakdown of the pre-existing, developmentally canalized systems underpinning *temperament*. Over fifty years later, work on the farm-fox experiment provides strong support for Belyaev's initial hypothesis, and has even begun filling in some of the details regarding the hormonal and other systems that are actually destabilized (**3.4.5**).

In terms of relating this mechanism to that of relaxed selection, three key points stand out from the work on the farm-fox experiment. Firstly, it identified *which* systems the key breakdown occurs in, those underpinning temperament. Secondly, it showed that a great many aspects of the domestic phenotype could appear as *side-effects* of that temperamental breakdown[31]. (Note, however, and this will be important below, that although they may *initially* be side-effects, once these various traits start to appear they become visible to selection in their own right, in the sense described in **2.4.1**. As such, if any of these traits turn out to be beneficial, we would expect them to spread further through the population, and possibly come to be enhanced.) Finally, it also served to illustrate one way in which that breakdown could occur: through the application of selective pressure on temperament that caused a directional change in hormonal and other regulatory systems (**3.4.5**).

With these three points in mind, we are now in a position to relate selection on temperament to relaxed selection. The key to this relationship is that the kind of breakdown of previously co-adapted and canalized systems that is so central to the farm-fox experiment *does not require explicit selection in favour of anything*. The reason for this is simple. As noted in section **5.3.5**, the majority of the action of natural selection is in a stabilizing or purifying mode, in which it acts to *maintain* currently adaptive traits in the face of deleterious variation. In other words, all that is minimally required for a previously co-adapted set of traits to breakdown is the relaxation of stabilizing or purifying selection. Indeed, an argument of just this kind

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[31] For example, that piebald coat colouration or the breakdown of seasonal mating patterns need not have occurred because they were themselves adaptive, but because they formed part of a correlated cascade of effects that followed the breakdown of previously canalized systems underpinning temperament.

was presented in relation to both the Bengalese finch **(2.4.10)** and a range of other domesticated species **(5.1)**. There is no necessity, therefore, to invoke any positive, directional selection in order to account for this kind of breakdown.

This kind of change, in which previously co-adapted sets of traits breakdown under circumstances of relaxed selection as a result of environmental buffering, is a phenomenon Deacon has termed *degeneration* (see **2.4**). Belyaev's concept of destabilizing selection and Deacon's concept of degeneration following relaxation have, then, a great deal in common. In particular, they both describe conditions in which a canalized set of co-adapted traits might breakdown. The first of these involves *directional* selection—whether artificial (e.g. **3.4**) or natural (e.g. **5.2**)—that specifically served to target the systems underpinning temperament. The second involves organisms finding themselves, for whatever reason (cf. the discussion in **5.1.4**), in an environment in which they were buffered from *stabilizing* selection, that had maintained those *same* temperament system in their previously canalized state[32]. As such, they might both be seen as two routes to the same destination.

However, there are also some significant differences between Belyaev's destabilizing selection and Deacon's relaxation-induced degeneration. The most important of these is that while both can explain the *breakdown* of a previously canalized state, only Belyaev's destabilizing selection can also explain the subsequent directional change in the population, such that not only does the earlier canalized state break down, but a *newly canalized state also emerges*. In the farm-fox experiment, this is represented by the shift from the initial wild-type temperaments in the original population, to the total spread of tame temperaments in later generations **(3.4.2)**. This difference derives from the fact that Belyaev's process operates through a

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[32] Many of the examples in which buffering and relaxed selection have been implicated also involve changes to the hormone systems that regulate temperament, similar to those seen in cases of selection against aggression, such as the farm-fox experiment (**3.4.5**). This is true for domesticates generally (**5.1.1.7**), as well as the Bengalese finch (**2.4.10**), and bonobos (**5.2.3.4**). Indeed, following some recently published work, it seem likely true of humans as well (Cieri et al., 2014). It is reasonable to conclude, therefore, that one of the key 'relaxations' concerns selection pressures that maintain the systems underpinning temperament. Of course, this does not rule out other relaxation-effects—such as those related to sensory and motor systems (see **5.1.1.4**)—but it does suggest that the relaxation of pressures with an influence on temperament may be particularly important.

directional shift from one canalized state to another, while Deacon's process operates as a 'random walk'—through a processes of drift—away from the initial canalized state as pressures that once maintained it become relaxed.

If the relationship between the two mechanisms outline above is right, then it has a range of implications for what we should expect to see in various instances of domestication. Firstly, we should expect that both selection against aggression and the buffered relaxation of selective pressures—such as predation, food scarcity and reduced necessity to be competitive (see **4.5.1.2** and **5.1** for further discussion)—should produce similar phenotypic outcomes. We should also expect, however, that selection against aggression should produce those outcomes much more rapidly than the relaxation of selection. Indeed, this is exactly what was found in the farm-fox experiment, in which domestication-typical changes swept through the population of selected tame-line foxes in under 50 years, but also appeared at a frequency an order of magnitude lower in the unselected, but still captive-living, control foxes (**3.5.6**). Finally, regardless of mechanism, we should expect that some of the side-effects of the domestication process should turn out to be beneficial and thus themselves become the object of selection. Given this final point, we might ask whether the two preconditions identified in chapter one should be thought of as side-effects or adaptations.

ii. Are the preconditions side-effects or adaptations?

The first preconditions was that cultural transmission should come to take on a greater role in influencing the communication system. This was explored in chapter two through a detailed examination of the Bengalese finch. In this section, I will recast the conclusions of that chapter (see **2.5**) in terms of the above discussion. The argument advanced in chapter two was that, in being transplanted to the domesticated environment, the ancestral munias were buffered from selective pressures—particularly species recognition (**2.4.10**)—that had served to maintain their song in a simple and stereotypic canalized state. In the context of domestication, with these pressures relaxed, this canalized state broke down. In other words, the *initial* breakdown of the canalized state was a side-effect of the buffered environment. Crucially, however, this breakdown of canalized simplicity, together with the increasing role for other influences, resulted in a greater phenotypic diversity—in particular, a greater diversity of song complexities. This then interacted with selective pressure stemming from female preference for more complex song. The result of this was that the descendent population of Bengalese finches came to have, on average, more complex song than their wild munia ancestors.

The second precondition related to inferential capacities, most fundamentally to recognising that something was meant communicatively in the first place. This precondition was explored in chapter three, through an extended examination of the domestic dog, as illuminated by the farm-fox experiment (**3.4**). The farm-fox experiment also shows the breakdown of a previously canalized state, although this time the breakdown is attributable not to relaxed selection but to selection against aggression. Regardless of the initial cause of the breakdown, however, one of the side-effects was that domesticated foxes came to exhibit a sensitivity to communicative intent, thus indicating how and why that same capacity likely arose in dogs (**3.4.4**). Where this case differs from the first precondition, however, is that, at least in the domesticated foxes, there seems to be no evidence that this ability has subsequently been found to be evolutionarily beneficial. In dogs, however, there is some evidence of differences between breeds. In particular, that while all breeds exhibit this same basic sensitivity to communicative intent, some breeds, particularly those that work closely with humans, also show enhancements over and above this basic capacity (**3.1.4**).

In both cases, then, the initial emergence of the precondition followed as a side-effect of the domestication process. The increased role for learning in the Bengalese finch appears as a result of the degeneration of biases that had previously canalized a simple, stereotypical song. Similarly, the sensitivity to communicative intent seen in dogs appears as a result of the breakdown of previously canalized systems underlying temperament. In both cases, too, although perhaps more so for the

Bengalese finch, there is evidence that this initial side-effect was then found to be beneficial in its own right. For the Bengalese finch, this involved the complexification of song in line with female preferences (**2.5**). For the domestic dog, this possibly involved the capacity to work with humans (**3.1.4**), perhaps facilitated by temperament-related changes in characteristics such as the willingness to look back at human faces (**3.1.2.1**). The parallel argument in the human case, therefore, would see *both* preconditions emerging as side-effects of domestication, with both of them—or rather, the *union* of both—coming to be beneficial, particularly as regards communication (see chapter one, section **1.4** onwards for a full discussion).

iii. Why *both* preconditions in humans, but only one in each of the comparative examples?

The claim that domesticated species typically exhibit a range of similarities—the domestic phenotype—has been a major theme of this thesis. There is also a need, however, to acknowledge the *differences* between domesticated species. This is a dimension that requires much deeper consideration than it has been given in the present work. This is particularly the case given that there is no comparative example of domestication leading to *both* preconditions emerging together in another species, and yet this is exactly what needs to be accounted for in humans.

One way this might be approached, is to focus on the specifics of the domestication process in each case. Might, for example, the particular 'pathway' to domestication (see **4.4**) taken by a species—whether, for example, they began as prey or as commensals—influence the final outcome? In addition, might this be an area where the distinction between domestication and *self*-domestication is important? For example, as seems to be the case in relation to the decline in brain size associated with the former but not the latter (**4.3.6**).

A second approach might be to focus on the differing evolutionary histories of the species prior to domestication. It has been argued, for example, that the evolutionary history of many lineages makes them unamenable to domestication at all (Diamond, 1997). Might it be important, for example, that the songbird ancestors of the Bengalese finch have long engaged in some form of cultural transmission, while the wolf ancestors of domestic dogs are known to have highly sophisticated social cognition? Might these differing phylogenies have laid the ground for different outcomes following domestication? In the human case, might the combination of primate social cognition with, at least in the gestural realm, the capacity of primates to learn new signals, explain why *both* preconditions could have emerged together? But if this were the case, what explains the difference between humans and bonobos?

These are hard questions to which I do not pretend to have a definitive answer. Nevertheless, considered in light of the discussion above, we should be able to make some tentative suggestions. Firstly, that the phenotypic outcomes of any particular process of domestication should be a function both of the mechanism by which that domestication occurred and of the previous evolutionary history of the lineage. This would explain why, as noted in **2.2.2**, domestication effects cannot account for the emergence of vocal learning in the Bengalese finch—indeed, the wild munia is itself a vocal learner—or the seemingly disparate[33] collection of other species in which vocal learning is found (see **1.4.1**). Rather, what we see is that domestication, by relaxing selection, serves to unleash the potential inherent in vocal learning that had previously been kept in check by selection pressures in the wild. Similarly, domestication can be seen to have unleashed the potential inherent in the advanced socio-cognitive capabilities of wolves, that had previously been kept in check by aspects of temperament (see **3.4.4**).

While many of the effects of domestication will, therefore, be seen across all domesticated species, some will only be seen in particular instances. What these more specific effects of domestication will be is likely determined by the *potentials*

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[33] Of course, I leave open the possibility that there is some unknown factor that connects all vocal learners. For now, however, I am unaware of any clear explanation of the currently observed pattern of vocal learning.

inherent in the evolutionary history of the lineage. More precisely, by the potentials that have thus-far been limited by aspects of temperament. It should be possible, therefore, to identify what these might be in particular instances, perhaps through an examination of behaviour. For example, Melis et al. (2010) found that chimpanzees who were seemingly unable to solve a co-operative dyadic task could do so if dyad-pairing was manipulated such that individuals with mutually high tolerance were paired together (see also **3.4.4**). The poor performance of chimpanzees, relative to dogs, on tasks of co-operative communication (see chapter three, particularly **3.2.2.3**) stands, then, as something that might be remedied through a change in chimpanzee temperament—exactly the kind of change that appear to underpin the domestic phenotype. Conducting a farm-fox like experiment on chimpanzees would obviously face numerous practical and ethical difficulties. The general point, however, is that experimental manipulations exploring behaviour may have the capacity to identify 'potentials' that could be released by a domestication-like process.

III. Are humans domesticates, or are humans and domesticates both something else?

Much of this thesis, particularly chapters four and five, has been focused on the question of whether it makes sense to think of humans as a domesticated species. The conclusion, based on both the *outcomes* view of domestication (see **4.4**) and a review of some of the various ways in which these outcomes might have come about in humans (see Chapter 5), was that it does indeed make sense to think of humans as domesticated. If accepted, this would allow us to move from the view of domestication illustrated in figure 6.1, to the view illustrated in figure 6.2.

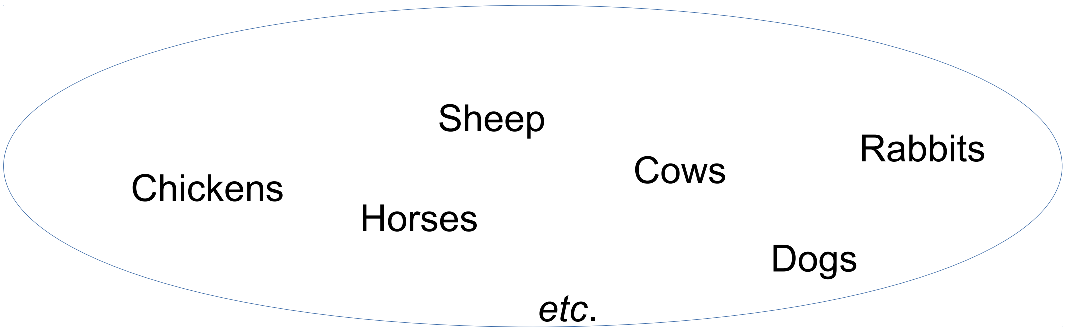

Figure 6.1: Conventional picture of domestication

Figure 6.1 depicts what we might think of as the conventional picture of domestication: Domesticated species are those that are controlled in some way by human beings. This very much accords with what was termed the *conditions* view of domestication in chapter four (see **4.4**).

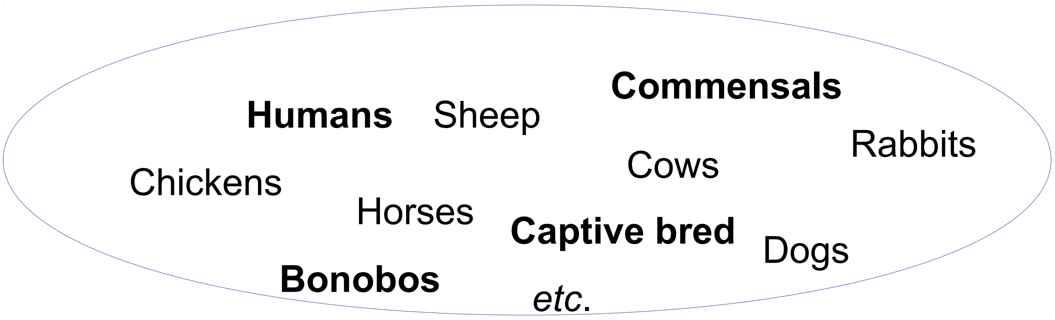

Figure 6.2: Expanded picture of domestication

In contrast, figure 6.2 depicts an expanded picture of domestication, largely based on an outcomes view (see **4.4**) and the shared domestic phenotype (see **4.2**, **4.3** and **5.1**). In addition to the conventional range of domesticated species, this expanded view brings in not only humans, but also commensal species (see **5.1.3),** the 'inadvertent domesticates' associated with captive breeding programs (see **5.1.2**) and bonobos (**5.2.1**). The advantage of this second picture over the first is that it allows us to make sense of a range of similarities that would otherwise have remained unconnected. In addition, this view also allows us to identify some falsifiable criteria by which we can decide whether the description of 'domesticated' should be treated literally in the case of humans.

The first of these criteria concerns the domestic phenotype itself. If it could be shown, for example, that humans do *not* in fact exhibit the typical outcomes of domestication, then that would be grounds to reject the claim that humans are self-domesticated. The second concerns the mechanism by which the domestic phenotype is produced. If the domestic phenotype in humans were the result of an entirely different evolutionary mechanism to that seen in other domesticates, then it would seem perverse to describe humans as domesticated. Important here, for example, would be evidence regarding whether humans have undergone similar changes in their hormonal and other systems that regulate temperament, and whether those changes are linked to the domestic phenotype. Some recent evidence suggests this may be the case (e.g. Cieri et al., 2014), but more is certainly required. Outside of these criteria, the concept of humans as 'self-domesticated' could either be relegated to metaphorical status, or abandoned altogether.

However, the major problem with this way of looking at the issue is that the choice between figure 6.1 and figure 6.2 is fundamentally dependent on the extent to which one accepts the *conditions* or the *outcomes* view of domestication. This is, at base, a *conceptual* choice. Indeed, it is a choice which, at its worst, threatens to descend into an argument about definitions rather than anything substantial about evolution. Once this happens, the whole debate moves out of the empirically testable realm. For example, if you were to reject the outcomes view of domestication—and thus reject the picture of domestication in figure 6.2—it is difficult to see what kind of *empirical* findings might make a difference to your opinion. If the debate is framed as a choice between figure 6.1 and figure 6.2, then it seemingly comes down to whether you are happy to use the same adjective—'domesticated'—in reference to a wider or narrower range of examples.

Quite clearly, however, the substantive question at issue is not about the use of an adjective, but about the evolutionary circumstances in which certain phenotypic outcomes are likely to occur. Keeping this in mind, the arguments presented in this thesis can be reformulated as shown in figure 6.3.

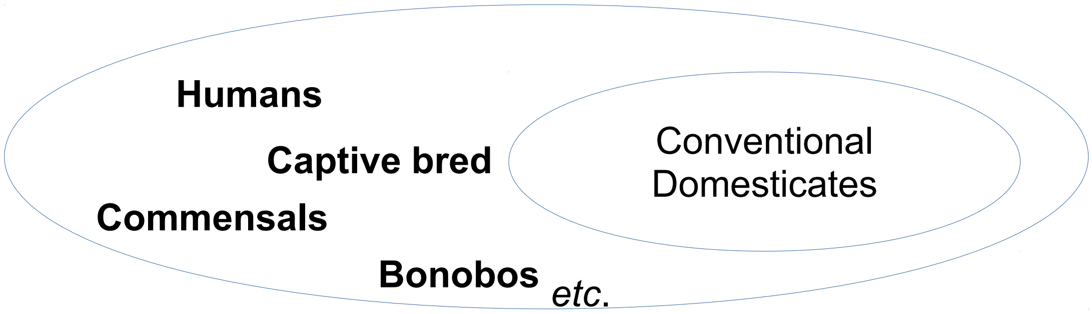

Figure 6.3: Domestication as a subset of a wider phenomenon

In figure 6.3, the range of species conventionally thought of as 'domesticated'—in effect, the whole of figure 6.1—is contained within the area, labelled 'conventional domesticates'. Rather than attempt to expand the usage of the term ‘domesticated’, this way of framing the argument notes the similarities between conventional domesticates and many of the other species discussed in this thesis—humans, bonobos, commensals, and animals in captive breeding programs—and takes that as evidence that all these cases belong to a wider set, of which conventional domesticates are but one major subset[34].

This way of framing the issue also puts us in a much better position to think about how the argument might be empirically tested. In particular, rather than haggling over the use of the term ‘domesticated’, we are now free to ask: *What is it that all these cases have in common that has lead to similar phenotypic outcomes?* With an answer to this question, we are in a position to make testable predictions of the kind found in historical-narrative science[35] (*sensu* Mayr, 1982, 1997). More specifically, we would be in a position to predict that *if and when we find other examples that share those same evolutionary conditions, we should also see similar phenotypic outcomes*.

What, then, are the evolutionary conditions shared by all those species in figure 6.3? As discussed above, one thing they likely share is the breakdown of previously canalized systems, particularly those relating to temperament. In some instances, this relates to selection acting directly on temperament itself; in many others,

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[34] I would very much like to thank Terrence Deacon for the discussion that finally crystallised this way of framing the topic.

[35] These are, in evolutionary terms, predictions about the *kinds of things we will find*, given our understanding of natural history and the processes by which it has occurred. One vivid example of this is the oft-quoted riposte, usually attributed to J. B. S. Haldane, that the discovery of a fossilised rabbit in Precambrian rock would shake his belief in, or even falsify, the theory of evolution by natural selection. Another famous example is Darwin’s (and, later, Alfred Russel Wallace’s) prediction—upon finding a Madagascan orchid with a nectary nearly a foot in length—that a pollinating moth with a similarly long tongue would also be found. More generally, and this is the logic being employed in the current instance, we can predict that organisms faced with similar conditions—that is, with similar 'design problems' (Dennett, 1995)—will likely converge on similar solutions (see also **2.1**).

however, the key conditions seems to relate to the effects of relaxed selection in a buffered environment. One point to note, however, is that many of the relaxation-degeneration examples in 6.3 show no sign of direct selection against aggression. In contrast, however, even the most clear-cut example of selection against aggression, the farm-fox experiment, shows signs that buffering also played a role (see **3.4.6**). Indeed, in the case of the bonobo, it seems likely that the (natural) selection against aggression was itself enabled by the fact that the geography of their feeding ecology buffered them, relative to chimpanzees, from the need to engage in aggressive and competitive social behaviour (**5.2.2.2**). These considerations suggest that buffering is the more common and, possibly the more fundamental, of the two mechanisms discussed above, and should likely be considered what, at base, is shared by all those in figure 6.3.

Given this analysis, we can predict that there should be many other examples of the same phenomenon. Other examples, that is, of species exhibiting a similar set of phenotypic changes, following evolution occurring in similarly buffered environments. And, indeed, other examples can be found. Palombo et al. 2008 report palaeontological studies of phenotypic change in a number of now-extinct ruminant species from the Mediterranean islands. Although these changes are linked to isolation on an island and not to domestication, the authors explicitly invoke the comparison with brain-size reduction under domestication because, they argue, the selective environment in both cases was fundamentally similar: including the near absence of predators and much reduced inter-species competition (Köhler & Moyà-Solà, 2004), all of which typify the environment of domestication (**4.5.1.2**). Once the arguments of this thesis are reformulated as shown in figure 6.3, it becomes clear that many further examples should also be found.

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