9-2015

Olfaction As The Paradigm For Perceptual Philosophy

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Recommended Citation

Keller, Andreas, "Olfaction As The Paradigm For Perceptual Philosophy" (2015). *CUNY Academic Works.*
https://academicworks.cuny.edu/gc_etds/1004

OLFACTION AS THE PARADIGM FOR PERCEPTUAL PHILOSOPHY

By

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A dissertation submitted to the Graduate Faculty in Philosophy in partial fulfillment of the
requirements for the degree of Doctor of Philosophy, The City University of New York
2015

This manuscript has been read and accepted for the Graduate Faculty in Philosophy in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

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by

Andreas Keller

Advisor: Professor Jesse Prinz

Plato wrote that smell is of a "half-formed nature" and that not much can be said about it, and Kant identified smell as the "most ungrateful" and "most dispensable" of the senses. Because contemporary philosophers share this distaste for smell perception, olfaction is often dismissed or ignored in philosophical accounts of perception. Instead, contemporary philosophy of perception is based almost exclusively on visual perception. The goal of this dissertation is to show that this focus on a single modality distorts our understanding of what perception is.

I am not the first to realize the potential of opening up perceptual philosophy to the non-visual modalities. Bill Lycan asked "how the philosophy of perception would be different if smell had been taken as a paradigm rather than vision." (Lycan 2000) (page 273). In this dissertation, I will try to answer this question. My analysis will show that philosophy of perception would be *very* different, were it based on olfaction. Many of the most basic concepts of philosophy of perception are based on peculiarities of visual perception that do not generalize to other modalities.

Acknowledgments

I would like to thank the many people who helped me in many ways during the planning, writing, and revising of this manuscript. Most important for the success of this project was the love, support, and encouragement from Dara Mao. Without her help, this project would not have been possible.

Many thanks also to my advisor Jesse Prinz for his guidance and support. David Rosenthal and Peter Godfrey-Smith also provided feedback and discussion that helped me improve earlier versions of this work. My prospectus and dissertation committees were rounded out by Massimo Pigliucci, Barbara Gail Montero, and Stephen Neale, who guided me through the process of finishing this work.

In the early stages of my interest in perceptual philosophy, I had the good fortune to be welcomed at the meetings of Thomas Metzinger's Mind group, which deepened my interest in the topics discussed in this dissertation and gave me the chance for many inspiring interactions. In many ways, my exploration of philosophical issues has been made possible through a Branco Weiss Fellowship from the Society in Science Foundation. I am grateful to them, as am I to Leslie Vosshall, in whose laboratory at Rockefeller University I worked throughout the writing of this thesis. I am also thankful to my MA thesis adviser Nicolas de Warren and to James Dodd at the New School for Social Research for teaching me about Husserl.

I had the chance to present parts of this work on many occasions, including several times at meetings of Thomas Metzinger's Mind group. I also presented parts of this work at the18th

Annual Meeting of the Association for the Scientific Study of Consciousness in Brisbane (Australia) in 2014, at the 10th Biennial Toward a Science of Consciousness Conference in Tucson (Arizone) in 2012, and as a panelist at the Workshop for Perceptual Learning and Perceptual Recognition at the University of Toronto (Canada) in 2012. At each of these occasions, the feedback and discussion has been interesting and valuable. I also have previously published some of the work presented here in chapter 1 (Quality-space theory in olfaction. *Frontiers in Psychology* 5:1; Keller A. (2014)). I want to thank the co-authors, editors, and reviewers involved with this publications for helping me shape my thoughts on the topics presented there.

My friends and colleagues Jessica Keiser, Svetlana Novikova, Ann-Sophie Barwich, and Benjamin Young have read parts of earlier versions of this manuscript and helped me to improve it. I am very thankful for that and hope to get a chance to return the favor some time.

Table of Contents

List of figures

Introduction

The main difference between this work and other works on perceptual philosophy is the focus on olfaction (Figure 1). The main advantage of olfaction as the paradigm for perceptual philosophy is that, compared with vision or audition, olfaction is a computational and anatomical simple modality. In addition to the focus on smells, the account of perception presented in this dissertation also differs from most other approaches in its appreciation of the fact that perception is an evolved mechanism. As such, we can only understand perception within an evolutionary framework. The questions addressed in this dissertation are the questions of perceptual philosophy. The answers to these questions that I will present combine insights and results from a variety of disciplines other than philosophy. Most of the interdisciplinary work surveyed here will involve empirical results from neuroscience, cognitive science, and psychology.

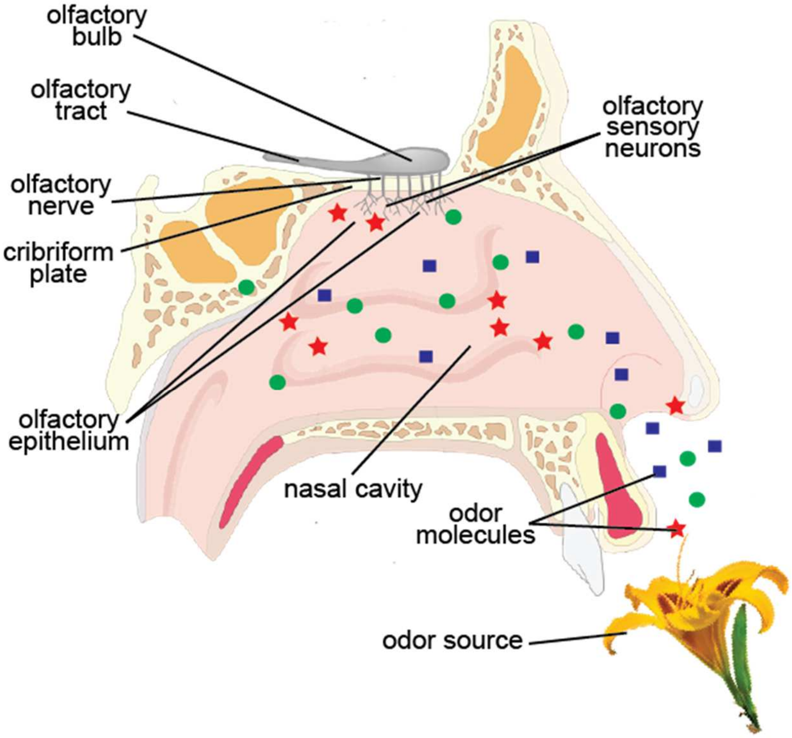

Figure 1: The olfactory system. Odor sources give off a mix of different types of odor molecules (represented in this figure by blue rectangles, red stars, and green circles). During sniffing, the odor molecules enter the nasal cavity. At the top of the nasal cavity is the olfactory epithelium, which contains the odor-sensitive endings of the olfactory sensory neurons. The olfactory sensory neurons form the olfactory nerve, which connects the nasal cavity with the brain through small holes in the skull (in the cribriform plate). In the brain, the olfactory sensory neurons terminate in the olfactory bulb, the first processing center for odor information. The olfactory bulb is connected to other brain regions through the olfactory tract. (modified from original work by The Emirr (diagram of nasal cavity) and Takkk (flower) (in the public domain under the Creative Commons license (CC BY 3.0))

This dissertation is divided into three parts: "Perceptual qualities", "Percepts", and "Cognitive processes". In the first part, I will discuss topics related to perceptual qualities[1]. Philosophically important issues related to perceptual qualities that will be addressed are the nature of perceptual qualities, modality-individuation, and the possibility of third-person access to perceptual qualities. I will discuss perceptual qualities as they are revealed by behavioral or psychophysical experiments in which different behaviors are shown in response to different stimuli. In the first chapter, I will suggest a strategy to arrange the perceptual qualities perceived by an individual perceiver in a perceptual space that reflects the similarity relations between the perceptual qualities. In the second chapter, the problem of comparing perceptual qualities between different perceivers is addressed. I will suggest that it is possible to compare perceptual qualities perceived by two different perceiver by aligning their perceptual spaces. Aligning two perceptual spaces is however only possible under certain conditions.

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[1] A variety of terms has been used for what I will call "perceptual qualities". Daniel Dennett lists "raw feels", "sensa", "phenomenal qualities", "intrinsic properties of conscious experiences", "qualitative content of mental states", and "qualia" Dennett, D. C. (1991). Consciousness Explained. Boston, Little, Brown and Company. (page 372). Each term tacitly imports assumptions about the phenomena that is labeled. I mean by "perceptual qualities" the mental qualities which are different in cases in which two colors, smells, tastes, and so on can be behaviorally discriminated.

Typically, perception is much more complex than a series of discriminable perceptual qualities. In the second part, these complexities will be addressed. Perceptual qualities can be combined in time and space, which is the topic of chapter 3. I will argue that olfactory perception has no spatial structure and that its temporal structure is impoverished compared with other modalities. In the modalities in which perception has a rich spatial and temporal structure, perception is often thought of as the perception of objects that are spatially and temporally extended and bounded. In chapter 4, I will apply common notions of perceptual objects to olfaction and show that odor perception is not the perception of objects. Chapter 5, which is a bit of a digression, will address the question of the evolutionary function of perception. I will argue that it is the function of perception to guide behaviors and defend this idea against alternative proposals. The general goal of the second part is to demonstrate that many of the complexities that are taken to be an integral part of perception in other modalities are absent in olfactory perception. These complexities therefore play no role in an account of perception that is based on olfaction.

Perception and non-perceptual cognitive processes are not always clearly separated. Perceptual systems coevolved with cognitive systems that process perceptual information and motor systems that execute an organism's behavior. Perception depends on these systems for being useful for the organism. Perception itself has no adaptive advantages unless it results in a stimulus-dependent modification of behavior[2]. In part III, I will address the tight connection

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[2] As an illustration of the uselessness of perception for perception's sake, consider sea squirts. Many species of sea squirts have a free-swimming larval form and a sedentary adult form. During the development from the free-swimming to the adult form, both the muscular system and the nervous system degenerate. The function of the brain is to guide behaviors and in the

between perceptual systems and non-perceptual cognitive systems. A review of the connections between olfaction and cognitive systems in chapter 6 will show that the connections between perceptual and cognitive processes are modality-dependent. The olfactory system evolved to be closely connected to emotional systems, but not to language systems. Other perceptual modalities are more closely connected to language than to emotion. In chapter 7, I will discuss the structure of the mind more generally. I reject common approaches to describing the structure of the mind and instead suggest a description of the mind as overlapping sets of functionally coupled networks.

Throughout this dissertation, perception is discussed with respect to its ability to guide behaviors and to make information available to cognitive processes. In many instances, the perception is conscious. However, the conclusions drawn throughout this dissertation are supposed to hold for conscious and non-conscious instances of perception (except when noted otherwise). Guiding behaviors and making information available to cognitive processes are functions that do not necessarily require consciousness. My goal is to investigate general features of perception that are independent of consciousness.

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absence of behavioral options, there is no need for a brain. Sensing a predator is only adaptive for an organism that has behavioral strategies for predator avoidance.

Part I: Perceptual qualities

The basic building blocks of perception are perceptual qualities with no spatial or temporal structure, like the redness of a tomato or the characteristic smell of a rose[3]. These perceptual qualities are mental qualities that, in humans, are usually considered to be conscious. The redness of the rose is experienced by the perceiver. Although this is the most familiar way in which we encounter them, perceptual qualities are not necessarily consciously experienced (Rosenthal 2010; Young, Keller et al. 2014; Rosenthal in press)). The fact that perceptual qualities can be either conscious or non-conscious is best illustrated by cases in which behavioral decisions are made based on perceptual qualities in the absence of consciousness. For example, at very low odor concentrations people often report verbally that they cannot detect any odor, although they discriminate stimuli successfully when they are asked to make a choice (Sobel, Prabhakaran et al. 1999). At slightly higher concentrations, when the sensory information is processed consciously, two odors are discriminated based on differences in their perceptual qualities. It is parsimonious to assume that the same two odors at lower concentrations are also discriminated based on differences in their perceptual qualities, even though the information is not consciously processed. Denying the existence of non-conscious perceptual qualities would require two theories of perception. One theory would have to explain how we can consciously distinguish a green object from a red object based on the different perceptual qualities associated with the objects. The second theory would have to explain how we execute stimulus-dependent behaviors in the absence of conscious processes. The second theory would have to be different from the first theory because if there are no non-conscious perceptual qualities, then the

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[3] As will be discussed in part II, these perceptual qualities often occur in complicated spatial and temporal arrangements. However, for the treatment in the first part, I will abstract away from spatial and temporal structures.

differential responses to different stimuli in the absence of consciousness cannot be based on perceptual qualities.

To avoid the need for two different theories of perception depending on whether the perception is conscious or not, one can also deny the existence of non-conscious perception. In olfaction, evidence for non-conscious perception comes from experiments that have shown that odors can have specific behavioral effects in the absence of conscious processing of olfactory information. For example, sniffs are shorter and shallower when an unpleasant odor is encountered than when a pleasant odor is encountered. This effect is independent of conscious experience (for a detailed treatment of this topic in olfaction, see (Young 2014)). Influences of unconscious perceptual qualities on behaviors are not peculiar to olfactory perception; they are also found in other modalities. In vision, masked priming effects, for example, depend on the features of the masked (e.g. not consciously perceived) stimulus (for reviews, see (Cruse, Kälberer et al. 2007; Hallett 2007). Evidence for non-conscious perception has accumulated over the last decade. However, the complete absence of consciousness is difficult to prove and some researchers are not convinced that non-conscious perception exists in humans
(Phillips). The account of perceptual qualities presented in part I does not depend on the existence of non-conscious perception and non-conscious perceptual qualities in humans. Instead, whether perception is conscious or not is irrelevant for this account because it is based on the outcome of behavioral or psychophysical experiments alone. The results of this analysis apply to perception in humans, birds, bacteria, robots, or any other system that shows differential responses to different physical stimuli.

Perceptual qualities are the building blocks of perception and all instances of perception involve perceptual qualities. All visual perception, for example, involves colors, although sometimes they are achromatic colors (black, white, and all the shades of grey). Similarly, all olfactory perception involves smells. There are myriads of colors and tones and smells. Attempts to bring order to the diversity of perceptual qualities go back to the earliest days of philosophy. The most promising approach has been to arrange perceptual qualities relationally according to their similarities in a multi-dimensional mathematical space (Goodman 1951; Clark 1993; Matthen 2005; Rosenthal 2014; Young, Keller et al. 2014). Using this approach, researchers have arranged all colors in a three-dimensional perceptual space (Figure 2), with the dimensions hue, brightness, and saturation. All tones have been arranged in a two-dimensional space according to their pitch and loudness[4].

Arranging things depending on their relations has been a successful approach to order biological diversity outside of perceptual research. The most prominent example is the arrangement of all living things based on their evolutionary relationships in a phylogenetic tree. One of the reasons

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[4] I am ignoring timbre in the context of perceptual spaces. Timbre is the quality of sound that allows us to discriminate between the sound made by a piano and by a guitar when they have the same pitch and loudness. Timbre has been called, "...the psychoacoustician's multidimensional waste-basket category for everything that cannot be labeled pitch or loudness." McAdams, S. and A. Bregman (1979). "Hearing musical streams." Computer Music Journal **3**(4): 26-43. (page 34). The rationale for ignoring timbre is that it is determined by temporal characters of the sound, like its onset and time envelope. The perceptual spaces discussed in the first part of this dissertation are meant to be arrangements of perceptual qualities, abstracted away from their temporal and spatial structure. Abstracting away from temporal structure is more difficult in audition than in other modalities. Pitch, which is usually included as a dimension of tone spaces, is determined by the frequency of a sound and therefore also dependent on the sound's temporal features. To include pitch but exclude temporal features that contribute to timbre is admittedly arbitrary. I do not think that expanding the tone space into a sound space by including the features that contribute to timbre would have important theoretical consequences beyond increasing complexity. However, this question may be worthwhile more consideration.

the phylogenetic tree is so important for evolutionary biology is that it includes *all* living things and the relations between them. The perceptual space that I suggest similarly includes *all* perceptual qualities, regardless of their modality. This is the philosophically most important difference between the approach presented here and previous approaches which it is based on (Goodman 1951; Clark 1993; Matthen 2005; Rosenthal 2014; Young, Keller et al. 2014). Previous approaches usually focused on constructing perceptual spaces for individual modalities (color space, smell space, etc.). It is my hope that a perceptual quality space that includes all perceptual qualities is an interesting alternative. In the first chapter, I will outline an approach to construct such a perceptual quality space that individuates perceptual qualities by arranging them according to the similarity relations between them. Each perceptual quality is individuated by its unique position in the perceptual quality space. I will suggest using triadic comparisons to determine relative similarity between three stimuli to arrange the stimuli in a multidimensional space. I will explain and justify this method and then speculate about the features that the resulting perceptual quality space can be expected to have.

The obvious disanalogy between the phylogenetic tree and the perceptual quality space is that there is only one phylogenetic tree. On the other hand, there are many different perceptual quality spaces. Individuals with red-green-colorblindness have a different perceptual space from normal-sighted individuals. Furthermore, an individual's perceptual quality space can change depending on experiences and changes or deterioration of the sensory systems. In the second chapter, I will first discuss this diversity of perceptual quality spaces to set up the problem of comparing perceptual qualities between different perceivers. I will then show that, under certain circumstances, individuating perceptual qualities without reference to subjective experience through quality spaces makes it possible to compare perceptual qualities that are perceived by different perceivers.

Chapter 1: Perceptual quality space

In this chapter, I will focus on how to construct the perceptual quality space for a given individual at a given point in time. I will not concern myself with questions about how stable this space is over time or how similar one individual's space is to another's. These topics will be addressed in chapter 2. In chapter 1, I will only attempt to develop and defend a strategy that arranges perceptual qualities in a way that reliably reflects the similarities between how they are perceived by an individual perceiver. Traditionally, the problem of putting order to the bewildering diversity of perceptual qualities has been addressed in two steps. In a first step, each perceptual quality was assigned to a sensory modality. In the second step, the perceptual qualities of each modality were arranged in a multidimensional space according to the similarities between the perceptual qualities. The result of this two-step process is a list of modalities and separate perceptual quality spaces for each modality. What is missing from this result is an explanation of similarities between stimuli in different modalities. It can be argued that there are no stable, meaningful similarity relations between tones, colors, tastes, and smells. However, empirical results that suggest that perceived similarities between perceptual qualities do not respect traditional modality boundaries. For example sugar, which is an odorless tastant, is consistently experienced to be more similar to the tasteless odorant vanillin than to salt, another odorless tastant (Rankin and Marks 2000). If all we have is a list of modalities and the structure of the perceptual quality spaces for each of the modalities, then we cannot account for this fact. To address this problem, I propose one-step strategy of arranging all perceptual qualities regardless of their modality in a multidimensional space based on their similarity relations. The resulting space will be exhaustive and relational "all the way down".

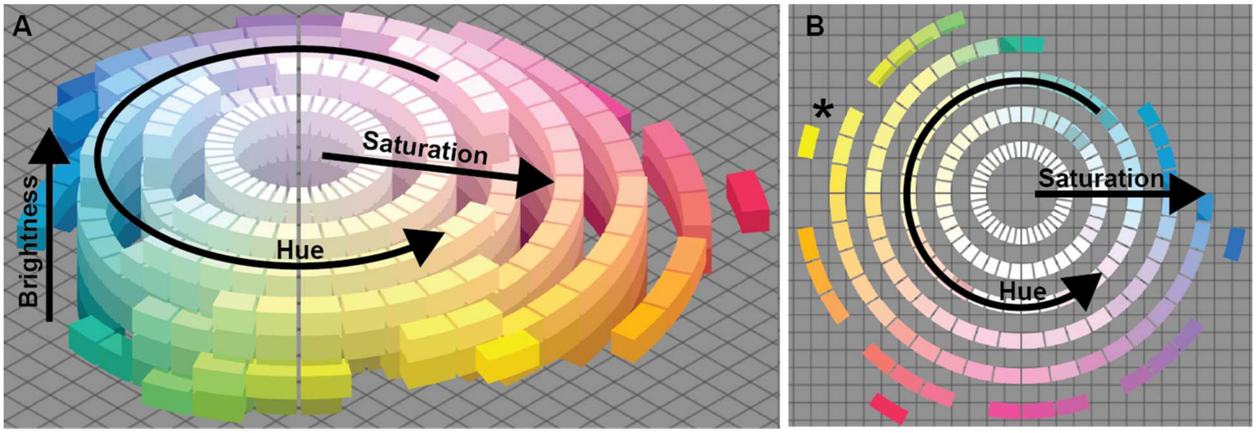

Figure 2: The perceptual color quality space. (A) The perceptual quality space is three-dimensional and asymmetric. By convention, the hue dimension is represented as a closed circle. The vertical dimension is brightness and saturation increases from the inside of the circle formed by the hue dimension. (B) A section through the perceptual color quality space at a given brightness. The asterisk marks the position of a color that does not exist in normal perception. A perceptual quality with this combination of hue, brightness, and saturation is not normally perceived by humans. (modified from original work by SharkD (in the public domain under the Creative Commons Attribution-Share Alike license (CC BY-SA 3.0))

1.1. Constructing an exhaustive perceptual quality space

An exhaustive perceptual quality space is a space in which all smells, colors, tones, tastes, and other perceptual qualities are arranged according to the similarity relations between them. Perceptual quality spaces consist of multi-dimensional coordinate systems in which different locations represent different perceptual qualities. Partial perceptual quality spaces for tones and colors (Figure 2) have already been established. As far as these partial spaces reflect similarity relations between the perceptual qualities of a modality, they will become part of the exhaustive perceptual space. A possible way to arrive at an exhaustive perceptual space is to first individuate the modalities, then construct perceptual spaces for each modality, and then arrange these perceptual spaces in a modality space. A modality space is a multidimensional space in which modalities are arranged according to the similarities between them (Keeley 2002; Gray

2013; Macpherson 2015). I think that this strategy does not address the problem I am interested in; the resulting modality space of perceptual spaces will not explain why sugar is more similar to vanillin than to salt (Rankin and Marks 2000). I therefore propose a one-step procedure of arranging all perceptual qualities in an exhaustive perceptual space based on psychophysical measures of similarity.

Determining similarity between perceptual qualities

It is difficult to overestimate the importance of similarity judgments for an organism's survival. Similarity judgments play a much more pronounced role in perception-based behaviors than discrimination. Discrimination is not very useful because we almost never encounter indiscriminable things. An apple can perceptually be discriminated from all (or most) other apples perceptually. It can also be discriminated from all bananas and all other things in the world. The capacity to discriminate a large, ripe, intact apple from another large, ripe, intact apple is not a useful evolutionary adaptation. What is useful is to be able to judge that one large, ripe, intact apple is similar to another large, ripe, intact apple. This allows us to respond similarly to things that are perceived similarly. That we are able to make very fine discriminations is a consequence of a perceptual system that evolved to judge similarities. As Quine wrote, "surely there is nothing more basic to thought and language than our sense of similarity; our sorting of things into kinds" (Quine 1970).

Experimentally, perceived similarities can be revealed in different ways (for a detailed discussion of the advantages and disadvantages of different strategies, see (Wise, Olsson et al. 2000)). Many of these experiments can be used in humans as well as in animals, and often they produce similar results (Chen and Gerber 2014). A reliable psychophysical method for determining similarity relations between stimuli are triadic comparisons. In triadic comparisons, three stimuli are presented to subjects who are instructed to pick the two stimuli that are the most similar (MacRae, Howgate et al. 1990; MacRae, Rawcliffe et al. 1992). Other methods for determining perceived similarities between stimuli include direct ratings of the similarity of two odors, and measuring similarity between verbal descriptors that are applied to odors (Wise, Olsson et al. 2000). Each of these methods has advantages and disadvantages and using different psychophysical methods to determine stimulus similarity will undoubtedly lead to slightly differently structured perceptual spaces. However, this dependence on the procedure used for its construction does not diminish the explanatory power of the perceptual quality space. This can be illustrated by comparison to the phylogenetic trees. A phylogenetic tree can be build based on skeletal anatomy, on genomic sequences, or on a combination of both. The resulting trees will be different. Mostly the differences will be small, but sometimes they will be consequential. The extent evidence is unlikely to be sufficient to resolve all uncertainties about shifts in populations that occurred hundreds of millions of years ago. There is a phylogenetic tree that accurately reflects all relationships between all living things; however, it is likely that science will never be able to represent all aspects of it in a phylogenetic tree with great certainty. This uncertainty does not diminish the importance of phylogenetic trees for biology. Similarly, there are, for a given perceiver at a given time, true similarity relations between all perceptual qualities. Different psychophysical methods or combinations of these methods will result in slight differences in how these relations are represented in a perceptual quality space. However, the importance of the perceptual quality space is not undermined by ambiguities due to different methods of constructing it.

Different methods can be used to establish similarity relations between stimuli. Using triadic comparisons has several advantages over other methods. One advantage of this method is that it requires only ordinal judgments. The similarity between stimuli does not have to be quantified, which is a cognitively very demanding task. Another advantage is that, as forced-choice tests, triadic comparisons are independent of conscious perception of similarities. Subjects that report that all three stimuli are the same may still perform non-randomly when asked to pick the two that are the most similar. A further advantage is that triadic comparisons, or equivalent stimulus generalization experiments, can be performed by all species and in all modalities. Presenting three stimuli in a row and asking subjects to group them according to similarity is possible in all modalities. Other methods to gain information about the similarity relations between stimuli are based on presenting two stimuli, for example colors, simultaneously. These types of experiments are only possible for modalities in which stimuli can be perceived simultaneously.

A complication for all attempts to constructing a perceptual quality space is the existence of perceptual qualities that are not directly associated with physical stimuli. There are, for example, "impossible" perceptual color qualities that can be only produced by combining the perception of the afterimage of one color with the perception of another color. If one looks at a pale blue-green surface and immediately afterwards at a maximally saturated orange surface, for example, the combination of the orange afterimage and the orange perception results in the perception of a hyperbolic orange that is more ostentatiously orange than every orange normally seen (Churchland 2005). Producing such color qualities poses a practical problem for constructing the perceptual space. Instead of simply presenting the stimulus, the whole sequence of stimuli that reliably leads to the perceptual quality has to be presented. However, as long as the perceptual qualities are predictably inducible, the problem is only practical. If some perceptual qualities are *only* perceived in hallucinations, and this perception is independent of a stimulus and impossible to predict, then these qualities cannot be captured by the method I propose.

Relation between similarity measures and discrimination tasks

Similarity-based psychophysics are not usually used to construct perceptual spaces. More commonly, perceptual quality spaces are constructed using just-noticeable-differences between stimuli (Goodman 1951; Clark 1993; Matthen 2005; Rosenthal 2014; Young, Keller et al. 2014). The just noticeable difference between two stimuli can be determined by forced-choice-discrimination tasks. The experiments start with two discriminable stimuli. The subject is asked to discriminate the stimuli and when they do so reliably, the physical properties of one of the two stimuli are gradually made more similar to the physical properties of the other stimulus. When the point is reached at which they can no longer be discriminated, the just-noticeable-difference between the two stimuli has been discovered. If the two stimuli cannot be made to be indiscriminable, then they belong to different modalities (Rosenthal 2014). The just-noticeable-difference-method results in a color space, a smell space, and several other quality spaces. It does not reveal anything about the relations between these spaces.

The results of forced-choice discrimination tasks are the subset of the results of triadic comparisons. When the subject in a triadic comparison task is presented with three stimuli, two of which are identical, then the grouping of the stimuli depends on whether the subject can discriminate the two identical stimuli from the third stimulus. When the difference between the stimulus that is presented in duplicate and the third stimulus is just noticeable, the subject will rate the two identical stimuli as being the most similar pair. When the third stimulus is then altered so that it can no longer be discriminated from the two identical stimuli, then the responses will be random, with each pair being identified as the most similar pair with equal likelihood. In this way, triadic comparisons provide information about just-noticeable-differences.

Triadic comparison delivers the same information that forced-choice discrimination tasks deliver. However, in addition to the information whether two stimuli can be discriminated, it delivers information about the relative perceptual similarity of discriminable pairs of stimuli. This information is necessary to arrange all perceptual qualities, even those that are associated with stimuli that cannot be altered so that they cannot be discriminated. This information is necessary to construct an exhaustive perceptual quality space and account for similarity relations between perceptual qualities in different modalities.

Despite the additional information that can be obtain through similarity-based psychophysics, psychophysicists are usually more comfortable with discrimination tasks than with similarity-based psychophysics. One reason why discrimination tasks are often preferred to similarity judgments is that discrimination tasks are the paradigmatic example of psychological measures of performance that probe human abilities. Similarity judgments on the other hand, are often considered to be based on the report of mental content rather than on performance (Wise, Olsson et al. 2000). However, when triadic comparisons are used to determine similarity relations, this is not the case. There are objectively correct facts about perceptual similarities and similarity tasks are a test of the ability to identify them. The length of three-inch nail is more similar to the length of a four-inch nail than to the length of an eight-inch nail. Similarly, of the distances between three perceptual qualities in a perceptual space, one distance is in most cases shorter than the other two distances. To deny that there are correct answers to triadic comparisons is to deny that the perceptual qualities involved in the triadic comparison can be arranged according to similarity in a perceptual quality space.

I said that, in triadic comparisons *in most cases* one of three distances between the three perceptual qualities is shorter than the other two. The only situation in which no distance is shorter that the other two is when all three distances are the same. They can all be zero, in which case the three stimuli are indiscriminable, or all three distances can have the same non-zero length. In this case, the stimuli can be discriminated, but the similarities between the stimuli are indiscriminable. This will most often occur when the three stimuli are all very dissimilar. With increasing dissimilarity, differences in similarity become irrelevant. The function of similarity judgments is to cluster, generalize, or categorize things, and when things are so dissimilar that they clearly are not in the same cluster, it is not necessary to be capable of comparing similarities. This failure to perform in triadic comparisons of three very different stimuli is not a bug, but a feature. Whether people can or cannot compare the similarities between stimuli has to be found out experimentally for individual cases. I predict that a triadic comparison between the color red, cold temperature, and bitter taste will not reveal anything about the similarity relations of these perceptual qualities. If this is the case, then the data from this triadic comparison will not contribute to the construction of the perceptual quality space. However, I may be wrong about it and people group cold temperature with bitter taste. Then this data-point can be used in the construction of the perceptual quality space.

Another common objection to using similarity judgments in psychophysics is that similarity can be judged along different criteria (Wise, Olsson et al. 2000). Imagine for example a triadic comparison of dark blue, light blue, and dark green. Some subjects may use darkness as a criterion whereas others may use hue. Imagine, as suggested by Matthen (Matthen 2005) (page 131), that you are asked whether the US, Russia, or China is more similar to Canada. Your answer will depend on the context in which the question is asked, and depending on the context, you will privilege different criteria (climate, political system, size, population, etc.) in answering. However, there is an important methodological difference between the cases of judging similarity between countries and between perceptual qualities. Unlike for countries, for perceptual qualities there are always comparisons available in which the perceptual qualities that are compared differ in only one criterion. Perceptual color qualities can be matched for brightness and saturation and then the similarity between them will be judged only according to hue. This is not the case for judging similarities between countries. It is not possible to compare two countries that differ in their population while they have the same climate, political system, and size. That similarities can be judged along different criteria is therefore not as big a problem for assessing similarities between perceptual qualities than it is for assessing similarities between countries. It merely is a practical problem in that it requires a very large number of comparisons to tease apart all the different criteria along which perceptual qualities can differ.

A further objection against similarity-based groupings is that similarity judgments are not stable over time. Instead, similarity judgments can be altered by experiences. In some cases, for example, odors that are presented in a mixture with another odor can take on some qualities of the odor they were mixed with. An odor smells different depending on what other odors it has been experienced with previously (Stevenson 2001). Presumably, this change in perceived quality results in changes in similarity judgments of the odors involved. It is certainly true that similarity-judgments depend to some degree on experience. However, these experience-dependent effects on similarity judgments are minute compared to the effects of innate standards of similarity[5]. Although similarity judgments for very dissimilar odors change slightly depending on what other odors they were paired with, it seems unlikely that one could get a subject to rate fir oil as smelling more like fish than like pine oil by repeatedly exposing the subject to a mix of fir oil and fish. There are strong innate mechanisms of similarity perception that are unchanging. Furthermore, experience-dependence of performance is common in all types of psychophysical testing. The capacity to discriminate odors, for example, is also affected by experience (Rabin 1988; Jehl, Royet et al. 1995).

In summary, for constructing a perceptual space that reflects similarity relations, similarity-based methods are the obvious choice. However, psychophysical similarity judgments can be problematic because they are cognitively more demanding than discrimination tasks. Humans are, for example, not good at comparing similarities between very dissimilar stimuli. For this reason, discrimination tasks are more stable and reliable and they have been the method of choice for constructing perceptual quality spaces. My goal is to construct an exhaustive perceptual quality space that includes the perceptual qualities of all modalities arranged by

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[5] As Quine pointed out, if all stimuli would be equally alike and equally different, we could never acquire generalized behavioral responses Quine, W. V. (1970). Natural kinds. Essays in Honor of Carl G. Hempel. N. Rescher. Dordrecht, D. Reidel Publishing Company., and all our behavioral responses are generalized responses that will be elicited by a group of similar yet discriminable stimuli.

similarity relations between them. I do not know how this could be accomplished using discrimination tasks. I therefore propose to give up the methodological advantages of discrimination tasks to gain the possibility of constructing a perceptual space that arranges perceptual qualities regardless of their modality according to their similarities. One can disagree whether this is a good trade. If there were no interesting similarity relations between different modalities, one would not gain anything from such a move. In the next section, I will speculate how the exhaustive perceptual space would look, in an attempt to show that interesting things about the relations between perceptual qualities in different modalities could be learned from such a space.

1.2. Features of the perceptual quality space

Using triadic comparisons to construct an exhaustive perceptual space is an ambitious empirical project. It would take a large number of triadic comparisons to reveal the detailed structure of this space. However, we already know enough about perceptual qualities and their similarity relations that one can speculate about the most important features of the perceptual quality space. In this section, I will speculate about the number of dimensions of the exhaustive perceptual space and about what the dimensions represent. I will then introduce a method of individuating modalities based on the distribution of perceptual qualities in the exhaustive perceptual quality space.

Dimensionality of the perceptual quality space

An important question about the perceptual space is how many dimensions it has. The number of dimensions is a direct result of the similarity relations (Clark 1993) (pages 84-89). For every set of similarity relations, the lowest-dimensional space in which all of them can be represented can be found. Figure 3 illustrates how arranging the same number of stimuli by similarity can require one, two, or three dimensions, based on the similarity relations between them.

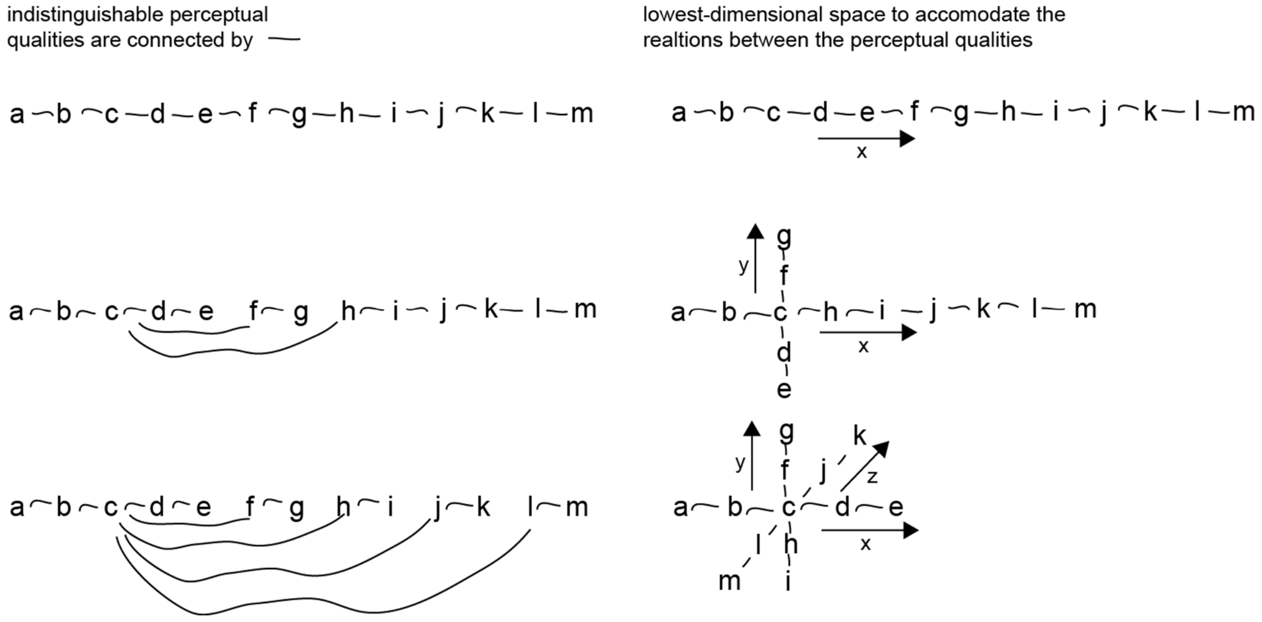

Figure 3: Determining the number of dimensions of a perceptual space. Depending on the experimentally determined relations between perceptual qualities on the left, one (top), two (middle), or three (bottom) dimensions are required to arrange them in perceptual space (modified after (Clark 1993) (pages 84 to 89).

To illustrate how the dimensionality of the perceptual space is revealed by the similarity relations between perceptual qualities, consider sets of qualities that are all equally similar to one another. Consider three perceptual qualities: A, B, and C. If A is as similar to B as it is to C and as B is to C, then these three qualities cannot be arranged in a one-dimensional space in a way that reflects all three similarity relations. The simplest way to arrange three equidistant perceptual qualities in space is to place them in the corners of an equilateral triangle. Triangles are two-dimensional structures and the existence of three equidistant perceptual qualities shows that the perceptual space they belong to has to be at least two-dimensional. The simplest way to arrange four equidistant perceptual qualities is to place them into the four vertices of a regular tetrahedron, which is the only possible arrangement of four equidistant points in three-dimensional space. This means that a perceptual quality space that contains four equidistant perceptual qualities has to be at least three-dimensional.

We do not know yet how many dimensions are required to accommodate all perceptual qualities. However, partial quality spaces in which perceptual qualities from a single modality are arranged have been constructed. These quality spaces illustrate the explanatory power of this approach by arranging large numbers of perceptual qualities in low-dimensional spaces. The millions of colors can be arranged in a space that has three dimensions (hue, saturation, and brightness) (Hardin 1988; Hilbert and Kalderon 2000). The approximately 340,000 tones can be arranged in a two-dimensional space (loudness and pitch) (Stevens and Davis 1938). Temperature space and pressure space presumably only have a single dimension. There are many more smells than colors and tones (Bushdid, Magnasco et al. 2014). Accordingly, no smell space has yet been constructed. However, it has been speculated that an olfactory perceptual space would have many more dimensions than the quality spaces that we know now (Auffarth 2013).

Having an X-dimensional perceptual quality space does not mean that each perceptual quality in the space can only be fully described by X dimensions. It is possible that some perceptual qualities have zero values for many of the dimensions. Just because an X-dimensional space is required to accommodate all perceptual qualities does not mean that the X-dimensional space is required to accommodate each perceptual quality (Figure 4). Greys are colors that differ only in their brightness. However, although the greys could be arranged in a one-dimensional quality space, they are commonly included in the three-dimensional space that can accommodate also those colors that have hue and saturation. Let us assume that the exhaustive perceptual space has ten dimensions. This does not mean that color perceptual qualities gain seven dimensions in addition to hue, brightness, and saturation.

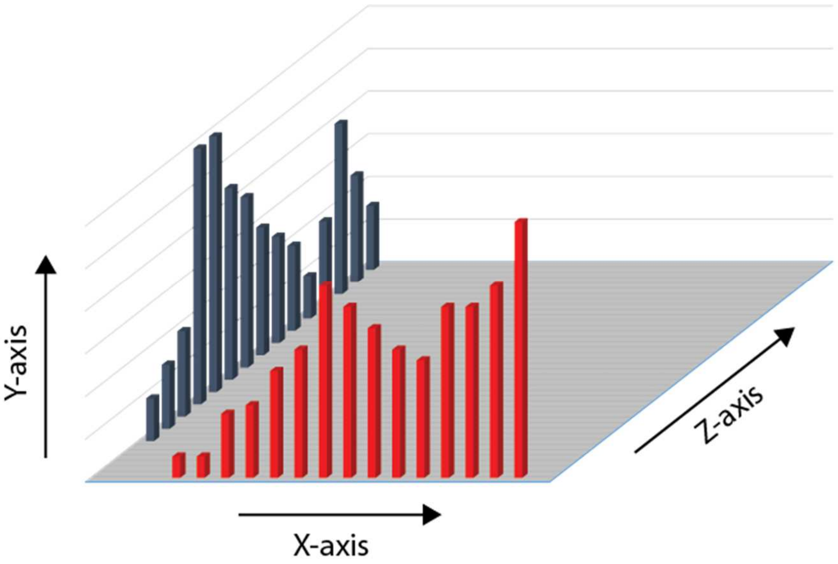

Figure 4: Not all dimensions in a perceptual space are shared by all perceptual qualities. A hypothetical distribution of perceptual qualities in a three-dimensional quality space is shown. The perceptual qualities form two clusters, shown in red and blue. Both modalities share the y-axis, but only the perceptual qualities in the red cluster vary along the x-axis and only perceptual qualities in the blue cluster vary along the z-axis.

Dimensions of the perceptual quality space

Once we know how many dimensions the perceptual space has, we will want to know what the dimensions represent; we will want to label the dimensions. Ultimately, it is a matter of convention how to label the dimensions of a perceptual space. The dimensions of the perceptual space may align with words that are used in pre-theoretic vocabulary to talk about perceptual qualities. However, it is also possible that the newly discovered dimensions of the perceptual space require new labels. Consider the labels for the dimensions of the color or tone space. "Hue" was an obscure Old English word for color that was revived by scientists in the 19th century to have a specific word for the perceptual property that is distinct from "color". In German, "hue" is "Farbton", which translates to "tone of the color", in analogy to auditory perception. "Pitch" was first used to describe perceptual auditory qualities in 1590, and the relations to the other meanings of the word are unclear. In German, "pitch" is "Tonhöhe", which translates to "height of the tone", reflecting the spatial position of tones in musical annotation. These examples show that labels for the dimensions of perceptual quality spaces were invented or re-appropriated by experts after the structure of the underlying perceptual space was understood. The same approach should be followed for labeling the dimensions of the exhaustive perceptual space.

That scientific progress brings with it a new vocabulary instead of relying on pre-theoretical language is a common occurrence. One example in which bringing systematic order to biological diversity required a new vocabulary is phylogenetic systematics and the naming of animal species. The pre-scientific vocabulary to refer to animals was not systematic. The many species of flying insects that bite or sting are called "mosquitoes". Myriads of small invertebrate species are referred to as "bugs". Only species that are of ecological importance to humans, like domesticated species or important pests, have common names. In some cases, cultivars or varieties also have proper names. With the rise of the biological sciences, a second vocabulary for talking about living things has been developed. Scientific names of species are based on the structure of the phylogenetic tree. The new names for the species were invented by scientists. This scientific vocabulary was developed without any regard as to whether it aligns well with the established ways of referring to living things. The scientific vocabulary had little impact on language. We still say that we have been bitten by a mosquito, not that we have been bitten by *Anopheles gambiae*. However, the scientific vocabulary has the advantage that it reflects the empirically determined structure of the phylogenetic tree.

New scientific discoveries commonly require a new vocabulary. Otherwise, there would be no need for experiments and one could deduce the structure of reality from language use. The lack of pre-theoretical verbal labels for the dimensions of the perceptual space is not a surprise and does not pose a problem because our vocabulary has "no more of a *representational* relation to an intrinsic nature of things than does the anteater's snout or the bowerbird's skill at weaving" (Rorty 1998) (page 48). Contrary to this insight, a strong preference for an account of perception that aligns with the pre-theoretical vocabulary has also been expressed:

> "It is therefore crucial to my thesis to emphasize that sense impressions or raw feels are common sense theoretical constructs introduced to explain the occurrence, *not* of white rat type discriminative behavior, but rather of perceptual propositional attitudes, and are therefore bound up with the explanation of why human language contains families of predicates having the logical properties of words for perceptible qualities and relations" (Sellars 1965).

My preferred strategy is to first construct the perceptual quality space and then attempt to describe it using non-scientific nomenclature. If this turns out to be impossible, a scientific vocabulary has to be invented. Admittedly, an account that would explain both perception *and* the way we talk about perception would be more powerful than an account of perception alone. However, I do not believe that such an account exists. Why we have words for some parts of the perceptual space and how these words relate to each other is a linguistic question. The structure of perceptual quality spaces, which can be constructed for bats or bacteria in the same manner they are constructed for humans, is independent of this linguistic question (for interesting treatments of the language used to describe perceptual qualities, see (Berlin and Kay 1969) for colors, and (Castro, Ramanathan et al. 2013) for smells).

Even though building a perceptual space proceeds without regard of pre-theoretic language, it is likely that at least some of the dimensions of the perceptual space can be interpreted in pre-theoretical language. One of the dimensions of the exhaustive perceptual space will presumably represent perceptual intensity. Intensity is a quality shared by perception in many modalities, and stimuli of similar intensity in different modalities are perceived to be more similar than stimuli of different intensity. It has for example been shown that darker colors are matched to stronger odors (Kemp and Gilbert 1997). It is also likely that stronger odors will be matched to louder sounds and stronger pains. These results show that intensity is an important feature of perceptual qualities across modalities. This will likely be reflected by the structure of the perceptual space. A separate dimension of the perceptual space may correlate with perceived pleasantness, which is also a quality of perception that is found in different modalities. Pleasantness, for example, plays an important role in the non-random matching of odors to sounds (Crisinel and Spence 2011). For tastes and smells, pleasantness may even be the dominant perceptual dimension (Khan, Luk et al. 2007)[6].

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[6] There is a question whether pleasantness should count as a dimension of perceptual qualities. The question mirrors by the question whether painfulness should count as a feature of perceptual qualities, which has been discussed by Austen Clark Clark, A. (2005). Painfulness is Not a Quale. Pain: New Essays on Its Nature and the Methodology of Its Study. M. Aydede. Cambridge, MIT Press**:** 177-197.. According to Clark, pain is accompanied by specific sensory qualities, but it is not one itself. The intuitive test whether one agrees with this is whether two equally painful pains, for example the pain of a sunburn and of a pulled muscle share a common sensory quality or not. The olfactory equivalent would be to ask whether two equally pleasant smells, for example the smell of bacon and that of vanilla share a common quality or not. Clark

Beyond intensity and pleasantness, correspondences between perceptual qualities in different modalities are more difficult to interpret using pre-theoretical language. Some crossmodal correspondences are easily explained through associations. The color green is matched to the smell of grass because the color and the smell are properties of the same object (Levitan, Ren et al. 2014). Other crossmodal correspondences, for example between pitch and smell, cannot be explained through associations and are grounded in perceptual similarities across modalities (for a review of crossmodal correspondences between smells and perceptual qualities in other modalities, see (Deroy, Crisinel et al. 2013)). However, ordinary language has no word for a perceptual quality dimension that is shared by pitch and smell that could be used to label this emerging dimension of the perceptual quality space. A new label has to be invented for this dimension and presumably also for many other dimensions.

Modality-representing clusters of perceptual qualities

Many methods of bringing order to perceptual qualities start by assigning each perceptual quality to one of the sensory modalities[7]. The method suggested here arranges all perceptual qualities according to their similarities in a perceptual space. The modalities, rather than being categories used to arrange perceptual qualities emerge from the arrangement of perceptual qualities.

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concludes that pain is not a perceptual quality, instead, the close connection between certain perceptual qualities and pain is that the sensory qualities are wired "directly into the creature's preference functions" ibid.. Whether something that is directly wired into perception is part of perception or not is part of the difficult problem of drawing the line between perception and cognition.

[7] A notable exception is Rosenthal, who uses the just-noticeable-difference-method to both construct perceptual quality spaces and individuate modalities Rosenthal, D. (2014). Quality spaces and sensory modalities. The Nature of Phenomenal Qualities: Sense, Perception, and Consciousness. P. Coates and S. Coleman. Oxford, Oxford University Press..

The coordinate system that contains the exhaustive perceptual space is not fully packed with perceptual qualities. Instead, it is sparsely populated by perceptual qualities that are interspersed by empty areas that do not correspond to any perceptual qualities. Presumably, there is no continuum of perceptual qualities between a color of a certain hue, brightness, and saturation, and a tone of a certain pitch and loudness. We cannot start with a perceptual color quality and change it in small steps until we have changed it into a perceptual tone quality. If this is correct, then the area between colors and smells in the coordinate system that contains the exhaustive perceptual space is empty. Presumably, there will be many other empty areas surrounding perceptual qualities[8]. It is very likely that the perceptual qualities are not distributed at random in the coordinate system; presumably, they form clusters. These clusters of perceptual qualities can be interpreted as modalities. If people perceive colors to be more similar to other colors than to any other perceptual quality, then all colors will be close to each other in a cluster that can be interpreted as the visual modality.

Modality-representing clusters of perceptual qualities emerge when perceptual qualities are arranged according to their similarities. However, because a variety of different formalized algorithms (Everitt, Landau et al. 2011) can be employed to detect clusters, cluster analysis

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[8] Some of the empty space in the coordinate system corresponds to *potential* perceptual qualities. The perceptual color space in Figure 2 shows that only certain combinations of hue, brightness, and saturation are perceived by humans. Very bright yellows are for example sometimes more saturated than maximally saturated less bright yellows. The asterisk in Figure 2B marks the position of a yellow that is never perceived because yellows of this brightness cannot be that saturated. The asterisk marks the position of a potential perceptual quality. Many other areas in the coordinate system that contains the exhaustive perceptual quality space, like the area between colors and tones, will not correspond to any actual or potential perceptual qualities.

allows for several different outcomes. The same arrangement can be interpreted as three modalities (Figure 5A), five modalities (Figure 5B), or three modalities with two of the modality-representing clusters subdivided into sub clusters (Figure 5C). The hierarchical organization of modalities that is shown in Figure 5C is probably the most accurate reflection of the relations between perceptual qualities. The best-known illustration of such a hierarchical structure is the arrangement of the perceptual qualities associated with touch. Touch includes every perception that is not vision, audition, gustation, or olfaction. Touch can therefore be further subdivided into proprioception (sensing relative positions of body parts), mechanoception (pressure), thermoception (temperature), nociception (pain), and maybe others.

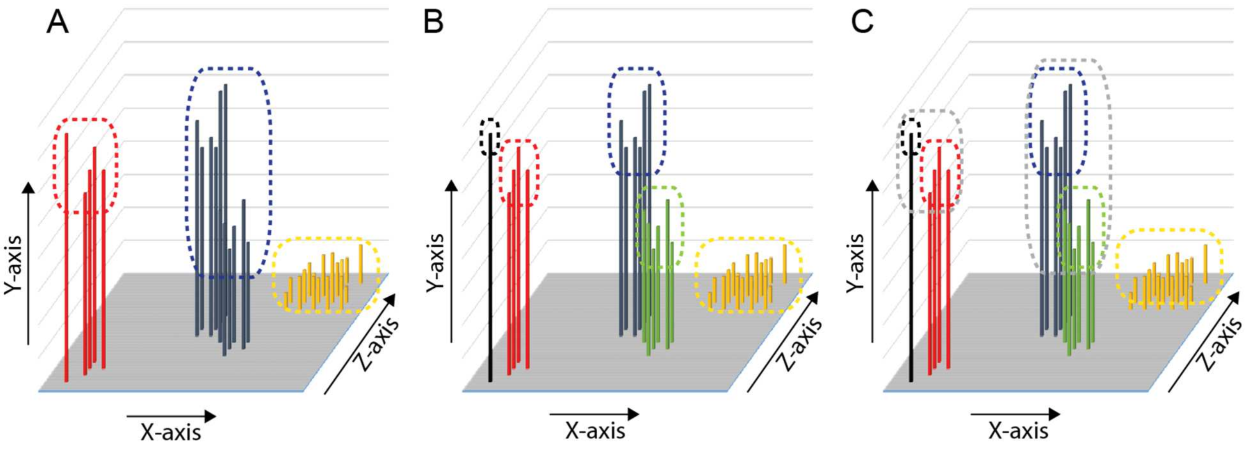

Figure 5: Modality individuating clusters of perceptual qualities. A hypothetical distribution of perceptual qualities in a three-dimensional quality space is shown. Depending on the parameters that one uses for identifying modality-representing clusters, this distribution can be interpreted as three (A) or five (B) modalities, or as three modalities, two of which can be further subdivided (C) .

Because the results of applying cluster analysis to the perceptual space depend on the criteria used to individuate clusters, cluster analysis cannot decide unambiguously how many modalities there are and where the boundaries between them are located. However, the advantage of cluster analysis is that it can be used to test accounts of modalities for their consistency. For example, the set of algorithms that clusters smells, tastes, colors, and tones all in their own modality-representing cluster can be investigated. If no algorithm in this set clusters all other perceptual qualities together in a single touch modality, then the classic account of the five human senses is wrong.

The big advantage of modality individuation through modality-representing clusters over other strategies of modality individuation is that it not only individuates modalities, but also reveals the relation between modalities. The distance between two modality-representing clusters in the perceptual space is a measure of the similarity between the two modalities. More interestingly, the cluster analysis also reveals the relative orientation of modality-representing clusters to each other. The distance between these clusters and how they are oriented with respect to each other represent similarity relations between perceptual qualities in different modalities. Consider again that sugar, an odorless tastant, is consistently experienced to be more similar to the tasteless odorant vanillin than to salt, another odorless tastant (Rankin and Marks 2000). The traditional two-step procedure of modality individuation and subsequent quality space construction cannot account for this fact. In contrast, the perceptual quality space that contains all perceptual qualities can account for all similarity relations between perceptual qualities, regardless of the modality-representing cluster they belong to. In Figure 6, a hypothetical arrangement of the cluster of gustatory perceptual qualities and olfactory perceptual qualities is shown. This arrangement preserves the distinction between the olfactory modality and the gustatory modality while also explaining why sweet taste is more similar to vanilla odor than to salty taste.

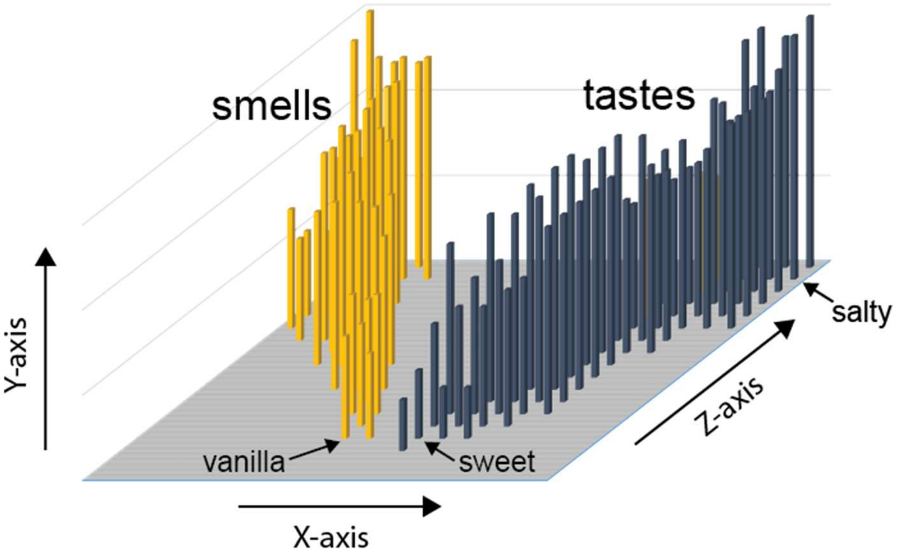

Figure 6: Similarity between perceptual qualities in different modalities. A hypothetical arrangement of smells and tastes in perceptual space that would explain why sweet taste is more similar to vanilla odor than to salty taste despite sweet and salty being perceptual qualities in the same modality is shown.

Interpreting clusters of perceptual qualities in the perceptual space as modalities is a form of individuating modalities based on behaviors, because the perceptual space was constructed through behavioral experiments. This is an unusual strategy. It is more common that modality individuation is based on representations, phenomenal character, the proximal stimulus, or the sense-organs (Grice 1962; Macpherson 2011)[9]. However, behavior-based modality individuation

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[9] How the sense modalities should be individuated has been a topic of philosophical investigations since Aristotle's *De Anima* Aristotle (2011). Excerpt from On the Soul (De Anima). The Senses: Classical and Contemporary Philosophical Perspectives. F. Macpherson. New York, Oxford University Press**:** 47-63, Sorabji, R. (2011). Aristotle on Demarcating the Five Senses. The Senses: Classical and Contemporary Perspectives. F. Macpherson. New York, Oxford University Press**:** 64-82.. Traditionally, modality individuation has been based on representations, phenomenal character, the proximal stimulus, or the sense organs. All four approaches largely agree when individuating vision and audition. Vision, for example, is the only sense that represents colors, the proper sensible of vision. Our eyes are at all levels of description

has also been suggested previously. Most notably, the just-noticeable-difference-method that has been used to construct quality spaces has recently been extended to provide a method for individuating modalities based on discriminative abilities (Rosenthal 2014). The just-noticeable-difference-method and the method proposed in section 1.1. have many similarities. The most notable difference between the two methods is that the method proposed in this chapter arranges perceptual modalities relative to each other according to the similarities between their perceptual qualities. As was pointed out above, the discriminative abilities that are revealed by the just-noticeable-difference-method are also revealed by relative similarity judgments. When subjects

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(anatomical, cellular, and molecular) sufficiently distinct from other sensory structures. Photons, the proximal stimulus, are also sufficiently distinct from other stimuli. The phenomenal character of all visual experiences allows distinguishing these experiences from other sensory experiences. However, it is merely a contingent fact of the biology of human vision that all four approaches agree on how to individuate it. With olfaction and other modalities they often produce contradictory results, as has been anticipated by Aristotle, who wrote "the distinguishing characteristic of smell is less obvious than those of sound or colour" Aristotle (2011). Excerpt from On the Soul (De Anima). The Senses: Classical and Contemporary Philosophical Perspectives. F. Macpherson. New York, Oxford University Press**:** 47-63. (page 52). One example of chemosensory perception that is difficult to categorize is the perception mediated by the TRPV1 receptor. TRPV1 is a type of molecular receptor that is sensitive both to hot temperature and to capsaicin, the pungent chemical found in chili peppers Caterina, M. J., M. A. Schumacher, et al. (1997). "The capsaicin receptor: a heat-activated ion channel in the pain pathway." Nature **389**(6653): 816-824.. This receptor is expressed in sensory neurons on the tongue and these neurons therefore respond equally to chili peppers and to hot water. If the sense organ criterion is applied, capsaicin and heat are considered two stimuli in the same modality. However, if the stimulus criterion is applied, then the TRPV1 receptor mediates perception in two different modalities. Two stimuli that are sensed by the same molecular receptor will result in the same neuronal activity and therefore in the same phenomenal character; therefore the phenomenal character criterion would judge heat and capsaicin to be two stimuli in the same modality. However, what is represented by the two stimuli is a botanical compound and hot air, respectively. TRPV1 is just one of many examples of chemical receptors that are sensitive to physically different stimuli Dhaka, A., V. Viswanath, et al. (2006). "Trp ion channels and temperature sensation." Annual Review of Neuroscience **29**: 135-161.. A prominent example from the olfactory system is the TRPM8 receptor, which is activated by the odor menthol as well as by cold air. In all these cases of receptors sensitive to two physically very different stimuli, the stimulus and representation criteria come to the conclusion that the receptor mediates perception in two different modalities whereas the phenomenal character and sensory organ criteria come to the contradictory conclusion that the two different stimuli are stimuli in the same modality.

are presented with three stimuli, two of which are identical and the third different, triadic comparisons mimic discrimination tasks. It can therefore be suspected that the modality individuation through both methods results in the same set of modalities. The method proposed in section 1.1. individuates the modalities in a similar way to the just-noticeable-difference-method and constructs similar perceptual spaces for each individual modality. However, it also arranges the modality-representing clusters of perceptual qualities in a way that reflects the similarities between perceptual qualities in different modalities.

1.3. Orderliness of the perceptual quality space

The perceptual tone space and the perceptual color space have explanatory power because they arrange a large number of perceptual qualities in orderly spaces. The approximately 340,000 tones (Stevens and Davis 1938) can be arranged in a two-dimensional space (loudness and pitch) and the millions of discriminable colors (Nickerson and Newhall 1943; Pointer and Attridge 1998) can be arranged in three dimensions (hue, saturation, and brightness) (Hardin 1988; Hilbert and Kalderon 2000). This means that each of millions of colors can be identified by three coordinates that represent hue, saturation, and brightness. Giving a full account of perceived colors therefore does not require a description of millions of colors, but only a description of three dimensions.

The reduction in complexity from hundreds of thousands or even millions of perceptual qualities to two or three dimensions is what makes the color space and the tone space useful. They would lose their usefulness if they were less orderly and arrange perceptual qualities in spaces with hundreds instead of two or three dimensions. If it were not possible to arrange all perceptual qualities in a low-dimensional space, the exhaustive perceptual space would not contribute to our understanding of perception. The perceptual qualities that so far have been most resistant to being arranged in a perceptual space are smells. There have been so many failed attempts to construct a smell space that some doubt that it is possible (Lycan 2000). If there would be no orderly smell space, there also would be no orderly space that includes all perceptual qualities and the project outlined in this dissertation would not succeed.

Orderliness in the olfactory perceptual space

After reviewing the many failed attempts to put order to the olfactory perceptual space, Lycan writes, "... smell may catch up to color and hearing in the orderliness of its quality space and in the accompanying explanatoriness of the underlying neurophysiology. But that is not *overwhelmingly* likely." (Lycan 2000) (page 280). Such pessimism is based on the failure of all previous attempts to arrange smells in a perceptual space (Berglund and Höglund 2012; Kaeppler and Mueller 2013). However, these failures could also be due to three main shortcomings in the attempts to build smell spaces.

One common mistake is that many approaches are not driven by perceptual qualities but by verbal labels for smells. Researchers often take odor labels like "burnt", "fragrant", and "spicy", and then arrange olfactory perceptual qualities according to how burnt, fragrant, and spicy they smell. An example that is still found in psychology textbooks is Henning's smell prism (Henning 1916), which is a triangular prism, the six corners of which are labeled "flowery", "foul", "fruity", "spicy", "burnt", and "resinous". All olfactory perceptual qualities are supposed to be located within this three-dimensional space. Projects like this conflate constructing a perceptual smell space with establishing smell categories. The dimensions of the three-dimensional perceptual color space are hue, saturation, and brightness. This space could have never been discovered using an approach in which color categories like "red", "green", and "blue" are taken to be foundational. On closer examination, it turns out that most of the projects that seem like failed attempts to establish a smell space were instead successful attempts to establish an "odor descriptor space" (Castro, Ramanathan et al. 2013). These attempts were successful in establishing the odor descriptor space. However, the odor descriptor space does not correspond to a perceptual space. This lack of correspondence is to be expected since it is also seen with the color space that the linguistic analysis of color terms does not result in in a better understanding of the structure of the perceptual color space.

The second problem faced by researchers trying to elucidate the structure of the smell space is the difficulty of finding the right odorants to use for such a project. The number and diversity of odorous molecules is immense. More than one billion different chemicals have a smell (Joel Mainland, personal communication). Choosing a few dozens of these stimuli to use in psychophysical experiments is a daunting task. Traditionally, there was no attempt to find representative stimuli for psychophysics. Instead, especially salient, interesting, and ecologically or economically important stimuli have been used. Avery Gilbert and Mark Greenberg succinctly summarized the danger of this predominant approach when they wrote that "we are creating a science of olfaction based on cinnamon and coffee" (Gilbert and Greenberg 1992) (page 329). This is equivalent to a color science based on the colors of earth, fire, and water. It is not surprising that attempts to construct smell spaces based on perfumery raw materials failed. Thanks to the work of Noam Sobel and his group, now sets of odorants that are representative of all odorants can be identified. Sobel and coworkers accomplished this by arranging odorous chemicals according to the similarity of their chemical and physical properties in a stimulus space. Once such a stimulus space has been established, sets of odorants that are representative for this stimulus space can be identified (Haddad, Khan et al. 2008). It is therefore, for the first time, possible to use representative odorants in psychophysical experiments and then generalize the results of these experiments to all of olfaction.

The third shortcoming of most attempts to construct a smell space is that they are based on individual odorous molecules (benzaldehyde, hexanal, vanillin, and so on) (Wise, Olsson et al. 2000). A perceptual space that is based on the smells of individual molecules only covers a tiny fraction of all olfactory qualities because mixtures of odorous molecules frequently have qualities that are different from the qualities of its components and of all other odorous molecules. To construct an olfactory perceptual space that covers all olfactory perceptual qualities, the olfactory qualities of odor mixtures have to be included. The perceptual qualities of odor mixtures are the qualities we are familiar with because the smells encountered in nature are usually mixtures. The characteristic scents of a rose (Ohloff 1994) (pages 154-158), coffee (Grosch 1998), and red wine (Aznar, López et al. 2001) are all complex mixtures of hundreds of components. The components of these mixtures interact in a variety of ways that are not well understood (Ferreira 2012; Ferreira 2012).

Previous attempts to reveal the structure of the smell space have failed. However, concluding from these failures that no orderly smell space exists would be premature. Before coming to this conclusion, it is worthwhile to try an approach that does not rely on our limited olfactory vocabulary and uses mixtures of representative odorants. Such a semantic-free approach, which is more similar to the approaches that were successfully applied to colors and tones, may result in the discovery of an orderly smell space.

Size of the olfactory perceptual space

How orderly the space that contains all perceptual qualities is depends on how orderly the smell space is. Most perceptual qualities that we can discriminate are olfactory perceptual qualities. There are more than one trillion discriminable olfactory stimuli (Bushdid, Magnasco et al. 2014). The actual number is higher because the estimate of one trillion is based on mixtures of 30 out of a collection of 126 different odorous molecules. However, many more than 126 different odorous molecules exist (Joel Mainland, personal communication) and molecules can be mixed into mixtures of more than 30 components. Furthermore, the odors can be mixed at different proportions. Whatever the actual number of olfactory qualities is, it is several orders of magnitude higher than the number of visual and auditory qualities.

A human takes less than one billion breaths in his or her lifetime. We encounter only relatively few ecologically relevant odors regularly. It is therefore surprising that we can discriminate so many different smells. We did not evolve to be able to distinguish such a large number of smells. Instead, we evolved to be able to discriminate minute differences between two olfactory stimuli. The large number of discriminable smells is a consequence of our evolved discriminatory capacity. Olfactory systems evolve to discriminate complex mixtures that differ in few of their components. In prehistoric times, it may have been important to distinguish the smell of several babies that were raised together to avoid feeding unrelated babies in times of scarcity. The body odors of related babies that live together are very similar. Body odors are complex mixtures that share many components but also differ in a few. Similarly, the odor of food and the same food that shows the first signs of being spoiled can be very similar. Again, the two different stimuli have many shared components, but they also differ in the components that are produced by the bacteria as the food starts to spoil. Detecting this difference can mean the difference between a nutritious meal and food poisoning. The ease with which we detect cork taint is a good example of the incredible resolution of our olfactory system. Detecting cork taint amounts to detecting the presence of a small amount of the chemical 2,4,6-trichloroanisole in the mixture of hundreds of diverse molecules that make up the wine aroma (Aznar, López et al. 2001).

Because minute amounts of chemicals that are added to complex mixtures of other chemicals usually lead to a change in the perceived smell of the mixture, and because the number of potentially odorous chemicals is in the billions (Joel Mainland, personal communication), it has been suggested that the number of distinguishable olfactory stimuli is "unlimited" (Wright 1964) (p. 80). If the number of perceptual qualities were indeed unlimited, no perceptual quality space that contains all of them could be constructed. However, a recent breakthrough in olfactory psychophysics showed that our ability to discriminate smells is limited. Tali Weiss and colleagues showed that mixtures with many components, when each component is diluted so that all components have similar intensity, converge perceptually. This means that mixtures of random odorous molecules with a large enough number of components smell similar and share an olfactory quality that has been called, in analogy to vision, "olfactory brown" or "olfactory white" (Weiss, Snitz et al. 2012). The reason why the complex mixtures of odorous molecules that we encounter when we smell roses or coffee do not smell similar is that the components of these mixtures are not a random sampling of odorous molecules and they do not contribute equally to the smell of the mixture. Instead, in many cases, the smell of a natural mixture is dominated by a few components. How many components are necessary in mixtures to render them indistinguishable from one another is not yet known (Weiss, Snitz et al. 2012). However, that larger mixtures converge perceptually shows that the resolution of the olfactory system is limited. The number of perceptual qualities is finite and they therefore can be arranged in a finite perceptual quality space.

There are two possibilities of how a perceptual space can accommodate a very large number of perceptual qualities. A large number of perceptual qualities can either result from a high resolution along the dimensions of the quality space or from a large number of dimensions. Quality spaces are mathematical constructs that have whatever number of dimensions is needed to capture the similarity relations of the relevant qualities (see Figure 3). It is unlikely that the odor space will have only two or three dimensions like the tone or color space. Smell space has been suggested to have a higher dimensionality than quality spaces in other modalities (Berglund and Höglund 2012; Auffarth 2013). It simply is not possible to arrange all olfactory qualities in a low-dimensional space. However, it is also unlikely that the number of dimensions of the smell space is very high. The number of perceptual qualities that can be accommodated in a perceptual space increases exponentially with the number of dimensions of the space. Maybe the smell space will reduce the complexity by a similar degree as perceptual spaces in other modalities. Approximately 5 million discriminable colors are arranged in a three-dimensional space and around 340,000 tones are arranged in a two-dimensional space. The cube root of 5,000,000 is 171 and the square root of 500,000 is 583, which means that each dimension of these spaces can be divided into a few hundred discrimination steps. If in the olfactory space 500 discriminable perceptual qualities are arranged along each dimension, then five dimensions would be required to accommodate a trillion olfactory perceptual qualities.

How orderly the exhaustive perceptual space is, is an empirical question that can only be answered with certainty after the psychophysical experiments required to construct the exhaustive perceptual space have been performed. Partial perceptual spaces are already known. The color and the tone space arrange a large number of perceptual qualities in spaces with three and two dimensions. It is likely that spaces for temperature or touch qualities will also have few dimensions. The only potential problem is how to arrange smell qualities. I have shown in this section that there are many more discriminable smells than other perceptual qualities. Accordingly, the smell space is likely have more dimensions than the color space or the tone space. However, although we will have to await the construction of the smell space to be sure, I am optimistic that the smell space will not have more than a few dozen dimensions. It is likely that the smell space will increase order by a similar degree as the perceptual spaces in the other modalities[10]. There is hope that it will reduce complexity enough to be a useful construct for perceptual philosophy. If this is the case, then the exhaustive perceptual space will be orderly enough to play an important role in our understanding of how perception works.

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[10] The procedure for constructing perceptual spaces described in section 1.1. will result in a perceptual space regardless of the similarity relations between the perceptual qualities. Any set of perceptual qualities can be arranged in a multidimensional space according to their similarity. It is therefore not possible that there is no perceptual smell space. However, a perceptual space in which a trillion perceptual qualities are arranged in a trillion-dimensional perceptual space would be nothing more than a list of the perceptual qualities and not a useful theoretical construct.

1.4. Conclusion: Perceptual qualities can be individuated by their position in a similarity space

All perceptual qualities perceived by a perceiver can be individuated based on their similarity relations with other perceptual qualities (Goodman 1951; Clark 1993; Matthen 2005). Sensory modalities can then be interpreted as clusters of perceptual qualities in this exhaustive perceptual space. The relational account of perceptual qualities that I developed here is based on the Quality Space Theory (Rosenthal 2005; Rosenthal 2010), but it uses different behavioral methods and therefore can account for similarity relations between perceptual qualities in different modalities. Relational accounts of perceptual qualities are alternatives to accounts that determine perceptual qualities by their intrinsic properties. Accounts that individuate perceptual qualities by intrinsic properties often lead to the conclusion that the only thing that can provide access to perceptual qualities is first-hand conscious experience. A relational account avoids this conclusion by showing how we can describe every perceiver's perceptual qualities.

Importantly, perceptual qualities are arranged in the perceptual space based on behavioral experiments and regardless of whether they are consciously perceived or not. What it feels like to perceive a certain perceptual quality is not used as a basis to construct the perceptual space. Instead, what it feels like to perceive a certain perceptual quality reflects its position in the perceptual space. The perceptual space is a mechanistic explanation of the qualities of subjective awareness. Individual instances of subjective awareness are not necessarily relational. At any time, we just smell a single odor. There are no relations to other perceptual olfactory qualities. However, how the odor smells is determined by its position in the perceptual space. This position can be expressed by coordinates along the dimensions of the perceptual space.

Chapter 2: Third-person access to perceptual qualities

In chapter 1, I have introduced a strategy to arrange all perceptual qualities according to the similarity relations between them that are revealed through behavioral experiments. The resulting exhaustive perceptual space makes it possible to individuate each perceptual quality through its position within the space. This is an important step towards a science of perceptual qualities because it makes it possible to identify and compare perceptual qualities without having to refer to the subjective experiences of the perceiver.

However, the strategy presented in the previous chapter does not give us a universal perceptual space, or *the* human perceptual space, or even the stable perceptual space of a given individual. This is not a shortcoming of the proposed strategy. There is neither a universal perceptual space, nor *the* human perceptual space, nor an individual's unchanging perceptual space. The experimental strategy introduced in chapter 1 produces an exhaustive perceptual space for a given perceiver at a given time. If one is interested in another perceiver's perceptual space, the strategy has to be repeated with the other perceiver. The perceptual spaces of two perceivers will differ. It is therefore necessary to develop a strategy of comparing perceptual qualities in different perceptual spaces. If no such strategy is available, then third-person access to perceptual qualities would not be possible and studying perceptual qualities in a systematic way would be a very daunting task.

In this chapter, I will present a strategy for comparing perceptual qualities that are perceived by different perceivers by first constructing and then aligning the perceptual spaces of the two perceivers. To set up the problem, I will first review the diversity of perceptual spaces and the different ways in which they can differ. In the second part of the chapter, I will then explain how other perceiver's perceptual qualities can be accessed under certain circumstances.

2.1. Diversity of perceptual spaces

Perceptual quality spaces can be constructed for every perceiver that can be made to respond differently to different stimuli. The perceivers can be humans, animals, plants, machines, robots, or extraterrestrials. Each perceiver has a different mechanism for perceiving and for processing sensory information. Different types of robots and machines are built according to different specification. Different species evolved different perceptual systems and brains that are adapted to the perceptual needs of their ecological niche. Different individuals of the same species can also vary considerable, and even the brain and sense organs of an individual change over time. This diversity of perceptual systems is reflected by the diversity of perceptual spaces.

The realization that there are as many perceptual spaces as there are perceivers could be discouraging and interpreted as a sign that perceptual spaces are not useful constructs for theorizing about perception. However, this would be the wrong response. The diversity and malleability of perceptual spaces does not reduce the explanatory power of these constructs. That diversity can increase explanatory power can be illustrated by the role of genomes in understanding phenotype determination. Like perceptual quality spaces, genomes are diverse. Different species have different genomes, and individuals of the same species carry different genetic variants of many genes in their genomes. Genomes also change over time due to mutations. Rather than diminishing the explanatory power of genomes, this diversity is the reason why genomes have become so important for our understanding of biology. Differences in genomes explain anatomical and physiological differences between species. The differences between the genomes of members of the human species explain why some humans have blue eyes while others are lactose intolerant. Changes in the genomes of our cells over time are the cause of cancer. That it is not possible to identify *the* genome, or *the* human genome, or *the* genome of a given individual does not diminish the important role that genomes play in understanding biology. Similarly, the diversity of perceptual spaces does not reduce their usefulness for our understanding of perception.

However, the diversity of perceptual spaces has to be acknowledged and the differences between perceptual spaces have to be known for perceptual spaces to be a useful theoretical construct. In this section, I will use the relatively well-understood color space as an example of how perceptual spaces differ between different perceivers. Perceptual spaces are arrangements of perceptual qualities according to similarities between them within a multidimensional coordinate system. Two perceptual spaces can have the same coordinate system, but differ in the arrangement of perceptual qualities within that coordinate system. Alternatively, perceptual spaces can differ in the coordinate system in which the perceptual qualities are arranged.

Diversity of the arrangement of perceptual qualities in perceptual spaces

In humans, the perceptual color quality space of has three dimensions: hue, saturation, and brightness. In this section, I will consider how color spaces that have these three dimensions can differ from one another. In the next section, I will then speculate about color quality spaces with different dimensions.

The color spaces of different mammalian species differ considerably. Color perception in these animals is the consequence of differential activation of sensory neurons that carry different types of cone photopigments. These cone photopigments, like all proteins, are encoded by genes and these genes, called opsin genes, are subject to evolution through natural selection. In mammals, there have been many dramatic evolutionary changes in the opsin genes (Jacobs 2009). Opsin genes can change, which can alter their sensitivity to light of specific wavelengths. More dramatically, opsin genes can duplicate and then change, which results in species that have more opsin genes than their ancestral species. Not only can species gain opsin genes, they can also lose them. An opsin gene is lost when a mutation that renders the photopigment non-functional occurs. Humans have three opsin genes and it is therefore said that they are trichromatic. Most other mammals have only two opsin genes. They are dichromatic. Some species, like the owl monkey, are monochromats that have only a single opsin gene. Some birds have more than three opsin genes. Most birds are tetrachromatic, while pigeons are pentachromatic. Behavioral experiments have shown that species with fewer opsin genes generally are worse at discriminating colored stimuli (for a review of comparative color vision, see (Jacobs 1981)). Additional opsin genes convey the ability to discriminate more color stimuli.[11]. The distribution

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[11] Having more types of receptors with different sensitivities does not always lead to more discriminable perceptual color qualities. The direct relation between the number of different receptors and the number of discriminable perceptual qualities only holds when the information collected by the receptors is processed in the same way. This has been illustrated by research into species of mantis shrimp that have up to twelve different photoreceptors, each sampling a different narrow range of wavelengths Marshall, J., T. W. Cronin, et al. (2007). "Stomatopod eye structure and function: A review." Arthropod Structure & Development **36**(4): 420-448.. Based on the large number of photoreceptors with different sensitivities, it has been speculated that mantis shrimp have a very large and complex color space. However, behavioral experiments revealed that this is not the case, which led to the suggestion that mantis shrimp do not use comparisons between different channels to discriminate between colors Thoen, H. H., M. J. How, et al. (2014). "A Different Form of Color Vision in Mantis Shrimp." Science **343**(6169): 411-413.. Assuming that the processing of color information is relatively conserved, a relation

of these qualities in the hue-saturation-brightness-space is different depending on the number of types of receptors with which light is perceived.

In addition to the differences between different species, there are also substantial differences between individuals that belong to the same species, as can be illustrated by human variability in color vision. There are different forms of color blindness in humans. Some humans are dichromats. They lack one of the three cone photopigments. Depending on which of the three cone photopigments is missing, this condition is known as protanopia, deuteranopia, or tritanopia. In Figure 7, how individuals with those conditions perceive the color spectrum is simulated. As can be seen by comparing the colors perceived by individuals with these conditions with the colors perceived by individuals with normal trichromatic vision (top of Figure 7), dichromats perceive fewer distinguishable colors. Some wavelength that are associated with yellow or cyan in trichromats are indistinguishable from white for them. Furthermore, they cannot distinguish some wavelength pairs that are easily distinguishable by trichromats. In protanopia, some colors that are perceived as green, yellow, or red by those with normal color vision are indistinguishable. Individuals with tritanopia cannot discriminate what in the normal case is perceived as yellow from what in the normal case is perceived as pink. If on would construct the color spaces for dichromats based on similarity relations between perceptual qualities, these spaces would be different from the normal color space shown in Figure 2. However, the colors that are perceived by dichromats all have hue, saturation, and brightness, like colors perceived by normal perceiver. Each perceptual color quality, regardless whether it is

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between the number of opsin genes and the number of colors that the species can discriminated can be expected in vertebrates.

perceived by human trichromats or dichromats can be individuated by its position in the color space that has three dimensions representing hue, brightness, and saturation.

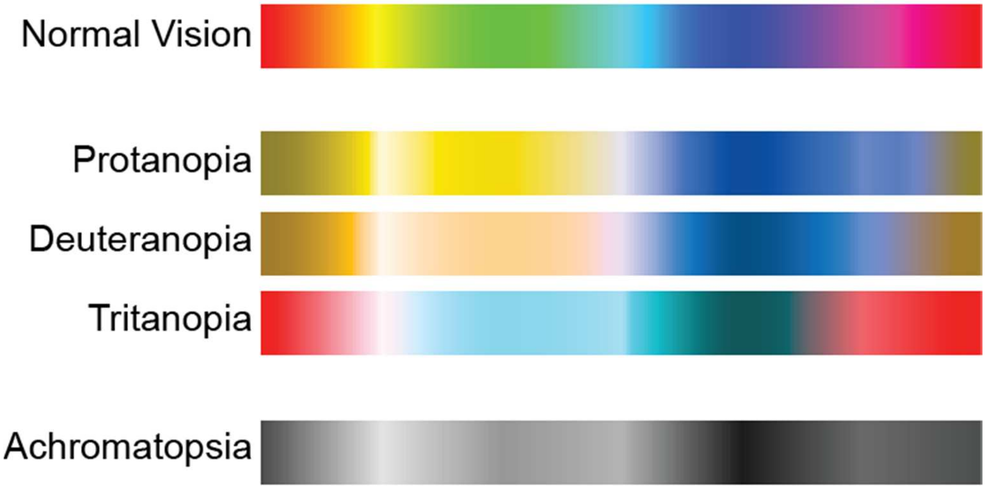

Figure 7: Variability in color perception between individuals. How lights along the frequency spectrum are perceived by humans with different systems for color perception is shown. A color blindness simulator was used to generate this figure. (modified from original work by Nanobot (in the public domain))

Diversity of the dimensions of perceptual spaces

Very rarely, individuals have even more impoverished color vision than dichromats. Individuals that suffer from total colorblindness, or achromatopsia, see the world only in different shades of grey. This condition can be caused by mutations that disrupt the molecular mechanisms with which cone cells respond to light. When this mechanism is disrupted, none of the three types of cone cells functions. Individuals with such mutations are not blind because in addition to cone cells, humans also have photosensitive rod cells. However, in the absence of functioning cone cells, humans only perceive different shades of grey. The visual perceptual qualities perceived by achromatopsic individuals all have the same hue and saturation. They differ from one another only in their brightness. The visual perceptual qualities of achromatopsic individuals can therefore be arranged in a one-dimensional space. The same is true for the visual perceptual qualities of monochromats such as seals and owl monkeys.

Brightness, the one dimension of an achromatopsic individual's color space is also one of the three dimensions of the three-dimensional color space of individuals with normal vision. The one-dimensional achromatopsia color space is a subspace of the three-dimensional normal color space. The one-dimensional achromatopsia color space can therefore be transformed into a three-dimensional normal color space by adding two dimensions (saturation and hue) and assigning each color the value zero for both of these dimensions. In general, a low-dimensional perceptual space that is a subspace of a higher-dimensional perceptual space can be represented in the same coordinate system as the higher-dimensional perceptual space. The difference in coordinate systems is then reduced to a difference in the number and arrangement of perceptual qualities.

Since there are some species with lower dimensional color spaces than humans, it is likely that some species have visual perceptual quality spaces that have more than three dimensions. We know that many animals can perceive features of light that we cannot perceive. Some species, for example, can perceive the pattern of polarized light in the sky. When this pattern is visualized in textbooks, the differences of polarization angle are represented as differences in hue or brightness of the color of the clear blue sky, which looks homogeneous and uniform to us. However, we would have to construct the perceptual color space for such a species to find out how the polarization pattern is actually perceived by them. It is possible that polarizations angles of light change the perceived hue, saturation, or brightness in species that are sensitive to polarization of light. However, it is also possible that the physical feature "angle of polarization" corresponds to a fourth dimension of color quality space that is inaccessible to humans. Similarly, we do not know whether pigeons, which are believed to be able to discriminate several billion colors, discriminate all colors depending on their hue, brightness, and saturation. Alternatively, the pigeon color space could have a fourth dimension that makes it easier to accommodate the large number of colors.

It would be arrogant to assume that no other species has a higher dimensional color space than us. However, it is also understandable. It is very easy to accept that the achromatopsic, who cannot perceive saturation or hue, is missing an important part of what makes visual perceptual qualities. However, it is much more difficult to imagine that we are also missing an important dimension of visual perceptual qualities. What else could there be to colors other than hue, saturation, and brightness? That this question is impossible to answer for somebody whose first-hand visual experience consists only of hue, saturation, and brightness illustrates the importance of relying on behavioral experiments rather than subjective experience in individuating perceptual qualities.

2.2. Third-person access to perceptual qualities

Every perceiver perceives similarities between perceptual qualities differently and the perceptual spaces between different perceiver therefore differ either in their dimensions, or in the arrangement of the perceptual qualities. These differences in perceptual spaces make it difficult to compare perceptual qualities between perceivers. However, comparing perceptual qualities between perceivers is necessary for third-person access to perceptual qualities which, in turn, is necessary for a science of perceptual qualities.

In this section, I will suggest that it is possible to compare perceptual qualities that are perceived by different perceivers even if their perceptual spaces differ. The question how similar two perceivers' perceptions of the color of a ripe tomato are can therefore be answered objectively. However, I will also show that comparing perceptual qualities between perceivers is only possible when the two perceivers' perceptual spaces can be aligned either directly or through intermediates.

Possibility of third-person access to perceptual qualities

How can we measure the similarity between perceptual qualities that are perceived by different perceivers? The similarity between perceptual qualities that are perceived by the same perceiver is represented by the distance between the two perceptual qualities in the exhaustive perceptual space. However, as discussed above, perceptual spaces differ between perceivers. This introduces a problem for comparing perceptual qualities that are not perceived by the same perceiver. As an illustration, consider a city map. I can mark locations on a city map and then compare one location to another. When the marks are close on the map, the positions they represent are geographically close. When the marks are far apart, then they represent geographically distant locations. Two marks at the same spot on the map represent the same location in the city. Now imagine that a friend of mine has the same city map and that she marks locations on her map. It will be easy, at least theoretically, to compare locations marked on the two maps. All that needs to be done is to transfer the marks from one map to the other identical map and then measure the distances between them. This is analogous to comparing perceptual qualities between two perceivers that have the same perceptual space. However, as reviewed above, no two perceivers have the same perceptual space. The analogous situation is therefore a situation in which different locations have been marked on two different maps of the city. Imagine that one map is a 1:10,000-scale map and the other a 1:20,000-scale map. In this situation, the two maps have to be aligned before locations that are marked on the different maps can be compared. In the case of a 1:10,000-scale map and 1:20,000-scale map, aligning them simply requires rescaling one of the maps. The solution to the problem of comparing perceptual qualities in different perceptual spaces is similar to the problem of comparing locations marked on different maps: the two perceptual spaces have to be aligned before perceptual spaces on them can be compared.

Consider a hypothetical example. In the top row of Figure 8A-C, the two perceptual spaces of two different perceivers and the position of the perceptual quality associated with a light stimulus of 430 nm in each of the spaces are shown. The question we want to answer is whether the perceptual quality that is associated with a light stimulus of 430 nm is the same for both perceivers. To answer this question, the two perceptual spaces have to be aligned based on their overall structure (lower row in Figure 8A-C)[12]. When the two spaces are aligned, the distance between the perceptual qualities associated with light of 430 nm wavelength in the two perceivers can be measured. In Figure 8A, the perceptual qualities of perceiver 1 and 2 are at the

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[12] The two spaces have to be aligned depending on their structure not depending on their dimensions. As Jerry Fodor and Ernie Lepore discussed in the context of State Space Semantics Fodor, J. and E. Lepore (1996). Paul Churchland and State Space Semantics. The Churchlands and their critics. R. N. McCauley. Cambridge, Blackwell Publishing**:** 145-159., attempts to align similarity spaces based on their dimensions merely succeed in shifting the problem from third-person access to perceptual qualities to third-person access to the dimensions of perceptual spaces. Instead of wondering whether your blue is the same as my blue, we wonder whether your saturation is the same as my saturation. Aligning the spaces depending on their structures avoids this problem.

same position in the combined perceptual space, which means that the same perceptual quality is associated with this stimulus in those two perceivers. In Figure 8B and C, different perceptual qualities are associated with the same stimulus in different perceivers. The perceptual qualities associated with light of 430 nm wavelength in perceiver 1 and 3 are similar (Figure 8B), whereas radically different perceptual qualities are associated with this stimulus in perceivers 1 and 4 (Figure 8C).

Another question one can ask is which stimuli elicit the same perceptual qualities in two perceivers. The strategy to answer this question is illustrated in Figure 8D-F. To answer this question, the two perceptual spaces have to be aligned and the position of the perceptual quality under study in them has to be marked (upper row in Figure 8D-F). Then, the physical stimulus that elicits this perceptual quality can be identified (lower row in Figure 8D-F). For perceivers 1 and 2, the same stimulus elicits the perceptual quality under study (Figure 8D). In perceiver 3, light of 460 nm wavelength elicits the same perceptual quality that is elicited by light of 430 nm wavelength in perceiver 1 (Figure 8E). In perceiver 4, light of 650 nm wavelength elicits the same perceptual quality (Figure 8F).

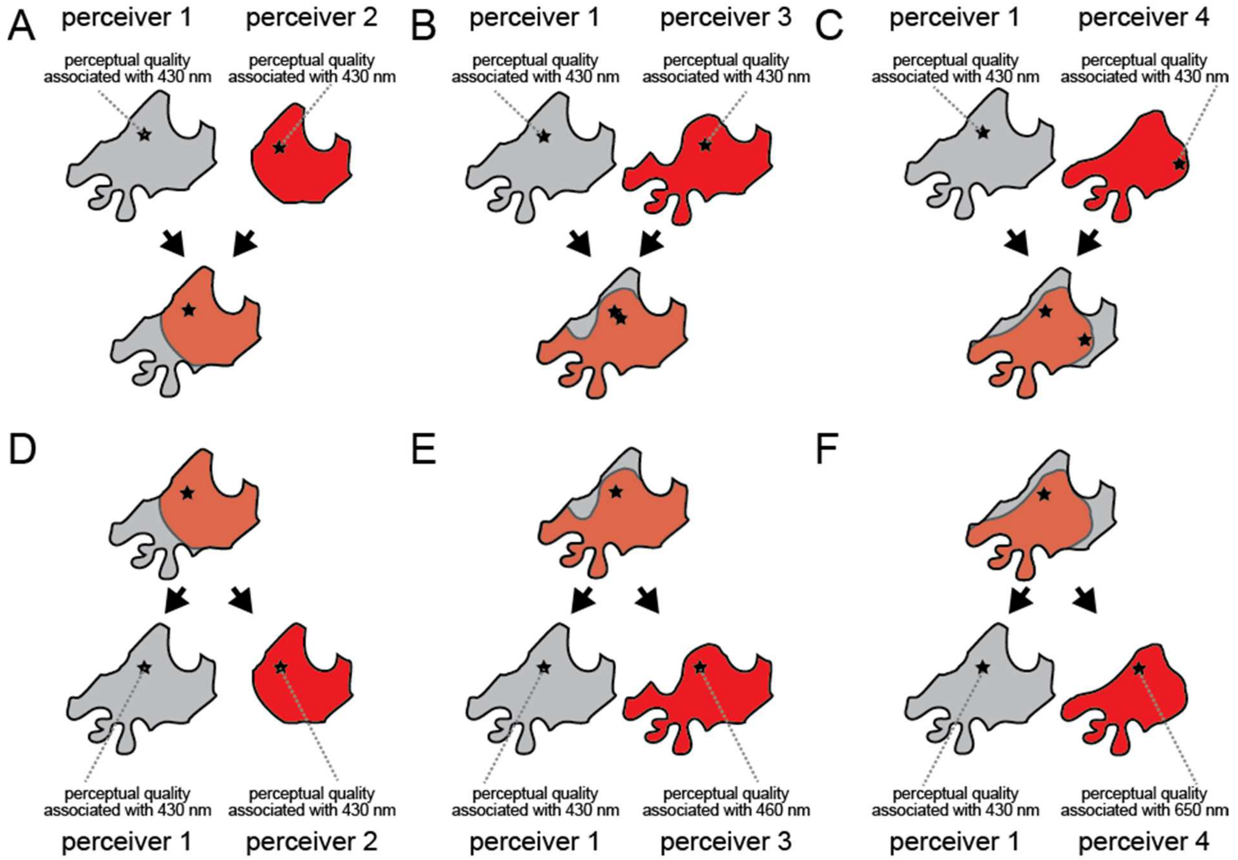

Figure 8: Determining similarity of perceptual qualities perceived by different perceivers. (A-C) The perceptual quality associated with light of 430 nm wavelength in perceiver 1 is compared to the perceptual quality associated with light of 430 nm wavelength in three other perceivers. (A) In perceivers 1 and 2, the same perceptual quality is associated with light of 430 nm wavelength. (B) In perceivers 1 and 3, a similar perceptual quality is associated with light of 430 nm wavelength. (C) In perceivers 1 and 4, very different perceptual qualities are associated with the same stimulus. (D-F) The stimulus that is associated with a specific perceptual quality in perceiver 1 is compared to the stimuli associated with the same perceptual quality in three other perceivers. (D) In perceivers 1 and 2, the same stimulus (light of 430 nm wavelength) is associated with the perceptual quality. (E) The perceptual quality associated with light of 430 nm wavelength in perceiver 1 is associated with light of 460 nm wavelength in perceiver 3. (F) The perceptual quality associated with light of 430 nm wavelength in perceiver 1 is associated with light of 650 nm wavelength in perceiver 4.

It is important to understand that the physical nature of the stimulus cannot play a role in aligning two perceptual spaces. It may be tempting to use salient physical stimuli that are perceived by both perceivers to anchor the two perceivers' perceptual spaces. One could for example align the perceptual color space of a bee and the perceptual color space of a human by distorting them so that the perceptual qualities that are associated with 480 nm light (blue for humans), 560 nm light (green for humans), and 710 nm light (red for humans) are in the same position. Then, one could identify the position of the perceptual quality associated with UV light (which can be perceived by bees, but not by humans) in the bee's perceptual space and measure what the closest perceptual quality in the human's perceptual space is. This, one might believe, would be a way to identify the human color perception that is most similar to how bees perceive UV light. However, this strategy is flawed because it assumes that the perceptual qualities blue, green, and red are elicited by the same stimuli in humans and bees, and there is no evidence supporting this assumption.

Let us return to the city map analogy. That the physical nature of the stimulus cannot play a role in aligning perceptual spaces in analogous to saying that the marks on the maps cannot play a role in aligning the maps. Imagine two different maps of the city. On one, I have marked the location of my home, my workplace, my barber, and my favorite restaurant. On the other, you have marked your home, your workplace, your barber, and your favorite restaurant. We want to know how close our favorite restaurants are. We cannot achieve this by distorting one of our maps so that the marks marking your home and my home, your workplace and my workplace, and your barber and my barber are at the same position and then measuring the distance between the marks marking your favorite restaurant and my favorite restaurant. The marks on the maps cannot be used to align the maps. Only features of the maps themselves can be used to align them. Similarly, the only way to find out which of your perceptual qualities is most similar to the perceptual quality associated with UV light in bees is to construct your own perceptual space and the perceptual space of the bee. If the two spaces can be aligned, the position of the perceptual quality associated with UV light in the bee can be compared to your perceptual space and the perceptual quality in your perceptual space closest to it can be identified.

Examples of third-person access to perceptual qualities

Consider, as an example of how two perceptual spaces can be aligned, the perceptual space of someone who suffers from specific anosmia for musks. Specific anosmias are conditions in which people with an otherwise normal sense of smell cannot smell a certain type of odor, for example musk odors (Amoore 1967). This condition can be caused by a disruptive mutation in the odorant receptor sensitive for these odors (Whissell-Buechy and Amoore 1973; Keller, Zhuang et al. 2007; Mainland, Keller et al. 2014). How could somebody with specific anosmia to musk find out something about the perceptual qualities that are associated with musk? Knowledge about the musk-sensitive odorant receptors and about the musk molecules is not going to be helpful because neither similarity between odorous molecules, nor between odorant receptors is a reliable predictor of similarities between olfactory perceptual qualities. The way to learn about the perceptual qualities of musk is therefore to build two smell spaces, one for an individual with a normal sense of smell and one for an individual with specific musk anosmia. The two smell spaces will be identical except that one will have a hole at the position at which the musk perceptual qualities are located in the smell space of the normal subject (Figure 9A, left). This hole represents the blind spot for musks and it is surrounded by the perceptual qualities that constitute the border of the hole. The smell of musk is between the smell of perceptual qualities on opposing sides of the hole that represents the musk blind spot. The individual with musk anosmia can find out what the physical stimuli are that are associated with the perceptual qualities around the blind spot and then smell them.

The advantage of specific anosmia as an example is that it is an actual condition. The disadvantage is that the smell space is not known yet and the example can therefore only be discussed in abstract terms. To complement the example of specific anosmia, imagine a fictional example that is similar to Hume's *Missing Shade of Blue*. Imagine someone having a normal auditory system with the exception of the inability of hearing the pitch D3. When somebody is playing a scale on a piano, there will be a moment of silence between C3 and E3 for this person. People with an intact auditory system will hear D3 between C3 and E3. The tone space is two-dimensional. One dimension is pitch and the other loudness. D3-deaf people will not hear anything at the pitch D3 at any loudness, so the tone space of the D3-deaf person will differ from that of a person with normal hearing by lacking a stripe along the pitch dimension. The tone space will be cut into two tone spaces, one space for tones higher than D3 and one space for tones lower than D3 (Figure 9A middle). Because in a scale, the perceptual qualities are ordered along the dimension (pitch) in which there is the specific blindness, the note before and after the moment of silence will provide information about the perceptual quality of D3 to the D3-deaf subject.

Consider a third example. People suffering from ageusia have no sense of taste. Constructing a perceptual quality space of such an individual will result in a space in which one modality-representing cluster, the one that represents taste qualities, is missing. It will likely be possible to align such a perceptual quality space with the perceptual quality space of a person that has all senses (Figure 9A right). There is no continuum of perceptual qualities between the gustatory qualities and qualities in other modalities, so there are no perceptual qualities that are directly adjacent to the missing taste qualities. However, there are proximity relations between perceptual qualities in non-gustatory modalities in the ageusia patient's perceptual space and taste qualities in the normal perceptual space the patient's perceptual space is aligned with. Unless the experiments are performed and the exhaustive perceptual spaces are constructed, the nature of the proximity relations between these perceptual qualities is unknown. However, it can be speculated that the alignment will reveal to the ageusia patient that the gustatory perceptual quality associated with chili peppers is similar to the perceptual quality associated with high temperature perceived at the tongue. The gustatory perceptual quality associated with sugar is close to the perceptual qualities associated with vanilla smell and soft touch perceived at the tongue.

These examples show that the strategy for third-person access to perceptual qualities outlined above can be successful. It is possible for the individual with musk anosmia to have information about how an individual with a normal sense of smell experiences musks. There is no ontological or epistemological barrier that precludes us from knowing other minds. This is a very important result because without a way to compare perceptual qualities regardless of who perceives them, there could be no objective science of perception. The fact that nothing precludes knowledge of other minds in principle does not mean that there are no practical problems with third-person access to perceptual qualities. In the next section, I will discuss these practical problems and show that some of them are unsurmountable and can be considered limits to third-person access to perceptual qualities.

Limits of third-person access to perceptual qualities

The strategy for third-person access to perceptual qualities outlined above depends on aligning the perceptual spaces of the two perceivers whose perceptual qualities we want to compare. Aligning perceptual spaces however may not always be possible. In other situations, there may be more than one possible alignment, so the two perceptual spaces cannot be aligned unambiguously.

In general, the more similar two spaces are, the easier it is to align them. In Figure 9A, three hypothetical examples of pairs of perceptual spaces with sufficient similarity in shape to align them are shown. The perceptual space pairs correspond to the examples of musk anosmia (left), D3-deafness (middle), and ageusia (right). In each of these three examples, the space on the right is derived from the space on the left by subtracting a small area. This makes it easy to align the two spaces. In Figure 9B, three pairs of perceptual spaces that are so dissimilar that it is not possible to align the grey space with the red space unambiguously are shown. In most cases in which two perceptual spaces have to be aligned, the decision whether it is possible to align them unambiguously or not is presumably not as clear-cut as in the examples in Figure 9 A-B. The perceptual spaces of two human individuals with normal perceptual capacities will presumably have very similar overall shapes. However, when zooming in, one will discover small differences between the spaces. Maybe the cluster representing colors is slightly elongated in one of the spaces, and the distance between the cluster of smells and tastes is not the same. It will certainly be possible to align the two exhaustive perceptual spaces, but it may be that several, slightly different, alignments are possible. One then has to use an algorithm to decide which alignment is the best. Which algorithm is chosen will be to some degree arbitrary. Another complication for deciding whether two spaces can be aligned is that it has to be decided which transformations of the spaces should be allowed to align them. If any type of transformation is acceptable, then every space can be distorted so that it will perfectly align with every other space. Because of these complications, there will be cases in which it is disputable whether two exhaustive perceptual space can be aligned or not. However, in other cases it will be clear whether two perceptual cases can be aligned or not.

When two perceptual spaces that clearly cannot be aligned directly are found in different animal species, a strategy to align them despite their very different structures is sometimes available. The strategy is to find intermediates that can be used to create a chain of aligned perceptual spaces. The two dissimilar perceptual spaces I and VIII in Figure 9C cannot be aligned directly. They are the same pair of perceptual spaces shown on the right in Figure 9B as an example of spaces that cannot be aligned. However, as is shown in Figure 9C, I and VIII can be aligned indirectly through the series of perceptual spaces II to VII. Perceptual space I can be aligned with perceptual space II, perceptual space II can be aligned to perceptual space III, and so on until spaces I to VIII form a chain of unambiguously aligned perceptual spaces. The direct alignment between I and VIII has not been possible because of the different shapes of the two perceptual shapes. This is symbolized by the red arrow connecting I and VIII directly in Figure 9C. The indirect alignment of I and VIII through a series of intermediates has however been possible. This is symbolized by the circle of black arrows connecting I and VIII indirectly in Figure 9C. To provide a hypothetical example, it may not be possible to align the human perceptual space directly with the perceptual space of the mouse. However, if the human perceptual space can be directly aligned with the monkey perceptual space, and the monkey perceptual space can be directly aligned with the rabbit perceptual space and the rabbit perceptual space can be directly aligned with the mouse perceptual space, it would still be possible to compare the perceptual qualities associated with 480 nm light in mice and in humans.

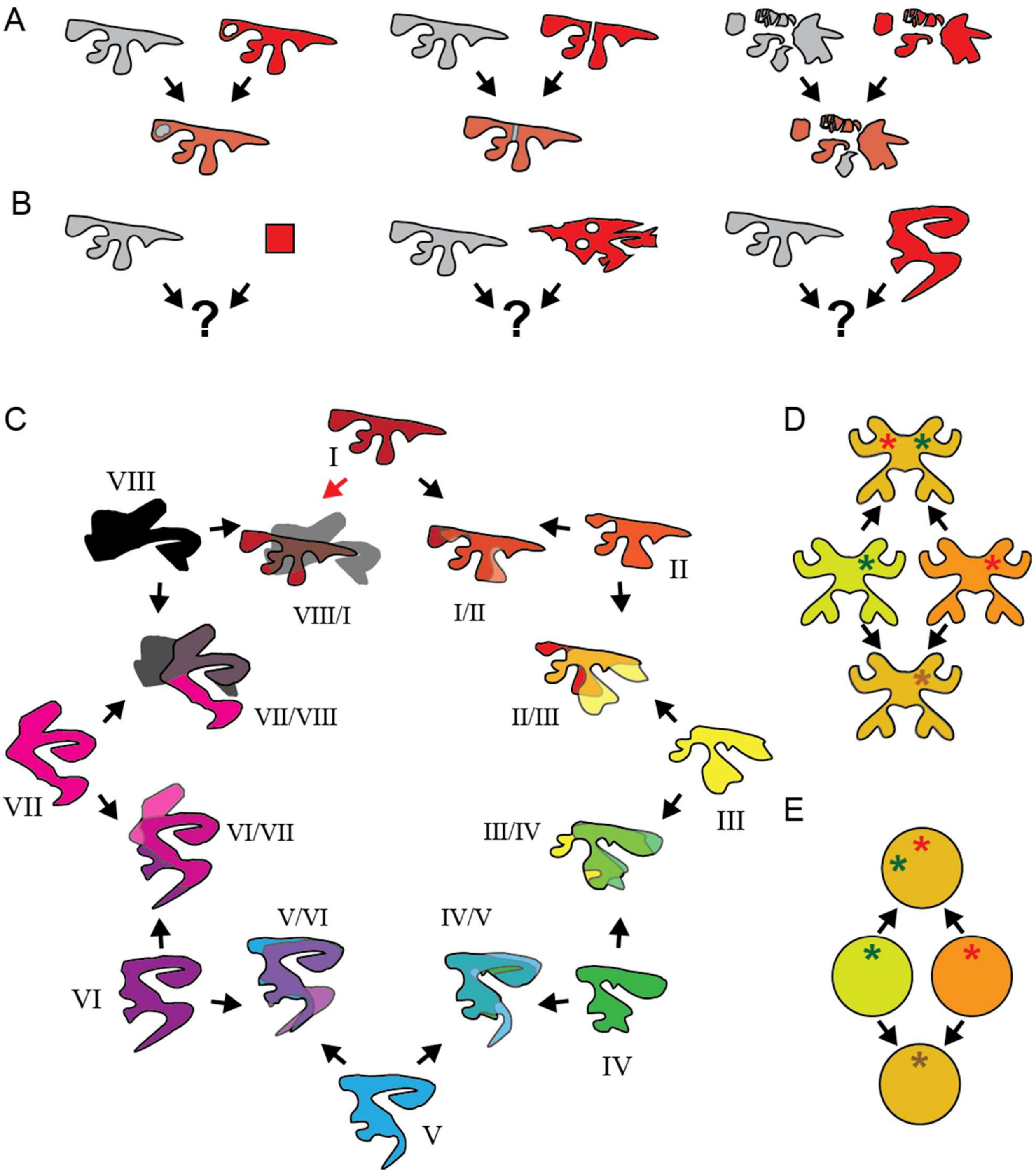

Figure 9: Aligning perceptual quality spaces. (A) Three pairs of perceptual spaces that are sufficiently similar in their shape to be aligned. (B) Three pairs of perceptual spaces that are too dissimilar to be unambiguously aligned. (C) Perceptual space I and perceptual space VIII are not similar enough to be directly aligned. However, through a chain of intermediates (perceptual spaces II to VII), they can be aligned indirectly. (D, E) Symmetrical perceptual spaces can be aligned in more than one orientation.

Perceptual spaces that are too different to be aligned are not the only possible problem for aligning two perceptual spaces unambiguously. Another possible problem for comparing perceptual qualities between different perceivers are symmetrical perceptual spaces that can be aligned in more than one orientation (Figure 9 D, E). Mirror symmetric perceptual spaces can be aligned in two different orientations (Figure 9D). Radial symmetric perceptual spaces can be aligned in any orientation (Figure 9D). Symmetry is more likely in simple perceptual spaces. In humans, neither the three-dimensional color space, nor the two-dimensional tone space is symmetrical. The structure of perceptual spaces in other modalities is not well known. Maybe the one-dimensional temperature space that goes from hot to cold is symmetrical. Your hot may be my cold. The exhaustive perceptual space that contains all perceptual qualities is complex and contains the non-symmetrical color and tone spaces, so the worry about symmetry is not pressing for the account of human perceptual qualities that I propose. However, if a symmetrical perceptual space were to be discovered in an animal species, the correct orientation could probably be found by studying the perceptual space of closely related species with a similar, yet not symmetrical, perceptual space. The most likely situation in which symmetry of the space will limit third-person access to perceptual qualities is when it comes to the perceptual spaces of machines, which can be purposefully designed to have symmetrical perceptual spaces.

In the philosophical literature, discussions of the possibility of symmetrical perceptual quality spaces has a long tradition since John Locke's discussion of the possibility of spectrum inversion in color perception (Locke 1689/1975) (for an overview of the literature, see (Byrne 2010)). Locke, writing long before the human perceptual color space had been established, discussed the hypothetical case of a symmetrical color space. In this case discussed by Locke, strawberries elicit the perceptual qualities that are elicited by cucumbers in normal perceivers. Cucumbers elicit the perceptual qualities normally elicited by strawberries. Locke goes on to assure the reader that despite this possibility of an inverted color spectrum, he thinks that the same object will elicit the same, or very similar, mental qualities in different individuals. Because the perceptual spaces of humans are not symmetrical, it is now possible to empirically test this proposal and search for individuals that perceive as green what others perceive as red. John Dalton discovered more than hundred years after Locke's hypothetical case that some individuals are red-green colorblind. In these individuals, cucumbers and strawberries elicit some of the same perceptual qualities.

Because the exhaustive perceptual quality space containing all perceptual qualities is not symmetrical, undetectable inversion is not possible in humans. However, it is possible in creatures with symmetrical perceptual quality spaces (if such creatures exist). This theoretical possibility of undetectable spectrum inversion is sometimes used in arguments against behaviorism and functionalism (Fodor and Lepore 1996). The argument is that, in undetectable spectrum inversion, two behaviorally or functionally identical perceivers could perceive different perceptual qualities in identical situations. It would however be impossible to prove the existence of an actual case of spectrum inversion (hence "undetectable" spectrum inversion).

2.3. Conclusion: Aligning perceptual spaces enables third-person access to perceptual qualities

Different perceivers perceive stimuli and the similarity between stimuli with different perceptual systems and they therefore have different perceptual quality spaces. This diversity of perceptual spaces complicates comparisons between perceptual qualities that are perceived by different perceivers. In this chapter. I proposed a strategy for third-person access to perceptual qualities that is based on aligning perceptual spaces. Quantifying the distance between perceptual qualities that are perceived by two different perceivers is possible by aligning the two perceptual spaces and then measuring the distance between the perceptual qualities in the combined space. This objective measure of similarity between perceptual qualities regardless of whom they are perceived by could provide the basis for the scientific study of perceptual qualities.

Because the strategy for third-person access depends on the ability to align the perceptual spaces of the two perceivers that are compared unambiguously, it is not always possible. One problem are perceptual spaces with structures that are so different that they cannot be aligned. The structure of the perceptual space of a perceiver depends on its perceptual systems and on the processing of sensory information. The perceptual systems of two biological perceivers are connected through the perceptual system of their last common ancestor. It is therefore unlikely to find perceptual spaces so radically different that they cannot be aligned among close relatives. It is also possible, when two perceptual spaces cannot be aligned directly, to use a chain of intermediates to align them indirectly. However, this is not always possible. Humans are evolutionary so distant from bacteria that it will very likely not be possible to align the human perceptual space through intermediate steps with the perceptual space of a bacterium. It is probably not possible to compare a given human perceptual quality with a given bacterial perceptual quality. The situation becomes even more hopeless when the two perceivers that are to be compared are not connected through a common ancestor. The perceptual space of an animal is unlikely to be similar enough to the perceptual space of a robot or of an extraterrestrial for the two spaces to be aligned unambiguously. It will therefore not be possible to find a stimulus that is associated with the same perceptual quality in a robot and in a bat.

Another problem case for the strategy of comparing perceptual qualities between perceivers by aligning the perceivers' perceptual spaces are symmetrical perceptual spaces. Symmetrical spaces can be aligned in more than one orientation. The exhaustive perceptual space in humans is not symmetrical, so this is not a concern when it comes to comparing our own perceptual qualities to those of other perceivers. However, it is possible that some perceivers have symmetrical perceptual spaces[13]. It is most likely that symmetrical perceptual spaces will be found in very simple organisms, or in machines, which can be purposefully designed to have symmetrical perceptual spaces.

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[13] Rosenthal argues that it is impossible for a space that is based on an individual's discrimination abilities to be symmetrical because a symmetrical space would collapse around the axis of symmetry Rosenthal, D. M. (2010). "How to think about mental qualities." Philosophical Issues: Philosophy of Mind **20**: 368-393.. This is not the case for the perceptual spaces discussed here. To illustrate that symmetrical perceptual spaces are possible, let us consider a simple perceiver that can only perceive two discriminable perceptual qualities. The perceptual space of this perceiver would consist of two points that represent the two perceptual qualities. This space would be symmetric because it is always possible to draw a symmetry axis between two points. If one would collapse this space around the axis of symmetry, the two perceptual qualities would fall into the same location. Since the two perceptual qualities can be discriminated, the collapsed space would not represent the similarity relations between the perceptual qualities accurately.

Part II: Percepts

In the first part of this dissertation, I have discussed perceptual qualities abstracted away from the spatial and temporal structure of perception. Perceptual qualities are the basic building blocks of perception. However, many normal instances of perception are much richer and more complex than a series of changing perceptual qualities. In this second part, I will describe how this complexity emerges through the combination of perceptual qualities. In chapter 3, I will describe how percepts are formed through the combination of perceptual qualities in space and time. In chapter 4, the notion of objecthood in the context of perception will be examined, and in chapter 5, I will discuss the function of perception. Specifically, I will argue against the proposal that it is the function of perception to collect correct information about the physical world. Instead, I will show that it is the function of perception is to guide behaviors.

In this part, I will cash in the promise from the title and focus heavily on olfactory perception. I hope that it will become apparent that notions like object-oriented perception and the idea of perception as a mirror of reality, which seem intuitive when considering visual perception, fail to capture the nature of olfactory perception.

Chapter 3: Olfaction in space and time

Percepts are formed by temporal and spatial arrangements of perceptual qualities. A visual scenery is a spatial arrangement of colors. A noise is a temporal arrangement of tones. In this chapter, I will discuss the structure of olfactory percepts. I will first discuss spatial structure and then temporal structure. As is always the case in perceptual philosophy, it is important to distinguish between the structure of the stimulus and the structure of the perception and I will therefore discuss these two topics separately. The review will reveal that olfactory percepts are much less structured than percepts in vision or audition. Olfactory perception has no spatial structure and a very impoverished temporal structure. For the most part, olfactory perception is the perception of a series of changing perceptual qualities.

3.1. Olfaction in space

Introspectively, it does not seem that the perception of odors is spatially structured. Olfactory perception has been called "a single unitary experience" (Stevenson 2009) (page 1010), "a state of consciousness, having neither geometry nor articulate individuation" (page 282) (Lycan 2000), and a "nominal sense" that simply provides "data of qualitatively different odors in our surroundings" (Köster 2002) (page 28). On the other hand, humans can indisputably use olfactory information for navigation. This is only superficially a contradiction because the ability to navigate using olfactory stimuli does not imply that olfactory perception is spatially structured.

Spatial structure of the olfactory environment

Our olfactory environment is spatially structured at different scales. At the largest scale, New Delhi, the Bavarian Forest, the Mexican resort town of Cancún, and the Mojave Desert in the southwestern United States can all easily be distinguished from one another based on the odorous molecules in the air at these locations. Each of these places has a different distinct smell. On a smaller scale, different ecosystems also have different smells. The ocean smells different from the tidal zone, which smells different from the beach, which smells different from the marshland. If one walks towards the ocean from a few miles inland, the odor environment will change in a predictable pattern. On a yet smaller scale, the bakery in the mall smells different from the shoe store. At an even smaller scale, my apartment smells different from the hallway and from my neighbors' apartments. Within my apartment, the kitchen, the bathroom, and the bedroom all have unique smells. Within the kitchen, the area by the oven smells different from the sink or the trashcan. Finally, my hands, feet, and armpits all have characteristically different smells.

The spatial distribution of odorants in the world is due to the spatial arrangement of the odor sources that release characteristic odorants. The concentration of the released molecules is, on average, higher close to the source than further away. Some odor sources remain at the same position in the environment and give off the same odorants for a long time. The ocean, for example, is a reliable olfactory landmark. Many other odor sources are much less permanent and reliable. The bakery in the mall will stop giving off bakery smells when it closes for the night. Apple trees may be good olfactory landmarks when they are flowering and then again when the apples are rotting under them, but not during the winter months. The difference between olfactory landmarks and visual landmarks, like trees, rivers, buildings, and mountains, is that olfactory landmarks are less stable over time.

The distribution of odorous molecules in the environment is especially unstable at the scale between meters and kilometers that is behaviorally relevant to humans. At this scale, the spatial distribution of odorous molecules is determined mostly by turbulent airflow (Weissburg 2000). At a lower scale between millimeters and centimeters, odor distribution is mainly determined by diffusion. The diffusion of odorants results in the formation of gradients and odor gradients can be used to locate the odor source. This is how insect larvae use smell for navigation. At a larger scale of tens or hundreds of kilometers, odor distribution is determined by climate events that produce stable spatial gradients in ratios of atmospheric trace gases (Wallraff and Andreae 2000). These stable gradients at a kilometer scales allow homing pigeons to smell their way home (Gagliardo 2013). At the human scale, stable patterns of odor distribution are comparatively rare, even in the presence of stable odor sources.

Dogs, rats, and other animals successfully use odors for navigation, which shows that, at least sometimes, odorants have stable spatial distributions at the scale that is behaviorally relevant for humans. However, dogs, rats, and all other terrestrial mammals normally do not use odorous molecules in the air for navigation. Instead, they use odors deposited on the ground as trails or markings. Trails and markings are much more stable over time than clouds of molecules. However, trails and markings are not accessible to humans because with the development of bipedalism our noses have been moved too high above the ground. Other species found solutions for similar problems. The elephant's olfactory epithelium is far from the ground, but it compensates for this with its trunk that constitutes a vacuum system to suck the odorous molecules from trails and markings on the ground up to the nasal cavity. Humans may be the only species of terrestrial mammals that is not aware of the trails and markings that structure the ground they walk on.

In summary, in the physical world, some non-random distributions of odorous molecules are stable over certain periods, for example odor gradients at the centimeter scale in soil. However, in the air several feet above ground, where our noses are, the distribution of odorous molecules is generally strongly influenced by turbulent airflows and very unreliable.

Spatial structure of olfactory perception

Our odor environment has a spatial structure and it would be possible that this structure is reflected in the structure of olfactory perception. However, laboratory experiments have shown that human olfactory perception is spatially unstructured. The simplest possible spatial structure of olfactory perception, a division of the perception into left nostril and right nostril, would be revealed by the ability to tell whether an odor is applied to the left or to the right nostril. Subjects fail even at this simplest task. It is usually not possible to discriminate between a stimulus being presented in the left nostril and the same stimulus being presented in the right nostril (Radil and Wysocki 1998; Frasnelli, Charbonneau et al. 2008). In seeming contradiction, it has also been reported that humans can compare the olfactory input between their two nostrils (von Békésy 1964; Porter, Anand et al. 2005; Porter, Craven et al. 2007). It has subsequently been shown that the performance in these experiments was not based on the spatial structure of olfactory percepts, but on chemesthesis (Kleemann, Albrecht et al. 2009; Croy, Schulz et al. 2014).

Chemesthesis is, by all accounts except those that individuate modalities solely on the physical properties of the stimuli, a different modality than olfaction. Chemesthesis is the chemical sensitivity of the skin or mucous membrane. The hotness when eating chili peppers, but also the burning when fingers touch the eye after handling chili peppers is mediated by chemesthesis. The sting when smelling vinegar and the perceived coolness of the smell of menthol are other examples of chemesthetic perception. Chemesthesis is mediated through receptors that mediate pain, touch, and temperature, which explains why chemesthetic experiences are described in terms of temperature and touch perception. The mucous membrane inside our nasal cavity has chemesthetic sensitivity. Like the entire surface or our body, this membrane is spatially mapped in our brain and we can tell whether the skin in our left or in our right nostril is being irritated. Chemesthesis in the nasal cavity is mediated by the trigeminal nerve. Experimentally dissociating olfaction and chemesthesis is notoriously difficult because at high concentrations many volatile molecules activate both the olfactory system and the trigeminal nerve. However, other than sharing the same stimuli, olfaction and chemesthesis have little in common (Figure 10). Olfaction is not involved in the ability to locate certain stimuli that was demonstrated by von Békésy and others (von Békésy 1964; Porter, Anand et al. 2005; Porter, Craven et al. 2007). We can tell that a jar of menthol is placed to our left because the skin in our left nostril feels colder than in our right nostril. The reason why we can tell that acetic acid is to our right is that it induces a stronger stinging in our right nostril than in the left. These perceptions are mediated by the trigeminal nerve. Abolishing olfactory perception by cutting the olfactory nerve would not affect this ability to locate the multimodal stimulus.

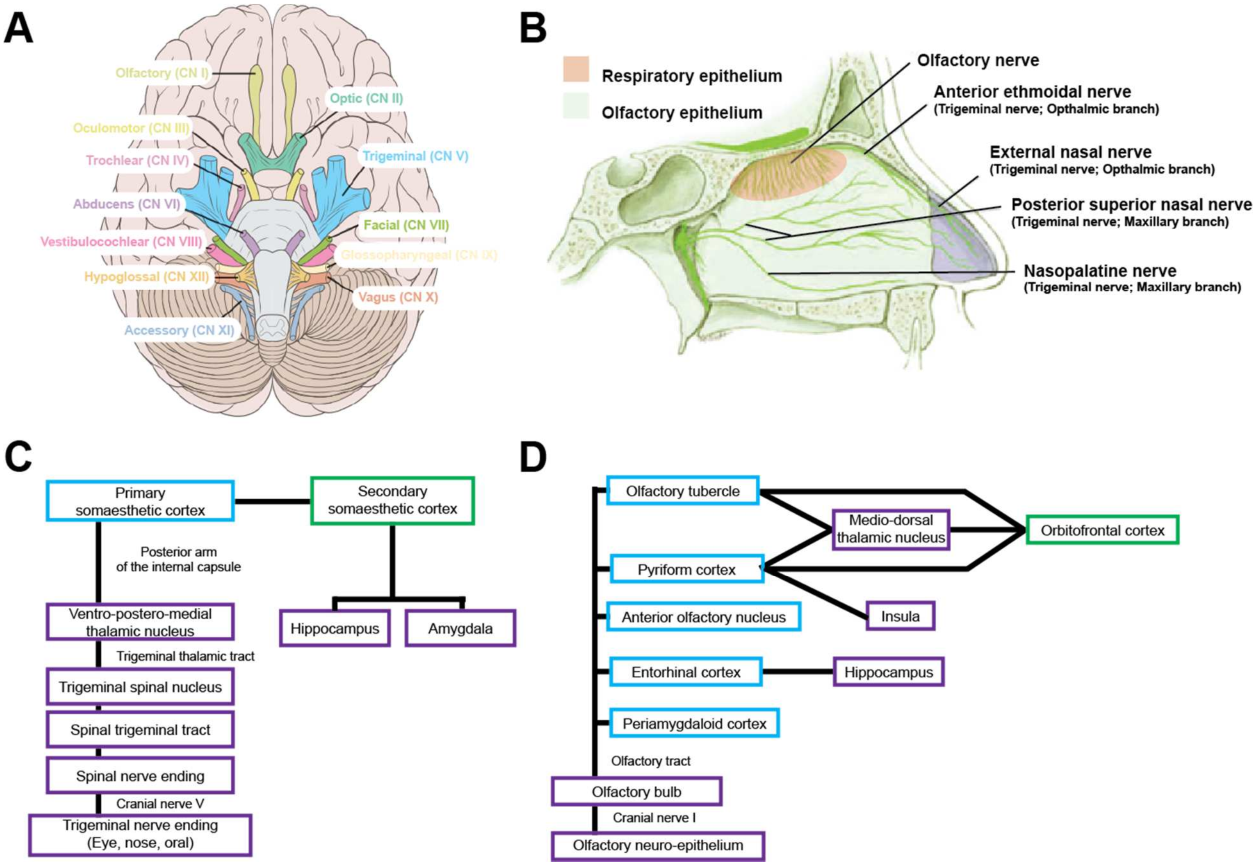

Figure 10: Perception mediated by the olfactory and by the trigeminal nerve. (A) The olfactory nerve and the trigeminal nerve enter the brain in different locations. (B) The olfactory nerve innervates the olfactory epithelium in the nasal cavity, whereas branches of the trigeminal nerve innervate the respiratory epithelium in the nasal cavity. (C, D) Different brain areas are involved in the processing of trigeminal information (C) and of olfactory information (D). (in (C) and (D) primary cortex is represented in blue, secondary cortex in green, and non-cortical regions in violet). ((A) modified from original work by Patrick J. Lynch (in the public domain under the Creative Commons license (CC BY 2.5); (B) modified from original work by FrozenMan (in the public domain under the Creative Commons license (CC BY-SA 4.0))

Odor-guided navigation without spatially structured perception

A possible objection to the thesis that our olfactory perception has no spatial structure is to point out that humans can successfully navigate using olfactory information. It is possible to find the source of an odor in a room. When humans navigate towards an object based on visual or auditory information, they use the spatial structure of the visual or auditory perception for guidance. The parsimonious assumption is that humans use the same strategy when using odor information to navigate towards an object. However, investigating instances of odor-guided navigation shows that this is not the case. Humans use different strategies for navigating based on olfactory perception than for navigating based on perception in modalities in which perceptions have spatial structure.

Although humans do not routinely use olfaction for navigation, there can be no doubt that it is possible. The paradigm example for olfactory navigation in humans is the nipple search behavior, in which infants use olfactory cues to orient towards their mothers' breasts (Varendi, Porter et al. 1994; Varendi and Porter 2001). There are also other examples. In dense tropical forests, visual navigation can be difficult, but there are many distinct odor sources available for olfactory navigation. Consequently, people living in this environment sometimes develop smell maps which they use for navigation (Classen, Howes et al. 1994) (pages 97-99). Smell can also provide valuable information about one's position with respect to an odor source, for example a lion. One can, using olfactory information, avoid areas that have a strong lion smell. Undoubtedly, this ability has saved many human lives.

These observations show that humans can use their sense of smell for orientation. That humans have the ability to navigate using odors has also been shown experimentally. It has been demonstrated that blindfolded human subjects have the ability to follow, crawling on all fours, a scent trail of chocolate essential oil (Porter, Craven et al. 2007). In another experiment, subjects were shown to be able to determine their position with respect to two odor sources by analyzing the ratio of the two smells (Jacobs, Arter et al. 2014). In institutions for mentally or visually handicapped people in the Netherlands, odorizing different hallways with different odors reduced the number of inhabitants that got lost trying to find their rooms (Köster, Møller et al. 2014).

That humans can use olfactory perception to navigate is not surprising. All perception of stimuli that are spatially structured in the environment provides the necessary information for navigation. If, in the experiment by Porter and colleagues (Porter, Craven et al. 2007) a salt trail would have been laid on the ground instead of a chocolate odor trail, blindfolded subjects presumably could have licked their way along the salt trail. Similarly, in a gustatory version of the study by Jacobs and coworkers (Jacobs, Arter et al. 2014), the floor of a room would have to be covered by a salt gradient and a perpendicular sugar gradient. In this situation, each location in the room can be gustatorily identified by the intensity and the salt/sugar-ratio.

However, that a stimulus is used for navigation does not mean that the perception of the stimulus has spatial structure. Even the most simple and unstructured signal can be used for navigation. Imagine an individual that gets headaches when standing close to a power line. Let us assume that the headaches have no spatial structure and that there are no qualitative differences between two headaches, but the intensity of the headache depends on the distance to the power line. This individual could use their headache to find a power line and to follow it from one city to another using electricity-guided navigation. If, while walking in a straight line, the headache decreases, the individual knows that they are moving away from the power line. The ability to use the taste of salt or an electricity-induced headache for navigation does not show that the salt perception or the headache have a spatial structure. Any perception of a stimulus can be used for navigation when the stimulus has spatial structure.

The strategy that humans most commonly use to navigate with the help of olfactory information is the same as used by the individual who uses electricity-induced headaches for navigation: active exploration of the spatial distribution of the stimulus through movement. We move our body, or at least our nose, to find out where the smell is coming from (Richardson 2011). When the intensity of a smell decreases during movement, we know that we are moving away from the odor source. This strategy of sampling odors at different positions and comparing the intensities is often applied for finding the source of an odor.

Another way of using olfactory perception for navigation despite its lack of spatial structure is to combine olfactory information with other sensory information. The wind provides especially useful information. When we perceive the odor of a barbeque and simultaneously perceive airflow from the left, then we can infer that there is a barbeque to our left. This is how many flying insects use olfaction to find an odor source. Smelling the odor they are interested in, most commonly pheromones released by other members of the species, elicits flight against the airflow. When they lose the trail, they change their flight path into a random search pattern until they pick it up again, at which point they continue to fly upwind.

The fact that some instances of perception have no spatial structure has drastic consequences for philosophy of perception, as has been discussed previously (Lycan 2000; Smith 2002; Matthen 2005; Peacocke 2008; Batty 2010). Due to the lack of spatial structure of olfactory perception, concepts depending on spatial relations such as position, orientation, directedness, and movement, which play a very important role in philosophy of perception that is based on visual perception, play no role in an alternative account of the philosophy of perception for which olfaction is the paradigm. As a consequence, many theories that have been developed with the visual system in mind are incoherent when the paradigmatic sense is olfaction. Views that consider the body and its movements to be central for perceptual consciousness (for an overview, see (Prinz 2009); for an example, see the sensory motor contingency theory (O'Regan and Noë 2001)), for example, may be plausible for vision or other forms of perception that involve "an actively-explorable anisotropic field" (Humphrey 2001), but not for olfaction.

Olfaction is probably the only major human sensory modality that never perceives perceptual qualities that are arranged spatially (although it is possible to design stimuli that result in spatially unstructured percepts in every modality). In vision, touch, and taste, sensory neurons are arranged spatially and their patterns of activation are mapped onto perception so that the spatial structure of the percepts resembles the spatial structure of the perceived stimulus. In vision and touch, this spatial mapping is central to the function of these senses. In gustation, the mapping does not seem to be central to the function of taste perception. However, although this information does not seem to be important, it is easy to tell the difference between a few grains of salt on the left part on the tongue versus on the right part of the tongue. In audition the main strategy for structuring perception spatially is to compare input to the two ears. This comparison makes it easy to auditorily distinguish a car approaching from the left from a car approaching from the right.

3.2. Olfaction in time

Although olfactory perception has no spatial structure, it certainly has some type of temporal structure. All perception has temporal structure because perception by definition involves changes depending on the presence or absence of a stimulus over time. There would be no adaptive value to perceiving an unchanging stimulus. The temporal structure of olfactory perception is determined by the temporal structure of odor stimuli and by the characteristics of the olfactory sensory system. The stimulus, odor molecules floating through the air, is much slower than light, sound, and other stimuli. As expected, the olfactory sensory system is therefore not optimized to sense stimuli with great temporal resolution. Although olfactory perception is temporally structured, the structure is much less complex and carries much less important information than the temporal structure of vision or audition.

Temporal structure of olfactory stimuli

The ratio of different types of odorous molecules in the air at a given position changes over time. Large cities often smell like rotten garbage during the summer and like burnt coal during the winter. Farther away from cities, the smell of flowers fills the air in spring, the smell of burnt grass in summer, and the smell of decaying leaves in fall. Some societies have used such seasonal regularities in the temporal patterns of odors to construct calendars based on olfaction (Classen, Howes et al. 1994) (pages 95-97). Different times of the day also have different smells. For some, mornings smells like coffee, mid-day like cafeteria food, and evenings like beer.

In addition to these regular annual and circadian fluctuations in odors, regularly occurring events are also sometimes associated with specific smells. These can be natural events, like the blooming period of a certain flower, or cultural events like Christmas or Thanksgiving. Successions of smells can also form olfactory events on shorter time-scales. An example of such a temporally structured olfactory event is the grilling of a steak. The smell of the meat will intensify as it heats up on the grill. Then the smell will change in quality from cooked meat to burned meat. After the steak is entirely burned, the smell will become less intense and eventually disappear.

Because of the difference in physical nature between odorant molecules, vibrating air, and photons, olfactory events unfold several orders of magnitude slower than auditory or visual events. To illustrate the difference, let us consider an event that can be perceived both visually and olfactorily: the removal of a bouquet of fragrant flowers from a room. The visual perception is mediated by the photons that are reflected by the flowers. When somebody comes in, picks up the bouquet of flowers, and takes it away, the photons that are reflected by the flowers no longer reach the perceivers eye. The photons that were reflected by the flowers before they were removed from the room have been absorbed by matter. In contrast, the olfactory perception is mediated by odorous molecules given off by the flowers. When somebody comes in, picks up the bouquet of flowers, and takes it away, all the molecules that have been given off by the flowers before the flowers were removed remain in the room. As long as the flowers were in the room, there was an equilibrium. The flowers gave off a certain amount of odorous molecules per time unit and a certain amount of odorous molecules escaped from the room through the gaps under the door, etc. After the flowers have been removed, the concentration of odorous flower molecules in the room will slowly decline. How long it will take until the concentration is appreciably reduced depends on the circumstances. It can take hours or days. A perfectly insulated room that is filled with an odorant will remain filled with the odorant for weeks or months. When a different bouquet of flowers is brought into the room, the odorous molecules from the new flowers will mix with the odorous molecules from the flowers that were in the room before. The stimuli in olfaction are, under normal conditions, rarely temporally separated. Instead sequential stimuli overlap and mix.

Temporal structure of olfactory perception

Not surprisingly, our olfactory sensory system is adapted to the slow-moving stimulus that it detects and not optimized for high temporal resolution. Before an odor molecule can be sensed, it has to be transported to the top of the nasal cavity through sniffing. Once it reached the olfactory epithelium, it has to diffuse through the olfactory mucus, a gel-like secretion that protects the sensory neurons from physical damage, but allows odor molecules to diffuse from the nasal cavity to the surface of the sensory neurons. The molecular processes at the surface of the sensory neurons through which odorants activate sensory neurons are also much slower than those through which photons activate photoreceptors.

In addition to the relative slowness with which it unfolds, olfactory perception also differs from other modalities in that it is temporally discontinuous. Olfactory perception is discontinuous because it depends on sniffing (Mainland and Sobel 2006). We perceive our chemical environment as parceled by sniffs: in short, discreet olfactory experiences every 1.6 seconds (Laing 1983; Mainland and Sobel 2006). Because of this discontinuity, human olfaction has been called "a constant state of change-blindness" (Sela and Sobel 2010). The analogy between olfaction and change blindness in vision is that change in an image is easy to detect when the altered image appears immediately after the original image. In contrast, when the two images are temporally separated by a mask, the change is more difficult to detect due to change-blindness (Simons and Rensink 2005). Similar phenomena have also been described in touch (Gallace, Tan et al. 2006) and audition (Vitevitch 2003). However, in olfaction, two percepts are always separated by a period of no perception. The special experimentally induced conditions under which change detection fails in other modalities are very similar to the normal condition of olfactory perception. Consequently, the detection of temporal changes in olfaction is more challenging than in other modalities. To overcome this challenge, the olfactory system has adopted an adaptation-based strategy of change detection (Wilson and Stevenson 2006). If sequential sniffs bring the same stimulus to the olfactory sensory neurons, the neurons will adapt to the stimulus and their response rate will decline. If a novel stimulus is encountered, neurons will start firing again. This is how change is perceived in olfaction.

The combination of the temporal structure of odor stimuli and the characteristics of the olfactory sensory apparatus result in a very impoverished temporal structure of olfaction. The main temporal aspect of odor perception is that intensity and quality of the perceived smell change over time. In vision and audition, in contrast, temporal structure can add much more information. Consider for example bird song, or language, in which the temporal sequence within an auditory perception carries all the relevant information. Similarly, the sequence within a visual perception makes the difference between a movement from left to right and a movement from right to left. In olfaction, neither the encoding of information in sequences that is seen in audition, nor the combination of spatial and temporal perception to perceive motion is possible. All that the temporal structure in olfaction informs us about is the change of the type and number of odorous molecules in our nasal cavity.

3.4. Conclusion: Olfactory perception is the perception of a sequence of spatially unstructured perceptual qualities

In this chapter, I have shown that olfactory perception has no spatial structure and a severely impoverished temporal structure. On the other hand, as discussed in chapter 1, olfaction has many more discriminable qualities than other perceptual qualities. This suggests that in olfaction, the nature of the perceptual qualities is the important information. In vision, it is how the perceptual qualities are arranged in space, and in audition, the important information is the temporal arrangement of perceptual qualities. The differences are differences of degree; however, they are the cause of how we tend to think about these three modalities. In this conclusion, I will illustrate these differences using thought experiments.

In visual perception, the behaviorally most relevant information is in the spatial structure of the perception. Wearing goggles that invert the visual field so that what is on the left in physical space is perceived to be on the right and *vice versa* severely reduces the ability to use vision to guide the behaviors it usually guides. Inverted visual perception is of no help in winning a fight, hunting a boar, or manipulating tools. Punching to the left when one's opponent is to one's right is not adaptive. Eventually, people adjust to inversion goggles and start to punch to the left when they perceive their opponent on their right. However, one can imagine goggles that present the visual field in continuously changing, random orientations. It is not possible to adjust to such goggles and to the individual wearing those goggles, vision will be almost completely useless.

The goggle leave the temporal structure of visual perception intact. Colors are also perceived the same with the goggles as they are perceived without them. This shows that disrupting the spatial orientation of the percepts alone, while leaving other aspects of perception unchanged, has a very strong impact on the usefulness of visual perception. Seeing a boar does not help in hunting the boar when one cannot see where it is. Seeing that a fist is about to strike does not help in blocking the blow when one cannot see from where it is about to strike. Seeing a tool does not help manipulate that tool when one cannot see where the tool is. It is only through its spatial structure that visual perception enables us to do all those things.

In auditory perception, the spatial arrangement of perceptual qualities is much less important than in vision. Instead, most of the behaviorally relevant information in audition is in the temporal sequence of perception. To illustrate the importance of temporal information for auditory perception, imagine headphones that temporally rearranged the sequences of perceived auditory perceptual qualities. This would make audition almost completely useless, because we usually recognize auditory events through their typical temporal structure. Listening to recordings backwards makes it difficult to identify auditory events. It is possible to learn to recognize temporally inverted events. However, when the perceptual qualities that make up those events are randomly rearranged, it will be very difficult to recognize them. The headphones that rearrange auditory perceptual qualities in time leave the spatial structure of auditory perception intact and do not change the pitch and loudness of tones. However, without the temporal sequence information, auditory information would be almost completely useless. The impact of such a manipulation of auditory perception on its utility would be much more severe than the impact of manipulating the spatial arrangement of auditory perceptual qualities. Redirecting the input that normally reaches the left ear to the right ear and *vice versa* will affect some behaviors guided by audition, like turning away from an explosion to protect one's face. However, many other auditorily guided behaviors, for example those dependent on communication, are independent of the spatial information reflecting the source of the sounds.

In olfaction, neither the manipulation that would dramatically disrupt visually guided behaviors nor the manipulation that would dramatically disrupt auditorily guided behaviors would have a noticeable effect. Redirecting the air that would normally go into the left nostril to the right nostril at random would not change perception at all, because humans cannot tell the difference between the two conditions. Dividing the olfactory stimuli into short temporal sections and then presenting these sections out of sequence would presumably be noticeable under certain circumstances, depending on how long the temporal sections are. However, in contrast to the effect on sound-guided behaviors, such a manipulation would not affect odor-guided behaviors dramatically. In olfaction, all the behaviorally important information is in what type of perceptual quality is perceived. This is why there are trillions of different smells and only a few hundred thousand tones.

Of course, the perceptual qualities are central to perception in *all* modalities. It is the arrangement of these perceptual qualities in space or time that provide the behaviorally most relevant information in vision and audition. If there were no perceptual visual qualities, they could not be arranged in space or time. The difference between olfaction and the other senses is that in olfaction the nature of the perceptual qualities carries *all* the behaviorally relevant information. Imagine goggles that change each type of color quality into a random other type of color quality. Bright and fully saturated orange would be perceived as dark, unsaturated blue. Many visually guided behaviors -- manipulating tools, hunting boars, fighting -- would be little affected by such a change. The effect of changing each type of perceptual quality in audition into another type would be similarly limited. Imagine headphones that change each type of auditory quality to a different type of auditory quality. This would not have a large impact on our auditorily guided behaviors. In contrast to the limited effect in vision and audition, if a device would change each type of olfactory perceptual quality into another type, olfaction would be completely useless. Perceiving vanilla smell as leather smell and rose smell as rotten meat smell will make it impossible for any adaptive behavior to be executed in response to olfactory perception[14].

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[14] The importance of the type of perceptual quality over their position in space and time that is found in olfaction is presumably the original, and most common, state of perception. When it is cold, we know to wear a coat or show other heat preserving behaviors, regardless of the spatial and temporal structure of the cold. When we taste sugar, we should swallow what is in our mouth because it likely has high caloric content. The spatial and temporal structure of the gustatory perception is not important for guiding this behavior. Human vision and human audition are highly specialized evolutionary derived instances of perception in which arrangement in space and time has become more important.

Chapter 4: Olfactory objects

In the first three chapters, I have discussed perceptual qualities and how perceptual qualities can be arranged in space and time to form percepts. Introspectively, it usually does not appear to us as if we perceive arranged perceptual qualities. Instead, it appears as if we perceive objects and their properties. Based on this introspective evidence, object-based accounts of perception have been developed. Objects of perception are most often associated with vision and touch. The traditional auditory counterpart to the visual object is the auditory event (Blauert 1997). In the name of identifying commonalities between modalities, talk of "auditory objects" has become more common both in neuroscience (Griffiths and Warren 2004; Bizley and Cohen 2013) and in the philosophy of perception (O'Callaghan 2008; Matthen 2010; Nudds 2010)[15].

The modality to which an object-based account of perception has been most difficult to generalize is olfaction[16]. Barwich writes: "The more we understand about the multidimensionality of olfactory experiences and the processes of smell perception with which they resonate, the more apparent it should become that object-based talk about perceptions is no longer tenable, if it ever was" (Barwich 2014). I agree with Barwich and in in the first part of this chapter, I will show that the common criteria for objecthood fail to pick out olfactory objects. It

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[15] As reasons why it is justified to think of audition as involving objects, it has been pointed out that "audible individuals are temporally extended and bounded, serve as the locus for auditory attention, prompt completion effects, and are subject to figure-ground distinctions in pitch space" O'Callaghan, C. (2014). "Auditory Perception." The Stanford Encyclopedia of Philosophy, from http://plato.stanford.edu/archives/sum2014/entries/perception-auditory/. O'Callaghan O'Callaghan, C. (2008). "Object perception: Vision and audition." Philosophy Compass **3**: 803-829. proposed that objects in vision and in audition are mereologically complex individuals. In vision, complexity is conveyed by the perception's spatial features, whereas in audition temporal structure makes perception complex.

[16] For a defense of olfactory objects, see Stevenson, R. J. (2014). "Object concepts in the chemical senses." Cognitive Science **38**(7): 1360-1383.

is possible to relax the criteria for objecthood so far that by definition all perception, including olfactory perception, is the perception of objects. In the second part of this chapter, I will show that under these circumstances, when olfactory perception is postulated to be the perception of objects, there are no satisfying candidates for what the objects of olfactory perception could be.

4.1. Is olfactory perception the perception of objects?

If a given instance of perception can be either the perception of objects or objectless perception, then criteria to decide whether a given instance of perception involves objects or not has to be developed. I will discuss in this section the two criteria that are most frequently applied. The first criterion, which dominates the scientific literature, is that perception is the perception of objects when it involves figure-ground segregation ((Kubovy and Van Valkenburg 2001) (page 102) (Stevenson and Wilson 2007) (page 1823)). The second criterion for perceptual objecthood that will be discussed in this section is that perception involves perceptual objects when the Many Properties Problem can be solved (Batty 2014; Carvalho). The Many Properties Problem is the problem of distinguishing stimuli in which the same properties are instantiated in different arrangements. That we can tell the difference between a painting of a blue triangle next to a red square and a painting of a red triangle next to a blue square shows that vision can solve the Many Properties Problem.

Figure-ground segregation

Seeing a person standing in front of a wall or a banana lying on top of a table are instances of perceiving a figure (the person or the banana) that can be distinguished from the ground (the wall or table). For smell, whether percepts have a figure-ground structure is less obvious than for instances of visual perception. It has been argued that there is figure-ground segregation, and therefore an object of perception, in olfaction (Stevenson and Wilson 2007). I will investigate this claim here. I will consider whether there is figure-ground segregation in olfaction first for olfactory perception without temporal structure and then for instances of olfactory perception in which the potential figure has a temporal structure.

At any given moment, a mixture of different odor molecules at different ratios activates our olfactory system. This ratio carries no spatial information (see section 3.1.). A rose under your nose will produce the exact same activity of the olfactory sensory neurons as an intricate spatial arrangement of 275 vials, each of which containing the appropriate concentration of one of the 275 chemicals that are found in rose oil (Ohloff 1994) (pp. 154-158). An apple under your nose in a vineyard can produce the exact same pattern of activity in the olfactory sensory neurons as a bunch of grapes under your nose in an orchard. More generally, a weak source of odor A that is placed close to the perceiver in front of a strong background of odor B can be indiscriminable from a weak source of odor B close to the perceiver in front of a strong background of odor A. Olfactory perception does not have a figure-background structure that reflects position of the stimuli in physical space like the figure-background structure in visual perception.

The conclusion that there is no figure-ground segregation in olfaction because olfactory percepts do not reflect positions of stimuli in physical space can be challenged in several ways. First, instead of being based on the perceived spatial relation between figure and ground, the distinction between figure and ground in olfaction could be based on intensity. Smells in nature are usually mixtures of many different odorants. When one of these odorants within the mixture dominates the perceived smell, it could metaphorically be thought of as "rising above the background". This could be interpreted as intensity-based figure-ground segregation. Imagine smelling a wine that smells strongly of apple as well as weakly of pineapple, cinnamon, and cherry. Smelling this wine could be described as a figure of apple with a background of pineapple, cinnamon, and cherry. Another way in which olfaction could accomplish figure-ground segregation is through differential familiarity. An odor mixture could acquire a figure-ground-structure when its components differ in their familiarity. Imagine smelling a wine that has a weak apple smell as well as weak cardamom, turmeric, and elderberry smells. Imagine further that you never before smelled cardamom, turmeric, and elderberry. This situation can be described as perceiving an apple object and an unidentifiable background. Finally, a similar phenomenology can emerge due to violation of expectation. A wine that smells like a normal wine but also has an unexpected fishy smell can be described as a fish object and a wine background. In all these examples of olfactory perceptions that could be considered as having a figure-background structure, the distinction between figure and background is based on the prominence of some aspect of the olfactory percept. The prominence can be conveyed through intensity, familiarity, or unexpectedness. The prominent aspect is interpreted as the figure while the less prominent aspects form the background.

To decide if any of these situations should be considered as evidence for figure-ground segregation in olfaction, it is informative to compare them to analogous situations in visual perception. The first case, strong apple odor perceived simultaneously with weaker other odors, corresponds to the visual scenery of looking at a tiled bathroom wall with differently colored tiles. The color of one tile is darker and more saturated than the colors of the other tiles. The second situation, apple odor together with an unknown mix of odors, corresponds to the visual experience of seeing a pile of unfamiliar-looking alien artefacts with a dead cow in between them. The third situation, unexpected fish odor mixed with regular wine odors, corresponds to the visual perception of a pink banana in a bunch of yellow bananas. A review of the literature on visual perception shows that such situations would be described as allocation of spatial attention depending on stimulus salience. They would not be considered instances of figure-ground segregation. Since salience-based attention allocation is not considered to be evidence for figure-ground segregation in vision, it should also not count as evidence for figure-ground segregation in olfaction.

My discussion of figure-ground segregation in olfaction so far has abstracted away from the temporal structure of perception. I have only shown that stationary olfactory snapshots do not have a figure-ground structure. Differential prominence of different features of an olfactory percept does not amount to figure-ground segregation. However, olfactory perception does also have a temporal structure. The figure-ground segregation in olfaction could be based on the fact that different sets of features of an olfactory percept covary over time (Wilson and Stevenson 2006; Carvalho 2014). This is an intriguing idea because our sense of smell is optimized to detect changes rather than states. We adapt quickly to any temporally constant odor and therefore stay sensitive to changes (Dalton 2000; Stevenson and Wilson 2007). The constant odor to which we are adapted, and therefor perceive only weakly, can be considered "background odor". Any change "in front" of this background can then be considered an object. Olfactory objects, according to this description, are similar to auditory events. There may be an olfactory background consisting of a mix of body odors and low-grade pollution and then a strawberry odor appears and lasts for a few moments before it disappears again. The strawberry odor that changed while the other odors remained constant can be thought of as an olfactory perceptual object.

As with prominence-based attention, it is informative to consider whether covariation over time would be considered as evidence for figure-ground segregation in visual perception. Consider the banana as a figure and the table as a background. Now imagine that there is some localized damage and skin abrasion to the banana. Over time, the damaged spots of the banana will turn brown while the rest of the banana and the table do not change color. This would not result in a reassessment of the figure-ground segregation so that the brown spots on the banana are now considered the object and the yellow part of the banana and the table the background. Temporal changes do not introduce figure-ground relations in vision. It is therefore parsimonious that such temporal changes also do not introduce figure-ground relations in other modalities.

Another reason to resist a notion of perceptual objecthood that is based on the temporal structure of perception is that such a notion would be so inclusive that "perceptual object" would become a synonym of "percept". If appearance and disappearance of a perception is sufficient to make it the perception of an object, then all perceptual systems that detect change over time detect perceptual objects. A hypothetical sensory system that consists of a single sensory neuron can distinguish objects from background, when objects are defined by their temporal structure. The neuron will permanently be activated at an intermediate level due to background levels of the stimulus. Occasionally, it will be strongly activated for a certain period of time when it encounters high levels of the stimulus. Afterward it will go back to the intermediate level of activation. The periods of strong activation can be interpreted as the objects that can be segregated from the constant background. Under this notion of perceptual object, all perception is the perception of objects and the dispute about objecthood becomes a dispute about terminology.

The Many Properties Problem

Instead of using figure-ground segregation as the criterion of objecthood in perception, it has been suggested that perception is only the perception of objects when the Many Properties Problem can be solved. The Many Properties Problem (Jackson 1977) is the problem of assigning properties to objects in situations in which several objects are perceived simultaneously. When we see a blue circle and a red square, we can solve the Many Properties Problem and assign the properties "blue" and "round" to one object and the properties "red" and "square" to the other object. The way the Many Properties Problem is solved in visual perception is by grouping properties together based on their location in perceived space. Properties that move through space together are properties of the same object. In olfaction, there is no perceived space. Regardless, two different identifiable smells can be identified at the same time. We can simultaneously perceive wine smell and sausage smell. If either the sausage smell or the wine smell has a spicy quality, can we assign the spiciness to one of the two smells? If we can, then olfaction can solve the Many Properties Problem.

It has been suggested that olfaction can solve the Many Properties Problem and that "spicy wine, and sausage" does in fact smell different from "wine, and spicy sausage" (Carvalho) (page 12). However, no biological mechanism on which this capacity could be based has been suggested.

The molecules that arrive at the olfactory epithelium and elicit the percept of "spicy wine and sausage" are identical to the molecules that elicit the percept of "wine and spicy sausage". One of the many molecules that are perceived as spicy is cuminaldehyde. Cuminaldehyde is found in some wines and it gives the smell of those wines a spicy note. However, cuminaldehyde is also given off by some spicy sausages. When the cuminaldehyde molecules reach the olfactory sensory neurons, they do not carry information about their source. The perception is the same regardless of whether the cuminaldehyde is given off by the sausage or by the wine. Olfaction cannot solve the Many Properties Problem (Batty 2010; Batty 2011). Because we cannot tell which property belongs to which potential olfactory object, we also cannot tell how many potential olfactory objects contribute to a given instance of perception. Instead of smelling spicy sausage and wine, or spicy wine and sausage, we may smell wine, sausage, and a jar of cumin oil.

The finding that we cannot assign properties to smells seems to defy everyday experience. When an anchovy and garlic pizza is delivered, we know that the anchovy smell and the garlic smell are both properties of the pizza smell. However, this knowledge is based on background knowledge and assumptions rather than on perceptual grouping of the anchovy and garlic smell. If the pizza that is delivered does not have anchovies on it, but the pizza deliveryman carries some anchovies in his pocket to snack on, we will incorrectly assume that both the garlic smell and the anchovy smell are properties of the pizza. This is because our assigning of properties to smells is not based on the structure of our percepts, but on our assumptions about the most likely scenarios. Similarly, an individual familiar with spicy sausages but not with spicy wine will interpret the stimulus discussed above as the perception of wine and spicy sausage. An individual that is familiar with spiced wines, but not with spiced sausages will interpret the same stimulus as the perception of spiced wine and sausage. Nothing in the olfactory percept itself enables us to assign the spiciness to either of the two smells.

Just like figure-ground segregation, solving the Many Properties Problem is possible in olfaction when the temporal structure of olfactory perception is taken into account. Covariance between the sausage and spice smell over time are good evidence that they are released by the same odor source and that they are properties of the same object. However, as discussed above, if temporal criteria would be sufficient for objecthood, then all perception with temporal structure would be the perception of objects and "object-based perception" would just be a different word for "perception".

4.2. What could be an olfactory object?

In section 4.1., I used two different criteria for objecthood to investigate whether olfactory perception involves the perception of objects. The result of this investigation was that the only conceptual framework under which olfactory perception is the perception of objects is one under which every instance of perception is the perception of objects. If such a definition of objecthood is endorsed, the question whether olfactory perception is the perception of objects is not an empirical question. Instead, olfactory perception is by definition the perception of olfactory objects. In this section, I will investigated what the objects of olfactory perception that are postulated by such an approach could be.

I will first discuss candidates for olfactory objects that have been suggested in the literature. The most obvious candidates for olfactory objects are the source of the odorous molecules, the clouds of odorous molecules that are given off by the source, and the molecules themselves. In the second part of this section, I will use phenomenal presence as the criterion for what the objects of olfactory perception are. This criterion has been suggested by Budek and Farkas, who propose that the causes of an instance of perception that are present in phenomenology are the objects of that instance of perception (Budek and Farkas 2014).

Potential odor objects

A straightforward proposal about olfactory objects is that the source of the odorous molecules is the object of the olfactory perception. Benjamin Young calls this view, which is based on naive realism about perception (Gibson 1966), the "ordinary object view" (Young) (page 46). According to the ordinary object view, the objects of the smell of lions are lions. One problem with this view is that the source of odorous molecules can be specified at different levels. What appears to be lion smell is mostly the smell of lion urine, so both the urine and the lions themselves are possible objects of the perception. Somebody driving by the zoo may think of the entire zoo as the object of the lion smell. Lion urine, individual lions, the pack of lions, the lion enclosure, and the zoo all can be considered as the source of the lion smell and therefore as its object.

Another problem of the ordinary object view of olfactory perception is that the link between the source of molecules that cause olfactory perception and the perception is much weaker and less direct than the link between the source of the light that causes visual perception and the corresponding visual perception. The smell of lions will linger for a long time after the lions have been moved to another zoo. The lion odor will also stick to their zookeeper's clothes so that when she comes home, she will smell of lions. Are the zookeeper's clothes now the object of perception? These examples show that smells, after they are given off by their sources, are no longer linked to them. It is therefore difficult to identify the "original" source of a smell, and practically often impossible to track a smell back to its source[17].

Because of these problems with applying the ordinary object view to olfaction, several alternatives have been proposed. One alternative suggestion is that the cloud of odorous molecules given off by the odor source is the object of olfactory perception (Lycan 2000). This cloud object view avoids the problems of unambiguously identifying the source of the cloud of molecules that make the ordinary object view unattractive for olfaction. The disadvantage of this view is that it cannot be integrated into an evolutionary account of perception. The perception of lions provides useful information that can guide behaviors that increase the perceiver's fitness by decreasing the likelihood of being eaten by a lion. The perception of a cloud of odor molecules,

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[17] How strongly the messengers of perception are linked to their source is a matter of degree. The difficulties pointed out here are not unique to olfaction; they are however much more pronounced in olfaction than in other modalities. An example of a weak link between the messengers of perception and their source in vision is our visual perception of objects that are very far away. We can see stars that no longer exist, because the light from the stars takes a long time to reach our eyes and sometimes a star will cease to exist while the light is travelling from it to the earth. Even the stars that still exist are perceived to be at the position in the sky where they were when they gave off the light and not where they are when we perceive them. The path of light can also be changed through gravitational deflection. All these phenomena make the link between light and its source less direct. In most cases of everyday perception, the connection between light and its source is however much more direct than the connection between an odor and its source.

on the other hand, is in most cases not adaptive (as has been pointed out by Ruth Millikan in conversation with Bill Lycan (Lycan 2014) (page 7)).

A more technical problem with the cloud object view is that an odor source usually gives off hundreds of different odorous molecules. Presumably, under the cloud object view, each type of molecule is considered to form its own cloud. The perception of the smell of lions therefore is the perception of hundreds of different objects. Alternatively, all the different types of molecules given off by the lions could be considered to form a single cloud. However, at any time, different types of molecules that have been given off by different odor sources are in the air. The only thing the different types of molecules that are given off by a lion have in common is that they have been released from the same source. The only way to determine which of the many molecules in the air belong to the lion odor cloud is therefore by reference to the odor source. This reintroduces all the problems of the ordinary object view that the cloud object view was supposed to solve.

An alternative to the ordinary object view and the cloud object view is the molecule object view, according to which the odorous molecules that bind to our odorant receptors are the olfactory objects. Benjamin Young has developed a proposal along these lines, although he does not consider the entire odorous molecule, but just its chemical structure, to be the object of olfaction (Young 2011). The advantage of a molecule object view over the cloud object view and the ordinary object view is that the perceptual qualities associated with olfactory perception are related to properties of the molecules, not to properties of the ordinary object or the cloud. Depending on the different chemical and physical properties of the molecules, they interact with different combinations of odorant receptors. This combinatorial code determines the perceived smell. Differences in molecules therefore result in differences in perception. With the molecule object view, the correlation between physical differences between two objects and differences in the perceptual qualities associated with the two objects is much higher than with the ordinary object view or the cloud object view.

Accounting for the differences and similarities in perceived smells is an important advantage of the molecule object view. However, the molecule object view faces the same problems faced by the cloud object view. It fails to provide a connection between perception and adaptive behavior. Smelling macrocyclic rings with two hydrogen bonds at the central oxygen conveys no adaptive advantage. Another problem that the molecule object view inherits from the cloud object view is the unsatisfying account of the perception of odorant mixtures. Wine gives off hundreds of different types of molecules that have different chemical structures (Aznar, López et al. 2001). If molecules (or their structure) are the objects of olfactory perception, then we perceived hundreds of different objects when opening a bottle of Chardonnay.

The ordinary object view, the cloud object view, and the molecule object view all have their advantages and disadvantages. Maybe it is not necessary to pick one over the others. Instead, the advantages of all three views could be combined. The zoo, the lions, their urine, the cloud of molecules that forms above the urine, and the structure of the molecules in that cloud could *all* be objects of olfaction. Such a layered account of objecthood has been suggested by Lycan (Lycan 2014; Lycan 2014). This layered account of objecthood is inspired by the layered accounts of referring. Lycan's example of a layered account of referring is that we can point at a chalk mark on a board and thereby refer to a number; thereby we refer to a room; thereby we refer to the occupant of that room. The analogous account for olfaction would be that by smelling a certain molecule, we smell the cloud of molecules it belongs to; thereby smelling the lions that gave off the cloud of molecules; thereby smelling the zoo in which the lions are housed.

Phenomenal presence as a criterion for objecthood

There are different suggestions about what the objects of olfactory perception could be. How can we decide which of the different proposals correctly identifies the olfactory object? It may be counterintuitive that we perceive hundreds of different objects when we perceive a Chardonnay. However, if a theorist is willing to accept this consequence of her view of olfactory objects, what procedure can be used to find out whether she is right? One proposal for identifying the object of an instance of perception is to use phenomenal presence as the criterion for objecthood. Following this proposal, the objects of an instance of perception are the causes of that instance of perception that are present in phenomenology (Budek and Farkas 2014) [18].

Every instance of perception has causes. The perception of rose odor is caused by the rose and by the clouds of odor molecules given off by the rose and by the binding of those molecules to

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[18] The investigation of phenomenal presence as a criterion for objecthood is the only part of this dissertation in which it is important whether perception is conscious or not. Phenomenal presence requires conscious perception, so non-conscious perception cannot involve objects. Even when unconscious perception involves the perception of figures with properties that are correctly assigned to them in front of a background, it is not the perception of objects. On the other hand, according to the proposal by Budek and Farkas, every instance of conscious perception is an instance of the perception of objects because in every instance of conscious perception *something* is phenomenally present. That something is the object of the instance of perception.

olfactory sensory neurons. One could consider these causes of the instance of perception to be its objects. Lycan's layered account of objecthood suggests something similar. However, calling the causes of an instance of perception its objects does not result in an interesting notion of objecthood. Instead, it merely results in a change in terminology from "causes" to "objects". The proposal suggested by Budek and Farkas is that only a subset of the causes of perception, namely those causes that are phenomenally present are the objects of that instance of perception (Budek and Farkas 2014). We may "see" that it is cold outside because it is snowing, but the temperature is not present in our visual phenomenology and therefore not an object of our visual perception. The snow, on the other hand, is present in our phenomenology, and is therefore an object of this instance of perception. The objects are whatever is phenomenally present in a given instance of perception. What would this be in the case of olfactory perception?

The methods of determining what is phenomenally present are problematic because the main evidence for phenomenal presence is introspection, and introspections differ between individuals. This variability has resulted in different proposals about the objects of visual perception. Some theorists have argued that in instances of visual perception only colors and shapes are present in phenomenology (for example (Tye 1995)). Others have reported that objects such as pine trees are present (for example (Siegel 2006)). I hope that in the case of phenomenal presence in olfactory perception things are so clear-cut that there are no disagreements about introspections.

For people who are unaware of the advances in smell research, the only things that can be phenomenally present in olfaction are ordinary objects. It has been a scientific discovery that odor perception is mediated through molecules that form clouds. Not that long ago, it was speculated that olfaction could be mediated by waves in a way similar to the way in which audition and vision are mediated. It is not uncommon to meet people who are not aware that olfaction is mediated by molecules. An even more recent scientific discovery was that the structure of a molecule determines its smell. This discovery is so recent that it is still disputed and not universally accepted. The alternative suggestion is that intramolecular vibrations of the molecule determine the molecule's smell (Turin 1996). What does this mean for the phenomenal presence of clouds of molecules and of features of those molecules? Is the object of olfactory perception for scholars who believe in the vibrational theory of olfaction the vibrations of the molecules, whereas it is the structure of the molecules for those who believe that the structure determines a molecule's smell, and for the vast majority of humans who have no knowledge about these things, it is neither? Such an account of perceptual olfactory objecthood as dependent on the perceiver's believes and knowledge about olfactory perception is unsatisfying. A scholar who believes in the vibrational theory of perception would perceive the odor molecules' vibrations, whereas a supporter of the shape theory of olfaction would perceive the odor molecules' shape. Which of the two perceptions is veridical (if any of them is) depends on yet unknown facts about the perceiver's olfactory system. The perceptual objects are perceiver-dependent.

Perceiver-depend olfactory objects have also been suggested in the context of the perceived valence of perceived odors. In this context, what the object of olfactory perception is does not depend on the perceiver's textbook knowledge about olfaction, but on the perceiver's attitude towards the odor. Yeshurun and Sobel write:

> We suggest that an odor object is the integration of the odor’s inherent pleasantness (...) with the subjective state at the moment of coding: mood, hunger, fear, etc. Therefore, an odor object is not the odor of the banana but rather an integration of the pleasantness of the banana odor with the subjective state at which it was encountered. (Yeshurun and Sobel 2010) (page 229)

A similar proposal suggests that the object of olfactory perception is the biological value to the perceiving organism (Castro and Seeley 2014). What is phenomenally present when an odor is perceived, according to these proposals, is the pleasantness, or the value, of the odor. As a consequence, if objecthood depends on phenomenal presence, what the object of a given instance of olfactory perception is does not depend on the physical features of what is perceived or on the perceptual system with which it is perceived. Instead, what the perceptual object of an instance of olfaction is depends on the current behavioral goals and motivational states of the perceiver.

4.3. Conclusion: Olfactory perception is not the perception of objects

I do not want to deny that most instances of perception appear to us as if they are the perception of objects. Consider for example the tactile perception of an object that is stuck in your throat, or under your eyelid. The object that is stuck under the eyelid has a certain size and it is located at a certain position. The object also has non-spatial properties. It may be hot or rough, for example. As we know, the perception of an object stuck under the eyelid is in many cases illusionary. Such a perception is often not caused by a physical object. Instead, the perception of something being stuck in the perceiver's throat or under her eyelid, similar to the perception of an insect walking over the perceiver's skin, is usually caused by localized irritation of the skin or mucosa. This illusion of objecthood shares many features with other types of illusions. The illusion of objecthood, for example, resists cognitive influence. Even when my doctor inspects the inside of my eyelid and informs me that the perception is caused by localized irritation and not by a physical object, the illusion of perceiving an object under my eyelid continues.

A thought experiment shows how tightly illusory objecthood is linked to the spatial arrangement of perceptual qualities. Imagine that the skin irritation under the eyelid starts to spread. Once the perceptual qualities have spread to cover half of the perceiver's face, they are not perceived as an object that covers a large area of the face. Instead, they are now perceived as spatially arranged perceptual qualities. Because the perception of perceptual qualities that are spatially localized has a strong tendency to induce the perception of illusory objects, olfaction, in which perceptual qualities are not arranged spatially, is an ideal system to investigate perceptual objecthood without this complication.

There are two ways to think of the role of objects in perception. One approach is to establish criteria for when an instance of perception involves objects and then investigate whether a given instance of perception is the perception of an object or not. The alternative approach is to postulate that all perception is the perception of objects. This makes sense when one believes that perception is best described in terms of perceptual objects. The question, when all perception is postulated to be perception of objects, is what the object of a given instance of perception is.

In this chapter, I investigated two criteria that allow for an empirical test whether an instance of perception involves objects or not. The two criteria for objecthood I investigated are susceptibility to figure-ground segregation and capacity to solve the Many Property Problem. I argued that olfactory perception fails to satisfy both criteria[19]. I have shown that those that claimed otherwise stretched the notion of figure-ground segregation so that it includes figures that are delineated only by temporal structure. Because every perception has a beginning and an end, this results in the conclusion that all instances of perception are instances of object perception. Any proposal of an empirical test that judges some instances of perception to be the perception of objects and other instances of perception to not be the perception of objects, judges olfactory perception to be not object-directed.

However, testing for objecthood can be dispensed off when the olfactory perception is postulated to be perception of objects. There are many notions of objecthood that are so loose that they include all instances of olfactory perception. Jonas Olofsson for example writes that the unified olfactory percept is "commonly referred to as an olfactory object" (Olofsson 2014) (page 2). This approach suggests that there is no difference between the perception of objects and other perception, but that it is preferable, for theoretical reasons, to think about all instances of perception as involving objects. The important question, when perception is postulated to involve objects, is the nature of those objects. It is not easy to see what could count as a criterion for objecthood in such a situation[20].

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[19] That olfactory perception in humans does not satisfy these criteria for objecthood is contingent on the structure of our olfactory system. If our body were covered in odor-sensitive cells, then some instances of olfactory perception could have a spatial structure and we could sometimes segregate odor figures from an odor ground. Olfaction's ability for figure-ground segregation would under these circumstances be similar to figure ground segregation in thermoperception. We can segregate the sun's heat radiation from background radiation. The sun is then the object of our perception of heat. Similarly, a hot potato that we hold in our hand can easily be discriminated from the temperature background.

[20] Lycan comes to a similar conclusion, that it is hard to argue for a claim for what vision does and does not represent Lycan, W. G. (2014). What does vision represent? Does Perception have

I have reviewed some suggested objects of olfactory perception: the odor source, clouds of odor molecules, and the molecular structure of the odor molecules. I then used phenomenal presence as the criterion to decide what the object of olfactory perception is. What is phenomenally present in olfactory perception depends on the perceiver. When a perfumer's olfactory sensory neurons are activated by the synthetic molecule Galaxolide, the Galaxolide molecule, or its structure, are phenomenally present for the perceiver. When the same molecule activates the olfactory sensory neurons of an average consumer, laundry detergent, or fresh laundry is phenomenally present. Galaxolide is added to laundry detergent to give it its characteristic smell. In 1964, before Galaxolide was first synthetized, the object of perception that is triggered by Galaxolide would have been "something smelly", because nobody could have associated the perceptual quality associated with Galaxolide with a specific molecule, or a specific source of odor molecules. In general, for all odors for which the perceiver neither knows the molecule nor the source, what is phenomenally present is "something smelly". This is unsatisfying, because it means that the perception of an unidentified extremely unpleasant and an unidentified extremely pleasant odor would have the same object. It has therefore been suggested to add an additional level of complexity by making the perceiver-dependent pleasantness of the odor a part of the olfactory object.

The proliferation of different concepts of olfactory objects and the suggestions to make the relation between the perceiver and the odorous molecule part of the olfactory object show that no

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Content? B. Brogaard. Oxford, Oxford University Press**:** 311-328.. So maybe these problems are not unique to olfaction.

candidate for olfactory object resembles the common notion of perceptual object. This, I suggest, is because olfaction is not an object-directed process. It is therefore not justified to postulate that all perception is the perception of objects. The notion of objects unnecessarily complicates the description of olfactory perception. An alternative view, which I endorse, has been proposed by Clare Batty, who holds that what we perceive in olfaction is not objects, but existentially quantified properties ("There is F-ness here") (Batty 2010; Batty 2011). According to Batty, olfactory perception does not involve objects that have properties. Instead, in olfaction, perceptual properties are "free-floating" or "object-less" (Matthen 2005; Batty 2010). Batty calls this view, which is motivated by many of the same considerations discussed in this chapter, the *abstract view* of olfactory content.

Chapter 5: The function of perception

An important step to understanding any biological system is to identify its evolutionary function. What is the evolutionary function of perception[21]? Why have so many living things evolved elaborate systems to distinguish perceptual properties and to arrange them in spatial and temporal patterns? In this chapter, I will argue, perhaps uncontroversially, that it is the function of perception to guide behaviors. I will contrast this proposal with the alternative proposal that it is the function of perception to collect accurate information about the physical world[22]. In many instances of perception, this seems like a false dichotomy. Is it not possible that perception guides behaviors *by* collecting accurate information about the world? In this chapter, I will show that this is not possible. In some situations, guiding behaviors and collecting accurate information about the world are in conflict. In these situations, behavior guidance is *always* given priority over perceptual accuracy. I therefore propose that perception was shaped by natural selection to guide behaviors adaptively. The fact that in many cases it also collects accurate information about the physical world is due to the constraint that in some, or maybe even most, situations, behavioral guidance requires correct information about the physical

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[21] There are diverse philosophical theories about what "functions" in biology are (for a collection of essays on the topic, see Buller, D. J., Ed. (1999). Function, Selection, and Design. Albany, SUNY Press.). Functions can be either teleological functions, or causal (or systemic) functions. The teleological function of a biological structure or mechanism is what it was selected for Millikan, R. (1984). Language, Thought, and Other Biological Categories. Cambridge, MIT Press.. The causal function of a mechanism is the role of a structure or mechanism within a complex system Cummins, R. (1975). "Functional analysis." The Journal of Philosophy **72**: 741-765.. This discussion is about the teleological function of perception. The teleological function is supposed to explain why something is there. The teleological function of something is the same as its adaptive value or the reason why it was selected.

[22] I chose “collecting accurate information” as the alternative possibility of what perception’s non-behavioral function cold be. However, there are many similar proposals. One suggestion would be that perception maps the physical world accurately another that it represents the physical world accurately. My arguments that it is the function of perception to guide behaviors works against all of these non-behavioral proposals equally.

features of the environment. The collection of accurate information through perceptual systems is not a direct product of evolution. Perception-dependent behaviors are the direct products of evolution and the collection of correct information is a spandrel[23].

Let me illustrate the difference between correctness of information and behavioral-guidance using subway maps as an example. The function of subway maps is to help people navigate the subway system. It is *not* the function of subway maps to provide accurate information about the physical location of subway lines and stations. Of course, in many cases subway maps do provide accurate geographical information. However, whenever the map designer has to make a decision between two designs, one of which is more accurate and the other more useful, she will decide to make the map as useful as possible for those trying to navigate the subway system. This is because it is the function of the subway map to help riders navigate the subway system. That is what the map is for[24].

How can it be that reduced geographical accuracy of a subway map increases its usefulness as a tool for navigating the subway system? For the answer to this question, one has to compare a city's subway map with a geographical accurate map of the same city. Take New York City as an

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[23] Evolutionary biologists call byproducts of the evolution of other characteristics that themselves are not direct products of adaptive selection "spandrels" Gould, S. J. and R. C. Lewontin (1979). "The spandrels of San Marco and the Panglossian Paradigm: A critique of the adaptationist programme." Proceedings of the Royal Society of London, Series B **205**(1161): 581-598.,

[24] Helping riders navigate the subway system is the function of the subway maps on display in subway stations. One can imagine other subway maps with other functions. There could be a map of the subway system used by the fire department for emergencies. In this map, geographical accuracy is important and it is irrelevant how helpful it is for navigating the subway system.

example. In Figure 11A, a section of the official Metropolitan Transportation Authority subway map of New York City is shown. In Figure 11B, the same section form an alternative, geographically more accurate, map is shown for comparison. The designers of the official subway map have sacrificed accuracy in the geographical information conveyed by the map to increase the map's usefulness in many instances. Most obviously, in the official map, Manhattan is represented as less narrow than it is. This makes it easier to discriminate and follow the many parallel train lines connecting uptown Manhattan to downtown Manhattan. The official subway map also smoothens the tracks of the lines, as can be seen for example in the section of the B and D train within the red rectangle in Figures 11A and B. In the red circle at the southern tip of Manhattan, it can be seen how the designers of the official map distorted the map to separate stations that are very close to one another. This makes it easier to identify and distinguish these stations.

Another geographical inaccuracy that has been purposefully introduced by the designers of the official subway map to make it more useful is that they exaggerated the width of the Harlem River that separates Manhattan and the Bronx (black rectangles in Figures 11A and B). How does representing the river to be wider than it is make the map more useful? The river is a barrier and people taking the subway should be made aware of this barrier so that they can plan to exit the subway at a station that is on the same side of the river as their destination. How wide the river is does not matter, what matters is that it cannot be crossed. This is a typical situation in which geographical accuracy of a map and usefulness of a map are in conflict. Whenever a decision between accuracy and usefulness has to be made, the designer decides to make the map as useful as possible.


A
B
Marble Hill 225 St
Kingsbridge Rd
Fordham Rd
183 St
Burnside Av
176 St
Mt Eden Av
170 St
167 St
161 St Yankee Stadium
Inwood–207 St
Dyckman St
190 St
181 St
175 St
168 St
157 St
145 St
137 St City College
125 St
116 St Columbia U
Cathedral Pkwy (110 St)
103 St
96 St
86 St
79 St
72 St
66 St Lincoln Center
59 St Columbus Circle
50 St
42 St Port Auth
34 St Penn Sta
23 St
14 St
Christopher St Sheridan Sq
Houston St
Canal St
Franklin St
Chambers St
World Trade Center
Cortlandt St
Rector St
Bowling Green
South Ferry
Wall St
Broad St
Whitehall St
Fulton St
MANHATTAN
CENTRAL PARK
Hudson River
East River
Allerton Av
Pelham Pkwy
Bronx Park East
BRONX ZOO
Harlem 148 St
Lexington Av/59 St
Grand Central
Times Sq
Union Sq
Astor Pl
Bklyn Bridge-City Hall
225 St
Marble Hill
Broadway-7 Av Line
8 Av Line
Metro-North
Jerome Av Line
Lenox Av Line
Lexington Av Line
Amtrak
Roosevelt Island
PATH
Amtrak/LIRR
42 St-Grand Central
Canarsie
CLOSED

Figure 11: Two ways of representing the subway stations and tracks in Manhattan. A section of the official MTA subway map of New York City (A) and the corresponding section of a geographically more accurate alternative subway map (B) are shown. There rectangles, red squares, and black rectangles mark corresponding locations on the two maps. ((A) modified from the official MTA subway map; (B) modified from original work by SPUI (in the public domain under the Creative Commons License).

Just as it is the function of subway maps to help riders navigate the subway system, the function of perception is to guide the perceiver's behavior. Subway maps often, but not always, use accurate geographical representations to help riders navigate the subway system and perception often collects accurate information about the physical world to guide behavior. However, collecting accurate information about the physical world is only one of many different strategies used by perception to fulfill its function. Collecting accurate information is the *intermediate* function of *some forms* of perception, whereas guiding behaviors is the *ultimate* function of *all* perception.

In this chapter, I will show that chemosensory perception, and perception in general, fails spectacularly at collecting accurate information about the physical world. By "accurate" or "correct" perception, I mean perception that reflects similarities in the physical world in similarities in perception. Similar things are correctly perceived when they are perceived to be similar. In section 5.1., I will review evidence that different individuals, especially when they belong to different species, often perceive the same stimulus or object differently. Identical things are usually not perceived identically by two different perceivers, which shows that at least one of the perceivers perceives incorrectly. In section 5.2., I will then show that even within the same perceiver similarity relations in the physical world are not accurately reflected in perception. In all the cases that I will discuss, perceivers have evolved to perceive the physical world less accurately than they could. In contrast, they perceive in all those cases the world in a way that ensures that they interact with it behaviorally in the most beneficial way for them. This discrepancy indicates that perception evolved to fulfill behavioral needs rather than to collect accurate information about the world. Those who resist a behavior-centered conception of the function of perception have responded to the type of evidence I will present in sections 5.1. and 5.2. by redefining "correctness". In section 5.3., I will discuss the alternative notions of correctness that have been proposed and show that they result in a notion of correctness according to which perception is correct when it elicits an adaptive behavioral response. When such a behavior-based notion of correctness of perception is endorsed, then guiding behaviors and collecting correct information are the same thing and the conflicts between them that exist when correctness of perception is based on a relation between what is perceived and how it is perceived disappear.

5.1. Perceptual variability

If all living things had evolved to collect accurate information about the physical world, one would expect all living things to collect very similar information, since they all live in the same physical world. In this section, I will show that this is not the case. I will provide a few examples of perceptual differences between different species, as well as examples of how the same stimuli are perceived differently by members of the same species, depending on their behavioral goals.

Perceptual variability between species

Comparative ecology has shown that different animal species often differ dramatically in how they perceive the physical world. Often this variability can be explained by the ecological niche inhabited by the species in question and by the behavioral repertoire with which the species interacts with the environment. Bees, for example, visit flowers, where they collect nectar. It is therefore important for bees to be able to distinguish flowers. Since many flowers have UV patterns, bees evolved the ability to detect UV light, so they can distinguish flowers using the UV patterns on the flowers' petals[25]. Another example of animal species that have evolved the capacity to sense stimuli that humans are blind to are those species that can perceive electrical stimuli. Because water is a much better conductor of electricity than air, electroreception is most often found in aquatic animals. Sharks, for example, can sense the weak electric fields generated by the nerve and muscle activity of potential prey. Some shark species, such as the lemon shark, use this information to coordinate their attacks. Other animal species lost some perceptual capacities because they moved into an ecological niche in which there was no need to detect certain aspects of the physical world. Some species of cavefish, which live in dark caves, have lost their eyes and therefore their ability to perceive light (Jeffery 2009). Similarly, carnivorous mammals, which have a sugar-free, meat-only diet, do not need to perceive sweet tastants. Consequently, many species like the cat, the spotted hyena, and the fur seal, have lost their sweet taste receptor, Tas1r2 (Jiang, Josue et al. 2012).

One could argue that in all these cases, the different species do not perceive the physical world differently; instead, they perceive different properties of the physical world. For example bees, with their capacity to perceive UV light, perceive the UV-reflecting property of the physical world. The blind cavefish, in contrast, do not perceive any light-reflecting properties of the physical world. However, in many cases, different animal species perceive the same properties of

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[25] The flowers provide from being visited by nectar-collecting bees because the bees carry pollen from one flower to the other, pollinating them. The bees' capacity to detect the UV patterns of flowers and the UV patterns of flowers therefore presumably coevolved.

the physical world, but the properties are perceived differently. Many examples have been discussed in section 2.1., where I discussed the diversity of perceptual spaces. However, not only the perceptual qualities themselves can differ between different species. The spatial and temporal arrangements of the perceptual qualities can also differ. Visual perception in fruit flies, for example, has higher temporal, but lower spatial resolution than human vision. The properties of the physical world that fruit flies and human perceive visually overlap largely, but how the two species perceive the physical world visually differs dramatically.

Perceptual variability within the same species

How the physical world is perceived differs not only between different species. Even members of the same species can have different behavioral goals and therefore different ways of perceiving their environment. In some species, for example, the perceptual systems differ between the sexes. The best-known examples are perceptual systems that are specialized for finding mates or facilitating courtship. Male moths, for example, have sensory organs that are specialized for the detection of the pheromones released by the females of the species. In other species, perceptual systems that are not involved in guiding sexual behaviors are sexually dimorphic. Some species of anglerfish, for example, show extreme sexual dimorphism. The male anglerfish are tiny compared to the females and spend most of their life as parasitic appendages attached to a much larger female. These males have very different behaviors than the females and therefore perceive the physical world very differently from them. Before the males attach to the female, they have large eyes that are specialized for detecting the bioluminescent lure of the female. After they attach to the female, the eyes degenerate.

Even within the same individual, the behaviors and therefore the demands on perception can change. Consider for example the fruit fly, which lives as a larva before it pupates and then emerges as an adult fly. The behaviors that need to be guided by perception for the larva are very different from the behaviors that perception has to guide in adults. The larva hatches from the egg on rotten fruit and spends the entire time before pupation eating. The adult fly that emerges from the pupae has a much richer repertoire of behaviors that includes finding a mate, mating, finding an appropriate site to lay eggs, laying eggs, and so on. Consequently, the same individual has a much richer perception of its environment as an adult. Most notably, adults fly whereas larvae cannot fly. The high temporal resolution of visual perception that flies need to execute flight maneuvers is therefor only found in the adult.

In other cases, perception changes with the behavioral demands within the same individual in the same developmental stage. Female mosquitoes, for example, have to find an animal to bite because blood is their main source of protein. They need protein to produce eggs. After filling up with blood, the mosquito has to find a puddle of water to lay eggs in. This abrupt change from having to find a source of blood to having to find a place to lay eggs is mediated by a change in the olfactory sensory neurons of the animal. These neurons become less sensitive to body odors and more sensitive to odors given off by potential egg-laying sites (Davis 1984). Similar changes in the activity of the most peripheral olfactory sensory neurons have also been found in other species (see for example (Root, Ko et al. 2011; Saveer, Kromann et al. 2012)).

In humans, a good example to illustrate the dependence of perception on changes in behavioral goals is the change in is the change in olfactory perception during pregnancy (for a review, see

(Doty and Cameron 2009)). A large number of self-reports indicate that the perception of food smells changes during pregnancy. The reason for this is that the most adaptive eating behavior is different during pregnancy. A pregnant woman has to not only feed herself, but also the embryo growing in her. An adult usually eats for energy, but during pregnancy, there is rapid tissue growth that needs to be sustained with a different combination of nutrients. In addition to the need to fuel the embryonic growth, pregnant women also need to be more vigilant than usual to avoid food that, although save for adults, might endanger the embryo. The most adaptive behaviors towards the same food items are therefore different during pregnancy as during other times. Consequently, the smell of these food items is perceived differently during pregnancy.

Different perceivers all encounter the same physical world. How they perceive this world differs dramatically. The largest differences are found between members of different species, but members of the same species can also differ dramatically in how they perceive the same stimulus. If correctness of perception is based on a relation between what is perceived and how it is perceived, then there are instances in which animals evolve to perceive the physical world less accurately, which is a strong indication that perceiving the world accurately is not the evolutionary function of perception.

5.2. Similarity of percepts and similarity of stimuli

> "Perception and desire have to meet certain standards of accuracy to enable creatures to survive in the world: they have to enable us to respond similarly to things that are similar and differently to things that are different, to avoid what is harmful, and to pursue what is beneficial" (page 73) (Nagel 2012).

In this quote from Thomas Nagel, two standards that have to be met by perception are mentioned. First, perception has to enable us to respond similar to similar things. Second, perception has to enable us to avoid what is harmful and pursue what is beneficial. These two standards are alternative formulations of the two proposals about the function of perception that are compared in this chapter. Retaining similarity relations is the criterion for accurate or correct perception. Avoiding harmful things and pursuing beneficial things is the criterion for guiding adaptive behaviors. Plainly, the two standards mentioned by Nagel are often in conflict with one another. The deadly coral snake and the harmless milk snake are very similar in their visual appearance. However, one is harmful and the other, for a hungry hunter, beneficial. We cannot simultaneously respond to these two visually similar snakes similarly, while also avoiding what is harmful and pursuing what is beneficial.

Situations in which perceiving what is physically similar as similar is in conflict with perceiving things that are harmful as different from things that are beneficial are interesting for understanding what the function of perception is. Examining such situations will reveal whether perception prioritizes guiding behaviors or collecting correct information. When evolutionary processes can shape our perceptual systems either to ensure that we avoid what is harmful and pursue what is beneficial *or* to respond similar to things that are similar, what is the outcome? In this section, I will show that the outcome is that evolution through natural selection selects the perceptual system that ensures adaptive behaviors over the alternative perceptual system that ensures correctness of the collected information. The chemical senses, especially the perception of bitter tastants, provide good case studies to illustrate this outcome[26].

Bitter tastants

Smell, taste, and other modalities combine to form the experience of flavor. One of the basic tastes that contribute to flavor is bitter taste. Extremely diverse chemicals, like hydrolyzed proteins, alkaloids, rancid fats, and poisons (Martin 2013) (page 65), all have a bitter taste (Figure 12). These bitter tastants are produced by a large variety of different plants. What most of the plants in which bitter tastants are found have in common is that they are inedible, unhealthy, or even toxic. As a consequence, whenever a bitter tastant is perceived, the appropriate behavioral response is to spit out what is in your mouth. Bitter tastants are therefore an excellent example of physically diverse stimuli that all require the same behavioral response. The perceptual qualities associated with these stimuli correlate much stronger with the appropriate behavioral response than with any physical feature of the stimuli. Hydrolyzed proteins and rancid fats are perceived as being similar, although they are physically very diverse. Non-rancid fat is physically more similar to rancid fat than hydrolyzed proteins. However, because rancid fat and hydrolyzed proteins have reduced nutritional value and because

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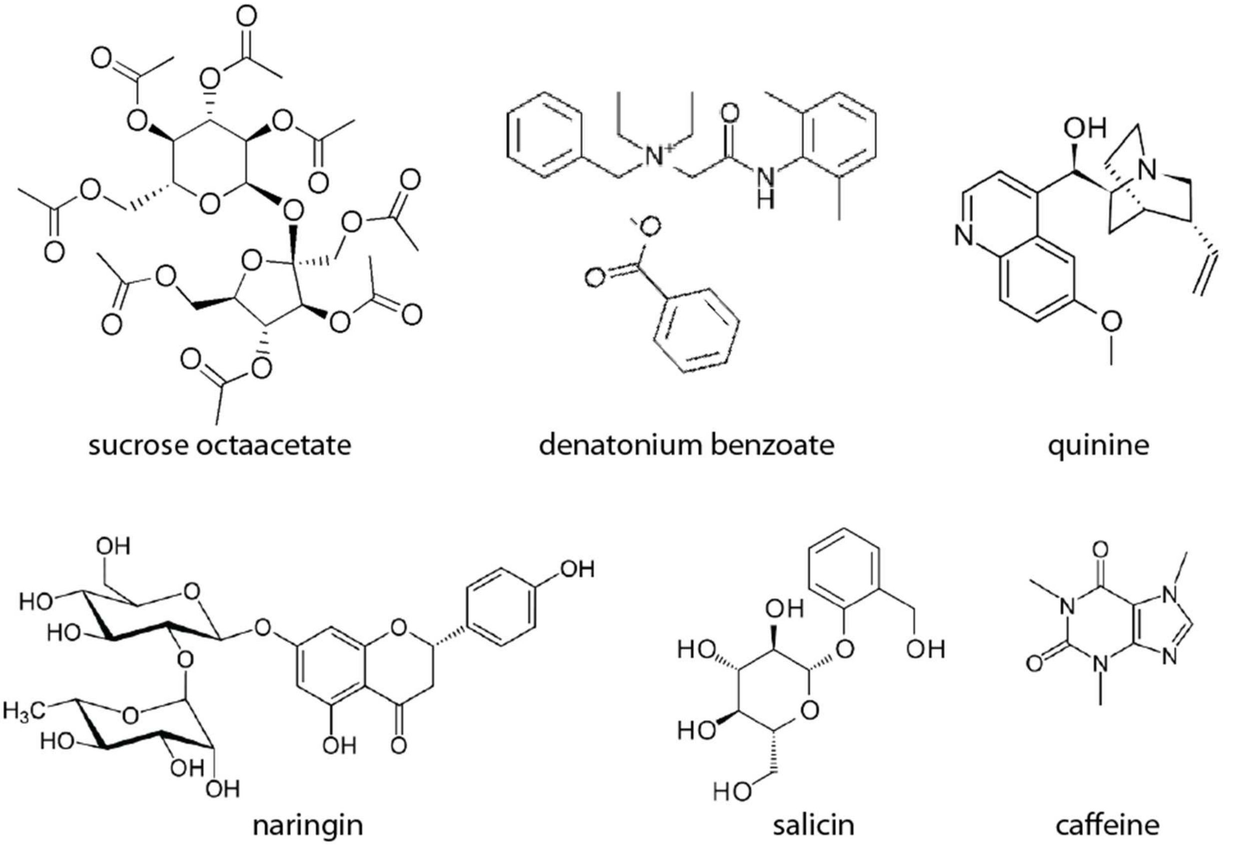
[26] The perception of temperature also provides excellent examples that have been discussed in detail by Akins Akins, K. (1996). "Of sensory systems and the "aboutness" of mental states." The Journal of Philosophy **93**(7): 337-372.. As Akin shows, the thermoreceptive system does not have the function of measuring the temperature in the environment as accurately as possible. Instead, its function is to help the perceiver execute behaviors that aim at avoiding damage through cold or heat. Evidence that this is the case is that the same physical stimulus is perceived to be of different temperature with different parts of the skin. Areas of skin that cover structures that are more delicate "exaggerate" temperature extremes. Similarly, the endpoint of (more dangerous) rapid temperature changes are perceived to be of different temperature than when the same endpoint has been reached through (less dangerous) gradual temperature change.

rancidification can produce toxic compounds, they are perceived as bitter. Because non-rancid fat is an excellent source of energy, it is not perceived as bitter. The physical similarity between the stimuli is not reflected by perception. This shows that, when efficiently guiding behaviors involves misrepresenting similarity relations between stimuli, as it is the case in bitter perception, then perception will misrepresent the physical world.


sucrose octaacetate

denatonium benzoate

quinine

naringin

salicin

caffeine

Figure 12: Six structurally diverse molecules that are perceived as bitter (Laska, Rivas Bautista et al. 2009).

The correlation between bitter perceptual qualities and the appropriate behavioral response of spitting out whatever is perceived is good, but it is not perfect. Sometimes, bitter foods and drinks are incorporate into our diet, which seems to contradict the idea that bitter taste is a signature of inedibility. Theobromine in chocolate and caffeine in coffee are two examples of bitter alkaloids consumed by humans. However, these chemicals are not examples of non-toxic bitter tastants. Instead, they have been incorporated into our diet *because* they are toxic. At low enough doses, these toxins, like many others, act as stimulants. To bypass the evolved response to bitter substances, large amounts of sugar can be added to coffee or chocolate to make bitter stimulants palatable.

Other bitter compounds are edible even at high doses. Evolution is an ongoing arms race between those who try to eat plants, and plants that try to avoid being eaten. A good defense against being eaten available to plants is to become toxic. Once toxic plants evolved, an equally good defense against being eaten is to taste like a toxic plant. This strategy of imitating the warning signal of a harmful species is known as Batesian mimicry. The similarity between harmless milk snakes and venomous coral snakes is the result of Batesian mimicry. Bitter tasting compounds that are edible may also be the result of Batesian mimicry. To avoid being eaten by humans, announcing that one is inedible through bitter taste is sufficient as long as many plants that taste bitter are actually inedible. Because our perceptual systems coevolve with the natural environment they perceive, the correlation between the perception of bitterness and the optimal behavioral response is not perfect. Some inedible compounds are not bitter and some bitter compounds are edible. However, the correlation between the perceptual quality and the appropriate behavior is much better than the correlation between the perceptual quality and the physical properties of the stimuli.

Evolution of perceived similarity

Bitter tastants are not the only case of perception that successfully guides behavior in the absence of a system that is concerned with collecting accurate information about similarity relations in the physical world. In olfaction, perceptual qualities are also more closely related to the appropriate adaptive behavioral responses than to the physical features of the stimulus (Castro and Seeley 2014). Consider for example molecules with a musky smell, which are found in glandular secretions of a wide variety of animals as well as in many different plants. The different molecules that are perceived as musky have very different chemical structures (Kraft 2004). The same is true for other smells like camphor or almond. In both cases, diverse sets of stimuli are perceived to have similar perceptual qualities.

One can speculate how chemical sensors that are sensitive to a wide variety of different chemicals that are physically different but require the same behavioral response, like the bitter tastant receptors, have evolved. The first step in the perception of tastants is that they are bound by a receptor molecule on the surface of a sensory neuron. There are different types of receptor molecules that bind to different types of taste molecules. Whether a given type of receptor molecule binds to a taste molecule or not depends on the receptor's molecular structure. The molecular structure of the receptor is determined by its amino acid sequence, which in turn is determined by the DNA sequence of its gene. Mutations in the receptor gene can alter the structure of the receptor and therefore change which chemicals can activate the receptor. Imagine that the first receptor in evolutionary history that bound a bitter tastant did bind to solanine, a bitter tasting toxin found in many plants. To be adaptive, activation of the receptor must have triggered the spitting out of the solanine-containing food that activated the receptor. Over time, random mutations have produced slight variants of this receptor. If any of these variants gained sensitivity to a second chemical that is found in a different inedible plant species, then the mutation was advantageous, because it increased the ratio of edible over inedible plants consumed. If the mutation made the receptor sensitive to a chemical found in edible plant species, it resulted in the edible plant being not consumed. This mutation therefore decreased the ratio of edible over inedible plants consumed and therefore was non-advantageous. In this manner, a receptor that detects the difference between edible and inedible plants can evolve. "Edible" and "inedible" are not features of the physical world, but they are properties that are relative to the perceiver[27]. As the hypothetical bitter receptor evolved into a reliable indicator of whether the perceiving organism should swallow or spit out the perceived food, it evolved away from accurately representing similarity of chemicals. The stimuli the receptor responded to became more and more physically diverse.

The mechanistic explanation of the evolution of a receptor sensitive to diverse molecules that all require the same behavioral response illustrates how a chemosensory system that guides behavior without collecting accurate information about similarity relations in the physical world can evolve from a system that collects accurate information. The mechanistic explanation also illuminates why cases like this are more likely to be found in the chemical senses than in vision. The reason for this difference is that the visual system perceives identity and location of objects, whereas the olfactory system only perceives identity of odorants. Just like many taste molecules require the same behavioral responses, there are instances of visual perception in which different visual objects require the same behavioral response. Whether somebody throws a rock, a book, or a shoe at you, the right response in all three cases is to move out of the object's trajectory. The

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[27] Whether a compound is edible and how nutritious it is for a given organism depends on the organism's digestive system and physiology. Cows have a specialized stomach for digesting grass. Termites can digest wood with the help of symbiotic bacteria in their guts. Neither grass not wood are good food sources for humans who lack the adaptations to make use of these food types.

same behavioral response is required regardless of *what* is perceived, just like in the case of bitter tastants. However, the required behavioral response to having any object thrown at you depends strongly on *where* the object is perceived. If it is perceived at eyelevel in the front, ducking is the best response. If it is perceived lower, stepping to the side will be more appropriate. If it is perceived to the left, the left arm should be raised to cover the face. If it is perceived to the right, the right arm should be raised to cover the face. When it comes to the perception of location, each location requires a different behavioral response because behaviors that are responses to the location of a perceived object are directed behaviors.

Consider a fictional situation to illustrate how the need for accurate presentation of the location of objects in vision results in a perceptual system in which similarity in the physical world is often reflected in similarity in perception. Assume that the presence of a lion, a rattlesnake, and an alligator all require the same behavioral response: freezing. Being able to discriminate these three animals is not advantageous because the optimal behavior in response to detecting them is the same. Now, if the three animals are perceived olfactorily, the olfactory system may evolve into a system that does not discriminate between lions, snakes, and alligators. An odorant receptor that mediates the freezing behavior could evolve to bind the different odors given off by the three different animals. We would lose the ability to discriminate these animals olfactorily because discriminating them has no adaptive value.

Now consider an alternative scenario. Assume that the appropriate behavioral response to lions, rattlesnakes, and alligators is running away from them. Further, assume that the animals are perceived visually. In this situation, we would not only need to know that we are encountering a lion, rattlesnake, or lion, but also where the animal is. Running *away* from it requires locating it in space. In this situation, the visual system would not lose the ability to discriminate the three animals, although discriminating them has no adaptive advantage. The reason for this is that how the animal's identity is perceived is severely constraint by the need to perceive its location. A system that has to perceive the location of objects will automatically also perceives the shape and the movements of objects, and rattlesnakes are shaped very differently from lions. They therefore also move differently through the visual space. This is why in vision and other modalities in which spatial perception plays an important role, guiding behaviors adaptively and collecting accurate information about the physical world often coincide.

The perception of space (and the perception of time, which I have not discussed here) is a notable exception to the rule that the similarity of percepts does not reflect similarity in the perceived stimuli but similarity in the adaptive behavior that the stimuli require. The reason for this exception is that successfully executing behaviors directed towards objects in the physical space requires accurate information about the position of the objects in physical space.

5.3. Alternative notions of correctness

Members of different animal species perceive the same physical stimuli vastly different. Even individuals of the same species evolved to perceive the same stimulus differently depending on their behavioral goals. Furthermore, when perceiving similar things similarly is in conflict with perceiving harmful things to be different from beneficial things, perceptual similarity reflects behavioral relevance rather than physical similarity of the stimuli. This type of evidence shows that perception is not about perceiving the physical world correctly, but about guiding beneficial behaviors. However, this conclusion only holds when *correct perception* is defined as perception in which the physical similarities in the world are reflected in similarities between percepts. A possible way to continue to resist a behavior-centered function of perception in light of this evidence is therefore to adjust the notion of perceptual correctness. Two alternative notions of correctness have been suggested in this context[28].

Perceptual system-dependent correctness

One alternative way of thinking about correctness in the context of perception is to define correct perception as perception that is triggered by its ordinary causes. When this definition is applied, then the gustatorily perception of bitterness is correct if it is triggered by the molecules that ordinarily activate the bitter receptor. This is akin to the proposal that perception represents open-ended disjunctive properties (Lycan 2014). The information that is collected by the perception of bitterness therefore is "What I currently have in my mouth is either sucrose octaacetate or denatonium benzoate or quinine or naringin or salicin or caffeine........". This information is correct when I have one of these chemicals in my mouth. An alternative and shorter way of saying the same thing is that the information about the physical world that I collect when perceiving bitterness is "What I currently have in my mouth is capable of activating the bitter receptor". This information is correct when something I have in my mouth is capable of activating the bitter receptor. Correctness of perception, under this notion, is dependent on the perceptual system. As the human bitter receptor evolves, the molecules it binds change.

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[28] Both of these possible responses are discussed by Akins as potential defenses of what she calls "the traditional view". She calls the first possibility I discuss in this section "the *a priori* defense" and the second the "appeal to biologically salient properties" Akins, K. (1996). "Of sensory systems and the "aboutness" of mental states." The Journal of Philosophy **93**(7): 337-372..

However, under the notion of perceptual system-dependent correctness, this change does not result in a change of how correct the receptor perceives the physical world. The old version of the receptor and the new version of the receptor perceive the world differently, but both perceive it correctly. The visual perception of an animal with a single photosensitive cell is as correct as the visual perception of the animal with the most sophisticated apparatus. Indeed, all perception by properly functioning perceptual system is by definition correct perception when correctness is defined in terms of the perceptual system (Akins 1996).

Perceiver-dependent correctness

A notion of perceptual correctness that, like perceptual system-dependent correctness, does not rely on the relation between the content of the perception and the stimulus is perceiver-dependent correctness. The difference between perceptual system-dependent correctness and perceiver-dependent correctness is that perceptual system-dependent correctness depends on the interaction between the stimulus and the perceptual system, whereas perceiver-dependent correctness depends on the interaction between the stimulus and the perceiver. The perception of bitterness is perceptual system-dependent correct when the perceived stimulus is capable of activating the bitter receptor. It is perceiver-dependent correct when the stimulus is inedible or toxic for the perceiver. In the first case the correctness depends on facts about the perceiver's perceptual system, in the second case, it depends on facts about the perceiver. This difference can be illustrated using the example of artificial sweeteners. The perceptual quality of sweetness is usually associated with tastants that have high caloric value. The appropriate behavioral response to it is to swallow. Sugars like glucose are typical examples of chemicals that taste sweet and have high caloric value. Artificial sweeteners are molecules that taste sweet but have low caloric value. Under the notion of perceptual system-dependent correctness, perceiving artificial sweeteners as sweet is correct perception because the perception is triggered by molecules that ordinarily activate the sweet receptor. Under the notion of perceiver-dependent correctness, the perception of artificial sweeteners as sweet is not correct because the behavior triggered by sweet perception (swallowing) is not adaptive for molecules with no caloric content. The reason why the sweet receptor misinforms us about the caloric content of artificial sweeteners is that these non-natural molecules were not present in the environment in which the perceptual system evolved.

Matthen has suggested perceiver-dependence of perceptual correctness in the form of species-specific standards of correctness (Matthen 2005). According to Matthen, every species has different perceptual systems and different ecological needs and therefore needs to perceive the physical world in a way specific to that species. As was reviewed above, perceptual systems and perception do not only differ between different species, but also between the sexes and life stages of the same species. Species-specific standards of correctness are therefore not enough. What is required are species-, sex-, life stage-, situation-specific standards of correctness.

Perceptual system-dependence and perceiver-dependence of perceptual correctness both propose that correctness of perception is independent of the relation between the stimulus and percepts. Instead of a mechanism that collects information about the stimulus, perception becomes a mechanism to collect correct information about the relation between the perceiver and the physical world. The molecule binds to *my* bitter receptor. The bitter plant is inedible *for me*.

5.4. Conclusion: Perception evolved for guiding behaviors

I have set this chapter up as a comparison between two proposals about the evolutionary function of perception: collecting correct information about the environment and guiding behaviors. Investigating chemosensory perception reveals that perception did not evolve to correctly represent, map, or collect information about the physical world. Instead, it evolved to guide adaptive behaviors of the perceiver. Adaptive behaviors are driving evolution with no regard to the correctness of the underlying perceptions, beliefs, or calculations. For example, there is no scientific evidence that an individual continues to exist in some form after death. Nevertheless, the belief in the afterlife, although almost certainly false, is widespread among human societies. It may have evolved not because it is a true belief, but because it is a false belief that induces behaviors that lead to increased fitness.

The impression that perception guides behavior *by* collecting accurate information about the physical world is most seductive when considering the perception of space in vision. Successfully hunting a boar requires information about the position of the boar in space accurately so that boar-directed movements can be executed. Other aspects of visual perception are constrained by this need for accurate spatial representation and much of visual perception therefore accurately reflects similarities in position and shape. As I have shown in this chapter, collecting accurate information about the physical world is not a function of chemosensory perception or other forms of non-spatial perception. The only function of perceiving smells and tastes is guiding adaptive behaviors. Collecting accurate information by itself has no adaptive value, and when perception guides adaptive behaviors by other means, collecting correct information provides no additional benefit for the organism.

The conclusion that collecting correct information is not the function of perception depends on a notion of correctness that defines correct perception as a perception in which similarities between stimuli are reflected in similarities between perceptions. Some scholars who resist the behavior-based function of perception have defended the collection of correct information as a function by redefining perceptual correctness. According to these alternative notions of perceptual correctness, whether a given instance of perception is an instance of correct perception does not depend on facts about the stimuli, but on facts about the perceiver. For example, different species need to respond differently to different stimuli. Whether a given chemical is toxic for the perceiver depends on the perceiver's physiology. A substance that is toxic for a human is not necessarily toxic for a trout and the other way around. The similarity in perception does not reflect the similarity of the chemicals, which would be the same for all perceivers, but the similarity in toxicity, which depends on the perceiver and differs between different species. Ultimately, these perceiver-dependent accounts of correctness define correctness as being dependent on behavior: the correct perception of something toxic is the perception that results in the evolved adaptive response to toxins.

Part III: Cognitive processes

So far, I have discussed the perception of perceptual qualities. I have also explored how these qualities can be combined in time and space, whether these combinations amount to something like perceptual objects, and what the function of perceiving and combining perceptual qualities is. Throughout, I have pretended that perception is separate from other cognitive processes and that the different perceptual modalities are not connected. Now, in the last part of my dissertation, I will acknowledge that the distinction between perceptual and non-perceptual processes is largely arbitrary. A satisfying account of olfactory perception has therefore to include an analysis of the relation between olfaction and non-perceptual cognitive processes, as well as of the relation between olfaction and other perceptual modalities.

In chapter 6, I will discuss the privileged connection between olfaction and emotional processes and the weakness of the connection between olfaction and language. I will contrast olfaction with vision to show that how perception is connected to specific non-perceptual processes depends on the modality under investigation. The connections between olfaction and emotional processes reflect the evolutionary history of olfactory perception. Because each modality has a different evolutionary history, it is not possible to generalize from the connectivity observed in one modality to the connectivity of all other modalities. In chapter 7, I will address the structure of the mind more generally. I will argue against using the concept of modularity to describe the structure of the mind and instead propose that the mind, much like the brain, is best thought of as a collection of overlapping functionally coupled networks. In the second part of chapter 7, I will investigate some of the functionally coupled networks involving olfaction with a special focus on cognitive penetration and crossmodal perception.

Chapter 6: Connections between olfaction and cognitive processes

Olfaction is often considered the most animalistic and primitive of our senses. Odor stimuli induce desires, emotions, and physiological responses that make us respond to certain smells in automatic ways. Reason is powerless to intervene. In contrast, vision is said to provide us with information that is used in rational analysis that leads to us deliberately choosing the most appropriate behavior. In this chapter, I will show that these caricatures of smell perception and visual perception have a basis in reality. The results of behavioral experiments, as well as neuroanatomical and functional evidence, demonstrate that olfaction has a privileged connection to emotional processing. On the other hand, plenty of evidence shows that the connection between olfaction and language centers is comparably weak. This heterogeneity of the relations between a given perceptual modality and different cognitive processes has to be acknowledged by any account of perception. There are no paradigm examples for the relation between perception and cognition. Instead, the relation between a given perceptual system and a given cognitive process depends on their shared evolutionary history.

In this chapter, I will discuss the connectivity between olfaction and two non-perceptual processes: language and emotional processing. This discussion will confirm that the connections between perception and non-perceptual processes differ substantially between olfaction and vision. This heterogeneity of the connections between perceptual systems and cognitive processes reflects the different evolutionary history of these systems and defies a generalizable account of the relation between perception and cognition.

6.1. Olfaction and language

> The sight in my opinion is the source of the greatest benefit to us, for had we never seen the stars, and the sun, and the heaven, none of the words which we have spoken about the universe would ever have been uttered. But now the sight of day and night, and the months and the revolutions of the years, have created number, and have given us a conception of time, and the power of enquiring about the nature of the universe; and from this source we have derived philosophy, than which no greater good ever was or will be given by the gods to mortal man. This is the greatest boon of sight.
>
> Plato's *Timaeus*

Plato tells us that visual perception is a requirement for language; without sight, "none of the words we have spoken about the universe would ever have been uttered"[29]. Language, in turn, is the tool of philosophy. Without vision, there would therefore be no philosophy, which is probably why philosophers concerned with perception have such a strong preference for vision over all other modalities. That Plato's intuition has some truth to it has been confirmed by psychology and neuroscience. It is easier for us to name and talk about colors then to name and talk about smells. There are two aspects of this difficulty to talk about smells. One problem is the lack of a smell vocabulary. Many languages have words for colors, like "blue" and "green"

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[29] A similar proposal has been made by Michael Tomasello in his *Origins of Human Communication* Tomasello, M. (2008). Origins of Human Communication. Cambridge, MIT Press.. Tomasello argues that human communication evolved from joint attention and shared intentionality. Joint attention is the phenomenon of an individual attending to an object after observing that another individual attends to the object. When we come across a group of people looking out the window, we are likely to join them to find out what interesting thing is going on outside. Joining others attention seems natural and does not require any conscious reasoning. However, being able to do that requires understanding what others perceive when their eyes are directed in a certain direction. This ability is sometimes referred to as "mindreading", because it requires inferring the content of another individual's mind in the absence of communication. This cognitively complex process is so sophisticated that it is rarely found in non-human animals. Joint attention in humans is only possible for visual attention. We can see what someone is looking at, but not hear what they are listening to, feel what they are touching, or smell what they are sniffing. Only through vision can one individual observe another individual in the process of perceiving Tomasello, M., M. Carpenter, et al. (2005). "Understanding and sharing intentions: The origins of cultural cognition." Behavioral and Brain Sciences **28**(5): 675-+..

(Berlin and Kay 1969). At least the English language does not have equivalent words for smells. Words used to describe smells are either judgments about the smell and its effects ("horrid", "soothing"), or, most frequently, the name of the source ("flowery", "leathery"). Why do we lack a smell vocabulary? It is possible that the lack of a smell vocabulary is caused by cognitive architecture. However, it is also possible that language coding is, for some reason, better suited to express some sensations rather than others. A third alternative explanation is that the cultural forces that shaped language happened to shape English in a way that reflects the relatively higher importance of colors compared to smells for the culture in which it evolved (for a review of these three possible explanations and of modality-dependent ineffability in general, see (Levinson and Majid 2014)). Because there are alternative explanations, the difference between our smell vocabulary and our color vocabulary do not show that there is an impoverished connection between olfaction and language centers. However, our limited abilities to talk about smells are not only due to the lack of an appropriate vocabulary. A second problem with talking about smells is that, even when there is an appropriate word to label a smell, we often fail to access it. This inability to access language to name smells or talk about them provides the evidence for a poor connection between olfactory processing and the language center that I will discuss in this section.

Naming smells

It is difficult for us to name a smell. To some degree, this is because, during development, we form much fewer associations between smells and verbal labels than between sights and verbal labels. Adults spend considerable time with preverbal children looking at picture books and pointing at drawn objects while saying, "this is a fire truck" or "this is a cow". Much less time is spent holding odors under children's' noses while uttering the odors' names. As a consequence, most of us have many more associations between visual appearances and names than between smells and names. However, for some odors, like coffee, sweat, gasoline, or garlic, there have been (for people with life histories similar to mine) many chances to learn the name of the odor. Interestingly, even for those very common and familiar odors, naming the odor is astoundingly difficult. In one experiment, the majority of participants were unable to name the smells of beer, urine, roses, or motor oil (Desor and Beauchamp 1974).

The inability to name an odor can have different reasons. The process of naming odors, just like any naming process, consists of three steps. First, the odor has to be identified. After the odor has been identified, the verbal label that is associated with the odor has to be activated. Finally, the response has to be generated (Johnson, Paivio et al. 1996). The identification step can be further subdivided. To identify an odor, it has to be detected, discriminated from other odors, and recognized. Odor recognition consists in matching the perceived smell to a previously perceived smell. Recognition does not imply the ability to name. One can recognize an actress in a movie from having seen her previously in another movie without being able to name her (Chobor 1992) (page 356). The poor performance of subjects in odor naming experiments could be due to difficulties at any of the steps involved in the naming process. The most likely explanation for the difficulties with odor naming is that accessing linguistic semantic information about odors is difficult (for the evidence that this is the case, see (Stevenson 2009)). This would mean that the subjects do recognize the odor, but are unable to name it. To test whether subjects recognized the odor but cannot name it, one would have to add a test for odor recognition that does not depend on verbal report to the experiment. One could, for example, ask subjects who could not name the odors of motor oil, urine, or beer, which one of the three they would rather drink. My prediction is that subjects would decide to drink beer more frequently than urine or motor oil. Similarly, I predict that they would be unlikely to pour the beer in their car's engine. If these predictions are true, then the deficits in odor naming are due to the difficulty of accessing linguistic labels for the odors. Either way, correct odor identification cannot be revealed by naming. Naming requires that, in addition to identification of the smell, the associated verbal label is activated and the response generated. From a failure to name an odor, it cannot be concluded that the odor was not identified correctly.

That the poor performance in odor naming is not due to problems in identifying the odor, but due to problems in making the connection between the perception and the appropriate verbal label is illustrated by the prevalence of the tip-of-the-nose phenomenon (Sulmont-Rosse 2005). The tip-of-the-nose phenomenon occurs when people are incapable of retrieving from memory the word that is associated with an odor, although they correctly identified the odor. The tip-of-the-nose phenomenon is named in analogy to the tip-of-the-tongue phenomenon, which is the failure to retrieve a word from memory in combination with the feeling that retrieval is immanent (Schwartz and Metcalfe 2011). Tip-of-the-nose phenomena are not caused by problems with odor identification, but by our inability to name odors. This is demonstrated by experiments in which subjects fail to name an odor correctly, but after they are provided with a list of odor names that includes the name of the odor that they have to name, or other semantic information about the odor, they can name the odor (Sulmont-Rosse 2005) (Gilbert 2008) (page 127).

Talking about smells

It is very difficult to name an odor, even for a subject who knows the odor name and does recognize the odor. Another striking difference between olfaction and vision with respect to language is how difficult it is to say anything about an odor that we recognize, but cannot name. In vision, we commonly talk about things we cannot name. We can talk about someone's visual appearance and behavior without knowing his or her name. In fact, knowledge of the person's name would not make a difference in what we are able to say about them. In vision, when an object cannot be named, it is still possible to retrieve a large amount of information about the object from memory (Lambon Ralph, Sage et al. 2000). We can describe the appearance of an actor whose name is on the tip of our tongue. We can list the movies he was in and describe his appearance in the hope that somebody else will help us out and provide the name of the actor that we currently cannot access. In olfaction, this is not the case. Very little can be said about an odor unless we are able to name it (Jönsson, Tchekhova et al. 2005). Stevenson writes: "What this suggests is that access to semantic information in vision is partially (if not fully) independent of the ability to name an object, while for olfaction a name appears necessary to access the same store of semantic information." (Stevenson 2009) (page 1008). It can be argued whether Stevenson is right and the problem is access to semantic information or more specifically access to linguistic semantic information. In an experiment that compared perfume experts with novices, it has been shown that the ability to perform actions that depend on semantic information like grouping of perfumes is to some degree independent of the ability to apply linguistic descriptors to those same perfumes (Veramendi, Herencia et al. 2013). This, like the speculation above that even subjects who are not able to name the odors of beer and motor oil are unlikely to drink motor oil instead of beer, suggests that it is not all semantic information, but specifically linguistic semantic information that is difficult to access in olfaction. Regardless of whether accessing any type of semantic information, or only accessing linguistic semantic information is problematic, the difficulty to access information about recognized odors that cannot be named further illuminates the fragility of the connection between olfactory perception and language processes.

It can be speculated that we did not evolve a stronger connection between olfaction and language because language is not necessary for olfaction to perform its function. Olfactory information is not used for abstract problem solving. Instead, olfactory-guided behavior is mainly concerned with executing simple behaviors when an odor is encountered (Herz 2001; Herz 2005). In addition to this speculative evolutionary explanation, several neuroanatomic explanations for the poor connection between olfaction and language have been suggested. The lack of a thalamic relay in olfaction (Herz 2005), the fact that odor information is predominantly processed in the right hemisphere of the brain (for a review, see (Royet and Plailly 2004)) whereas language is predominantly expressed in the left hemisphere (Binder, Frost et al. 1997), and potential competition for computational resources (Lorig 1999) have all been suggested as contributors to our diminished capacity to name and talk about odors.

Whatever the reason for our inability to semantically process odor information is, it dramatically influences verbal reports about multimodal perceptions. Visual information always dominates when a verbal report is produced based on sensory information from different modalities. When visual and olfactory information are in conflict, the verbal report unfailingly reflects visual perception. This has been demonstrated in an experiment that set up a direct competition between conflicting visual and olfactory perceptions. Students of the Faculty of Oenology of the University of Bordeaux were asked to describe the taste of different wines. They tasted, in different sessions, a red wine (a cabernet-sauvignon/merlot) and a white wine (sémillon/sauvignon), as well as the same white wine, but with odorless red color added to it. The students described the taste of the white wine using words that are usually used to describe white wines. The red wine was described using words that are commonly found in descriptions of red wines. The interesting outcome of the experiments were the words that the students used to described the taste of the wine that tasted like white wine but looked like red wine. The description of this wine was more similar to the description of the red wine than to the description of the white wine (Morrot, Brochet et al. 2001). In other words, when visual information is available, the experts' description of wine taste is dominated by color rather than smell.

As part of the same study, the authors also analyzed the words used in thousands of wine tasting comments that they obtained from wine critics. They divided the tasting comments into those about white wines and those about red wines. What they found is that "the odors of a wine are, for the most part, represented by objects that have the color of the wine" (Morrot, Brochet et al. 2001). Descriptors like "honey", "lemon", "grapefruit", "straw", and "banana" are often used to describe white wines, but never to describe red wines. On the other hand, the most common descriptors that are more frequently applied to red wines than to white wines are "cherry", "blackcurrant", "raspberry", "violet", and "redcurrant". Morrot and colleagues did not test the winemaking students whether they are capable of telling which of the three wines taste the same. It is likely that the students would have been able to distinguish between the red wine and the white wine with the red food color despite the color of the two wines being indiscriminable. Despite the inability to base verbal reports on olfactory perception, humans have an excellent sense of smell and perform very well in olfactory discrimination tasks (Bushdid, Magnasco et al. 2014). That experts can be tricked into verbally describing the taste of a white wine that is colored red as if they would describe a red wine is not a consequence of an underdeveloped sense of smell. It is a consequence of the dominance of vision over olfaction when it comes to producing a verbal report. Vision has a privileged connection to language processes and therefore has a stronger impact on verbal reports than conflicting information from other modalities such as olfaction[30].

6.2. Olfaction and evaluation

While olfaction has little impact on verbal reports about perception, it is often thought to play an important role in inducing and regulating certain emotions. Nabokov wrote, "Smells are surer than sights or sounds to make your heartstring crack." The same thought has been less poetically expressed by the psychologist Rachel Herz: "... the sense of smell and emotional experience are fundamentally interconnected, bidirectionally communicative and functionally the same." (Herz 2007) (page 15). That smell and emotions are "functionally the same" means that there are striking similarities between how both odors and emotions motivate behaviors. It has been said that "More than any other sensory modality, olfaction is like emotion in attributing positive

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[30] Dominance of vision over information from other modalities during multi-modal perception is often observed. A famous example is the ventriloquism effect. Although the voice attributed to the ventriloquist's dummy comes from the speaker's mouth, it is perceived as coming from the dummy's mouth because visually, the dummy's mouth is perceived as moving whereas the speaker's mouth is not. What is special about the cases discussed here is that vision does not appear to change the olfactory perception as much as it specifically changes the verbal report.

(appetitive) or negative (aversive) valence to the environment." (Soudry, Lemogne et al. 2011) (page 21). Humans use olfactory information mainly to evaluate food, locations, and other humans (Stevenson 2009). These evaluations result in changes in affective states and they are associated with highly adaptive behaviors.

Paradigmatic examples of the olfaction-emotion-connection (which has been reviewed in detail before: (Ehrlichman and Bastone 1992; Köster 2002; Herz 2007; Stevenson 2009)) are the influence of odors on emotions involved in romantic love and sexual arousal (Herz 2007; Stevenson 2009), and the close connection between olfaction and disgust (McBurney, Levine et al. 1977; Stevenson 2009; Stevenson, Oaten et al. 2010). Disgust, love, and sexual desire are examples of evaluative emotions, and the parallels between emotions and olfaction are only found for simple evaluative emotions. Regulating more complex emotions that are based on understanding complex social relations and other people's intentions require a semantic analysis that cannot be performed based on olfactory information. These more complex emotions are therefore mainly regulated by visual and auditory input that can convey social relations and intentions. Listening to a dark and tormented poem is more efficient at inducing sadness than any olfactory stimulus. Jealousy or gratitude are usually induced and regulated by visually observing people act in certain ways.

The simple evaluative emotions that are closely connected to olfaction are also usually associated with physiological responses. Being disgusted increases the likelihood of shuddering, retching, and vomiting. Being sexually aroused increases heart rate and blood flow to the genitals. Emotions also are closely related to moods, which can be considered longer lasting states that increase the likelihood of specific emotions. Squeamish people are more easily and frequently disgusted and people with a high libido are more frequently and easily sexually aroused. It is an important and unresolved question what the relations between moods, emotions, and physiological responses are. The most notable dispute is whether, as proposed by William James, emotions are the perception of physiological responses. For the purpose at hand, it will not be necessary to answer these questions. Instead, I will limit myself to providing evidence for an exceptionally close connection between olfactory processing on the one side and evaluative emotions, moods, and physiological responses on the other side.

Olfaction as inducer and regulator of evaluative emotions

Odor perception is largely the perception of odor valence. Plato suggested that "pleasant" and "painful" are the only odor categories (Plato). More recently, multidimensional scaling techniques uncovered that valence is the most important perceptual dimension in olfaction (Haddad, Khan et al. 2008). For colors and tones, valence is not an important perceptual dimension. When we are asked to arrange several odors in a one-dimensional space, we will likely order them at least in part according to their pleasantness. Colors, on the other hand, are more likely to be ordered from blue to red, and tones from low to high. This does not mean that all colors or all tones are equally pleasant. Very high tones are usually considered unpleasant and people tend not to like yellow-greenish colors. However, the difference in valence between the smell of rotting corpses and vanilla smell is larger than the difference in valence between yellow-green and your favorite color. Most people would rather live in an apartment in which the walls are painted in the least pleasant color than in an apartment that is filled with the least pleasant smell.

A well-known effect of the strong affective quality of smells is olfaction's capacity to elicit vivid memories. Odor-induced memories are often very emotive and produce a strong feeling of "being there" (Stevenson 2009). This capacity of odors to generate detailed vivid memories is called "Proust effect" after the author Marcel Proust (Chu and Downes 2000). Proust described in *In Search of Lost Time*, involuntary vivid childhood memories that were induced by the smell of madeleines. Memories like those described by Proust are so remarkably vivid because the close connection between olfaction and emotion can give even mundane odors strong affective relevance. Affectively relevant memories, like those of weddings and car crashes, are always more vivid than other memories. In odor-triggered vivid memory, everyday situations can gain the same vividness by hi-jacking the affective power of odors.

Further evidence for the close connection between olfaction and evaluative emotions is that emotional and physiological responses are more difficult to voluntarily modulate when they are odor-induced than when induced by other means. Olfaction induces evaluative responses in an unmediated, direct, and automatic fashion. The smell of a preferred food is a potent inducer of salivation and subsequent consumption of the food. The smell of rotten corpses is a potent inducer of vomiting and subsequent behavioral odor avoidance. In comparison, pictures of food and pictures of rotten corpses are far less potent in inducing salivation or vomiting. Furthermore, the emotional and physiological responses induced by visual stimuli are easily modified by background information. The sight of a rotting corpse will not induce a strong affective response when the perceiver knows that it is an actor in make-up or a digital special effect in a movie. For smells, such background information is powerless to attenuate the affective response. The smell of decaying bodies can be recreated in the laboratory from synthetic molecules that have names like "putrescine" and "cadaverine". Exposing people to the synthetic corpse smell is likely to induce vomiting even when the subjects of the experiment have been told prior to the experiment that the smell they are about to perceive is a mixture of molecules that were synthesized in a factory, rather than the odor coming off rotten corpses. Overcoming visually-induce emotions is much easier than overcoming odor-induced emotions. This difference shows that the connection between visual perception and emotional processes is much more flexible and fragile than the connection between emotion and olfaction.

All of the observations and experiments discussed above suggest that there is a privileged connection between olfaction and evaluative emotions. Skeptics will ask for an experiment in which the modalities are directly compared. However, comparisons between modalities are difficult because the results of the comparisons depends on the stimuli that were chosen for comparison (Ehrlichman and Bastone 1992). In one experiment, it was shown that odor stimuli elicited stronger affective responses than the corresponding visual stimuli. Subjects were asked to smell an odor, for example the odor of freshly brewed coffee, or view a corresponding scene, for example somebody pouring coffee from a pot into a cup. Then they were asked to write down "whatever immediately came to mind". Subjects wrote shorter reports in response to the olfactory stimulus that in response to the visual stimulus, indicating that verbal reports are dominated by visual input. However, the reports in response to the olfactory stimulus contained more affective words than the reports in response to the visual display (Hinton and Henley 1993).

Shared neuroanatomy of olfactory and emotional processes

Mechanistically, the close connection between olfaction and evaluative emotions can be explained in terms of neuroanatomy. There is large overlap between the brain regions that process emotions and smells (for a review, see (Soudry, Lemogne et al. 2011)). Much of the processing of emotions and olfactory information occurs in an evolutionary ancient brain structure called the limbic system[31]. Many of the brain structures in the limbic system play important roles both in the processing of olfactory information, and in the processing of emotions. Consider for example the amygdala, an almond-shaped group of nuclei that is part of the limbic system. The amygdala is involved in the regulation of emotion (Aggleton and Young 2000; Salzman and Fusi 2010). Especially well studied is the role of the amygdala in regulating fear and aggression. In addition to this role, the amygdala also processes olfactory information. The amygdala receives strong direct input from the primary olfactory cortex, but very little direct input from the visual system (Zald and Pardo 1997; Gutiérrez-Castellanos, Martínez-Marcos et al. 2010; Pessoa and Adolphs 2010). In rats, around 40% of the neurons in the amygdala are responsive to odors (Cain and Bindra 1972). Even more intriguingly, the connection between the primary olfactory cortex and the amygdala is bidirectional (Zald and Pardo 1997).

A second brain structure that is involved in both olfactory processing and the processing of emotions is the olfactory bulb. The olfactory bulb receives direct input from the olfactory sensory neurons. It is where the first steps of olfactory information processing happen. The

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[31] This part of the brain is also known as "reptilian brain", because we share it with reptiles, or "rhinencephalon" (literally, "nose brain"), because it processes smells. It is not a functionally unified system but rather a set of neighboring brain structures including the primary olfactory cortex, the limbic lobe, the hippocampus, and the amygdala.

olfactory bulb also plays a role in emotional regulation, which is surprising for such a peripheral structure that is only one synapse removed from sensory neurons. The olfactory bulb is so important for the processing of emotion, that rodents in which the olfactory bulb has been removed surgically are an animal model for depression. The behavioral, endocrinological, and molecular changes seen in these animals are similar to those observed in patients with depression. Furthermore, these changes can be reversed by the same interventions that are used to treat patients suffering from depression, including antidepressants and electroconvulsive shock. The depression-like symptoms in mice without an olfactory bulb are not merely a response to the lack of olfactory input. Mice with an intact olfactory bulb in which olfactory input has been interrupted through other methods do not show depression-like symptoms. These results suggest that the olfactory bulb, which is the first and most important center of olfactory processing, also plays an important role in regulating emotions (for a review, see: (Song and Leonard 2005)).

The part of the neocortex that processes olfactory information is the orbitofrontal cortex, which is located above the orbits in which the eyes are situated. The orbitofrontal cortex is only found in mammals (Gottfried 2007) and it is, unlike the visual cortex, not well connected to the frontal areas that are involved in semantic analysis (Price 2007). The role of the orbitofrontal cortex in olfactory processing is a matter of ongoing research. A lesion study of a single patient showed that brain injury that was largely limited to the right orbitofrontal cortex did completely abolish conscious processing of olfactory information. The patient's ability to modulate his sniffing behavior in response to olfactory stimuli was unaffected and he showed normal skin conductance responses to odors (Li, Lopez et al. 2010). Based on this study, which is broadly consistent with previous studies of patients with orbitofrontal damage or lesions (see references in (Li, Lopez et al. 2010)), it has been proposed that the orbitofrontal cortex is the neural correlate of olfactory consciousness. Others have suggested that the main role of the orbitofrontal cortex is to process the hedonic value of smells (Rolls, Kringelbach et al. 2003). In addition to its role in olfactory perception, the orbitofrontal cortex also plays a key role in regulating affect, emotion, and motivation (Zald and Rauch 2008; Gottfried and Zelano 2011). The main role of the orbitofrontal cortex in this context seems to be to link reward to hedonic experience (Kringelbach 2005). Damage to the orbitofrontal cortex can lead to disinhibited behavior that can include gambling, swearing, drug addiction, and hypersexuality.

The amygdala, the olfactory bulb, and the orbitofrontal cortex are just three examples of brain structures that play important roles in olfactory processing as well as in the processing of emotions. Other structures within the limbic system show similar profiles. The large overlap of brain regions that process emotions and brain regions that process olfactory information provide the mechanistic explanation for the privileged connection between olfaction and the processing of evaluative emotions.

6.3. Conclusion: Olfaction is well connected to emotional, but not to linguistic processing

The evidence presented in this chapter shows that olfaction has a strong impact on evaluations and emotions, while our capacity to process olfactory information linguistically is very limited. This is not a new insight. Over 2,000 years ago Plato wrote that odors "have no name and they have not many, or definite and simple kinds; but they are distinguished only as painful and pleasant" (Plato). Today we know that the reason for the privileged connection between olfaction and evaluative emotions is that the same neuronal networks in the brain that process olfactory information also process emotions. The connection between olfaction and emotions is presumably not the only privileged connection between a perceptual modality and a non-perceptual cognitive process. Vision seems to have a privileged connection to language processes. An analysis of proprioception, the sensing of the relative position and movement of body parts, would reveal a strong connection between proprioception and motor regulation. That one can find this type of modality-specific connections shows that sensory information from a given modality is made available only to those processes that can use the information for adaptive behaviors. The motor system needs to know the current angle between the forearm and upper arm, so that it can execute directed arm movements. The language system does not need to know the current elbow angle because being able to report the position of your forearm verbally does not convey strong adaptive advantages.

The sense of smell has evolved to be an evaluative rather than a descriptive sense. Olfactory information is used mainly to make decisions about rejecting or accepting food or mates (Stevenson 2009). Describing verbally the smell of spoiled meat is not crucial for survival; having a negative emotional response to spoiled meat that is stronger than hunger is crucial for an adaptive, odor-guided, behavioral response. The connection between olfaction and emotion is so close that Rachel Herz wondered "whether we would have emotions if we did not have a sense of smell; *I smell therefore I feel?*" (Herz 2007) (page 14). Herz's thoughts mirror those of Plato, who wondered whether we would have reason without vision and those of Michael Tomasello, who wondered whether we would have language without vision. Summarizing the different relations between perceptual modalities and cognitive processes, Trygg Engen wrote:

"Functionally, smell may be to emotion what sight or hearing is to cognition" (Engen 1982) (page 3).

The philosophical impact of the heterogeneity in the connections between perceptual systems and non-perceptual systems is that epistemological accounts that deal with perception have to confront the fact that they dealt with only one form of perception. However, the more profound point is metaphilosophical. The privileged connection between vision and language is the main reason why I felt that it was necessary to undergo the current research project to expose and correct the misguided ideas in the philosophy of perception that are based on the exclusive engagement with visual perception. The tool of philosophy is language and the connection between vision and language is stronger than the connected between other modalities and language, which gives vision privileged access to the minds of philosophers.

Chapter 7: The structure of the mind

The privileged connection between olfactory perception and emotional processing that I discussed in the previous chapter is a result of the interdependence and coevolution of the two processes. It is just one example of a non-perceptual process that evolved together with the sensory system from which it receives its input. The proprioceptor system, which provides information about the relative position and movement of body parts, would not have evolved in the absence of a motor system that can use the information provided by it. On the other hand, the motor system would not have evolved the capacity to quickly adjust and correct ongoing motor patterns, if it had evolved in the absence of a sensory system that provides the information about the position of body parts that is necessary for guiding these corrective movements. A perceptual system only conveys an adaptive advantage in the presence of a non-perceptual system that can make use of the information that the perceptual system provides. Similarly, cognitive systems can only contribute to guiding adaptive behaviors when they receive information about the environment from sensory systems.

To which other systems a perceptual system is connected determines how the perceptual system functions and what role it plays for the organism. In this chapter, I will therefore consider the structure of the mind and olfaction's position in this structure. The first section of this chapter will be methodological. I will discuss how to individuate the parts of which the mind is made up and discuss how connections between the parts can be discovered. I will argue against the popular strategy of dividing the mind into modules and instead propose to think of the mind in terms of functionally coupled networks. In the second section, I will address two specific questions using the methods developed in the first section. The first question is whether there is information flow from non-perceptual parts of the mind to olfaction. The second question is whether there is flow of information between olfaction and the other sensory modalities.

7.1. Uncovering the structure of the mind

Before strategies to uncover the structure of the mind are considered, one should question whether the mind is structured in an interesting way that is worth discovering. Strong evidence for a structure of the mind is provided by the study of individuals with localized damage to the brain. The effects of localized brain damage are often restricted to specific mental processes. In many cases, perception in a specific modality is compromised while the other modes of perception remain intact. Language comprehension or production can also be specifically impaired. In many cases, memory formation or retrieval are impacted without a strong effect on other mental processes. This shows that the mind is divided into relatively independent parts. One part can be damaged while the others remain intact. The functional decomposition of the mind into distinct parts is only one aspect of the structure of the mind. The parts of the mind are also interconnected in interesting ways. It is not the case that every part of the mind is connected to every other part of the mind equally, as I have shown in the previous chapter, using the connections between olfaction and language and between olfaction and emotion as examples. The structure of the mind therefore consists of parts and connections between the parts. There are tensions between dividing the mind into parts and describing connections between the parts. When two parts of the mind have a very strong exclusive connection, on what basis can they be described as two connected parts as opposed to a single part of the mind? I will argue below that the best way to account for these tensions is to describe the structure of the mind as a collection of networks. Before I discuss this suggestion, I will critique the common strategy to describe the mind as a collection of modules.

A critique of the concept of modularity

Current accounts of the structure of the mind usually refer to the parts of the mind as "modules". In this context, "module" is a technical term that can be defined in different ways. Most of its definitions are unrelated to the word's dictionary definition that considers modules to be "distinct, self-contained units from which are larger structure can be build". The terminology of modularity of the mind goes back to Fodor (Fodor 1983). Fodor defined modules as those parts of the mind that satisfy nine criteria. The nine criteria, as paraphrased by Prinz (Prinz 2006), are:

(1) Localized: modules are realized in dedicated neural architecture

(2) Subject to characteristic breakdowns: modules can be selectively impaired

(3) Mandatory: modules operate in an automatic way

(4) Fast: modules generate outputs quickly

(5) Shallow: modules have relatively simple outputs (e.g., not judgments)

(6) Ontogenetically determined: modules develop in a characteristic pace and sequence

(7) Domain-specific: modules cope with a restricted class of inputs

(8) Inaccessible: higher levels of processing have limited access to the representations within a module

(9) Informationally encapsulated: modules cannot be guided by information at higher levels of processing

The different definitions of "module" that can be found in the literature are derivatives of Fodor's original definition. Different definitions mainly differ in which criteria they emphasize. The two criteria that have received the most attention are informational encapsulation and domain-specificity (Samuels 2006). A part of the mind is informationally encapsulated if it does not receive information from higher centers of processing in the brain. Fodor, in later writings, focuses on informational encapsulation as a sufficient criterion for modularity (Fodor 2000). A part of the mind is domain-specific when it processes a restricted type of information, for example olfactory information or information about linguistic rules. Many theorists consider domain-specificity to be the most important, if not only, criterion that needs to be satisfied for a part of the mind to be a module (Cosmides and Tooby 1994; Sperber 1994). Others have picked different subsets of the criteria for their definition of "module". For Carruthers, for example, five of Fodor's nine criteria are relevant to decide whether a part of the mind is a module (Carruthers 2006) (page 12).

Not surprisingly, how the structure of the mind is described depends on the definition of "module" that is employed. If parts of the mind have to be informationally encapsulated to be considered modules, then the mind is not modular, except for the perceptual systems, which are modules (Fodor 1983). If modules are identified as parts of the mind that are domain-specific, then the mind is a large collection of modules (Sperber). The thesis that the mind is modular through and through, known as the massive modularity thesis, has been especially popular with evolutionary psychologists (Pinker 1997). If modules have to satisfy all of Fodor's nine criteria for modularity, then no part of the mind qualifies as a module (Prinz 2006). Other combinations of the modularity criteria that have not been explored in detail presumably will result in different distributions of modules in the mind.

This is only a very brief overview over the concept of modularity and how it has been used to investigate the structure of the mind (for a more detailed review, see (Robbins 2010)). However, it should be sufficient to unpack the concept and see what it can contribute to uncovering the structure of the mind. The strategy for identifying modules of the mind is to test parts of the mind whether they satisfy certain criteria. What is rarely discussed is that this strategy can only be applied *after* the parts of the mind have been individuated through some other process. Only after the mind has been divided into parts can the parts be tested for modularity. Many disagreements about the modularity of a certain part of the mind are, on closer inspection, based on disagreements about what the part that is tested for modularity is. Take for example the question whether vision is modular, when "module" is defined as an informationally encapsulated part of the brain. The main argument against informational encapsulation are top-down influences on visual perception. Pylyshyn avoids the discussion of these top-down influences by dividing vision into "early vision" and the rest. He then moves on to argue that early vision is informationally encapsulated (Pylyshyn 1999). Instead of discussing whether a given part of the mind is informationally encapsulated or not, the parts of the mind are individuated so that they fit the desired outcome. If we accept that early vision is informationally encapsulated, then we will also accept that edge-detection in the visual system is informationally encapsulated. Why is edge-detection in the visual system then not considered a module?

In another example how conclusions about the modularity of the mind depend on how the parts of the mind are individuated, Prinz and Samuels exchange silly examples of potential domains that would influence conclusions about the domain-specificity of parts of the mind (Prinz 2006; Samuels 2006). Prinz suggests, "the particular animal used by Lawrence to cross the Arabian

Desert", while Samuels offers "camels in London on Tuesdays" and "planning wheat-free picnics in 2005". Neither of them offers an individuation procedure that would avoid the result that there are parts of the mind concerned with these domains. I hope that these examples suffice to show that we need to know what the parts of the mind are, before there can be a fruitful discussion about which parts qualify as modules. Furthermore, we have to be careful not to confuse testing parts of the mind for modularity for individuating parts of the mind.

The structure of the mind consists not only of the parts of the mind, but also of the connections between those parts. Modules, as discussed, are a subset of the parts of the mind that satisfy the criteria required for being a module. We have seen that the relation between modules and the parts of the mind is that some parts of the mind, for example those that are domain-specific or those that are informationally encapsulated, are modules. What is the relation between modules and the connection between the parts of the mind? The two most frequently discussed criteria for modularity, informational encapsulation and domain-specificity, are both network properties that concern the inputs received by a module. Fodor's criteria that do not concern a module's role within a network, but the module itself (that it is fast and automatic, and that the underlying neuroanatomy is localized in the brain and develops in a characteristic way) have largely been abandoned.

The analysis of the relation between modules and the structure of the mind shows that the concept of modularity is only of limited usefulness when the goal is a comprehensive description of the structure of the mind. There are two limitations of the concept of modularity. First, modules are parts of the mind with certain properties, which means that the modular structure only captures the parts of the mind that show a certain property (or set of properties). Whatever property is used as a criterion for modularity, it is certainly wrong to postulate that the portions of the mind that do not fulfill the criterion cannot be structured. Nobody would argue, I think, that there can be no structure in the absence of informational encapsulation or in the absence of domain specificity. This structure is not included in an account of the structure of the mind based on modules. The second inadequacy of using modularity as a framework to describe the structure of the mind is that, although the most common definitions of "module" all define modules as parts of the brain that have a certain position within a network, modularity does not explicitly acknowledge the network structure of the mind. I suggest that describing the mind in terms of overlapping functionally coupled networks instead of in terms of modules will give a more accurate view of how the mind is structured.

Functionally coupled networks that connect parts of the mind

Functionally coupled networks that connect the parts of the mind can be investigated using different methods. One possibility is to use introspection. When smelling food is more likely to make us hungry than touching food, this can be interpreted as evidence for a closer connection between olfaction and hunger regulation than between touch and hunger regulation. However, introspection has three disadvantages. One disadvantage is that it is better suited for discovering connections between parts of the mind than for individuating parts of the mind. It is not clear how introspection could be useful to decide between the proposal that there is a part of the mind concerned with planning wheat-free picnics in 2005 and the proposal that there is a part of the mind that is concerned with planning in general. The second disadvantage is that a project to elucidate the structure of the mind based on introspection would come up with a very impoverished structure. Just because we are not aware that one process influence another process does not mean that there is no such influence. Investigating the structure of the mind will therefore miss many connections. Finally, it is a disadvantage of using introspective evidence to discover the structure of the mind that there is no procedure for weighing the evidence in cases of disagreeing introspections between individuals.

Another possibility to study the networks of the mind is with behavioral experiments. Behavioral experiments avoid two of the problems of introspective evidence. When touching food makes us eat more food in a behavioral experiment, then this is evidence for a connection between the parts of the mind that process tactile information and the parts of the mind that regulate food intake, regardless of the subjects' self-reports about the existence of such a connection. Furthermore, in behavioral experiments the sample size is larger than in introspection and it is therefore possible to discover inter-individual variability or agreement. The structure of the mind is likely to be partly hard-wired and partly shaped by previous experiences and it is interesting to distinguish innate and acquired structure.

A limitation that behavioral experiments share with introspection is that they are better suited to discover connections between parts of the mind than to individuate the parts of the mind. I cannot imagine a behavioral experiment that could distinguish between the proposal that vision is one of the parts of the mind and the competing proposal that early vision is one of the parts of the mind. A further disadvantage of using behavioral experiments to reveal the structure of the mind is that behavioral experiments treat the mind as a black box. When a behavioral experiment shows that smells induce emotions, it shows that olfaction and emotional processing are connected. However, the results do not show how they are connected. There may be a direct connection, but many alternative explanations are possible. There may be, for example, connections between olfaction and memory and between memory and emotion. Smells may elicit memories and memories, in turn, elicit emotions. Combining evidence from introspection and from behavioral experiments can be helpful to decide between the alternative structures that may underlie the behavior.

In addition to introspection and behavioral experiments, neuroanatomy, and especially functional neuroanatomy can also provide evidence about the structure of the mind. Like the other source of evidence, functional neuroanatomy has its disadvantages. The most troubling problem with drawing conclusions about the structure of the mind from observing the brain is that it presupposes an association between brain areas and parts of the mind. That there is such an association has become apparent when methods of visualizing brain activities were invented. The associations between brain and mind are most robust in sensory areas. Activity in the olfactory bulb is much more likely to be associated with smelling than with seeing whereas the visual cortex is most active during visual perception. Many structure-function-associations have also become apparent in the central brain. Activity in the amygdala is more likely to be associated with experiencing fear than with counting. The functional mapping of the brain is a large and ongoing research project with more than 1,000 new publications added to the literature every year (Smith 2012).

The big advantage of using evidence from functional neuroanatomy to discover the structure of the mind is that it can potentially provide a basis for individuating parts of the mind based on specified criteria. This would not be possible using introspection or behavioral experiments. The general approach for individuating parts of the mind through functional neuroanatomy that I have in mind is to group mental activities that are associated with the same patterns of brain activities together as parts of the mind. Obviously, much more work would have to be done to show that this approach would be successful. There are many problems, both theoretical problems and practical problems. Theoretically, it has to be decided what counts as the same pattern of activation. Practically, the limited temporal and spatial resolution of functional brain imaging limits the precision with which patterns of brain activity can be compared. Regardless of these problems, considering the lack of alternatives, I believe that functional neuroanatomy provides a promising path to individuating parts of the mind.

Once the parts of the mind have been individuated in such a way, the functional connections between them can be studied. A powerful method of elucidating connections between different brain regions is intrinsic functional connectivity magnetic resonance imaging (Buckner, Krienen et al. 2013). This method visualizes brain activity in the resting state and uncovers the spatial patterns along which activity spreads through the brain. Activity in one area of the brain that regularly follows after activity in another area of the brain is evidence for information flow between the two areas. The two areas are functionally coupled. Functionally coupled networks in the brain are a subsystem of the anatomical networks and they are severely constraint by them. When two regions are not anatomically connected, then they are not directly functionally coupled. However, a direct anatomical connection does not imply that the two regions are functionally coupled. To illustrate how the study of functional coupling goes beyond the study of neuroanatomy, consider a hypothetical example. Region A may be anatomically coupled to region B and region B to regions C, D, E, and F. Visualizing brain activity may however reveal that, after region A is active, region B is active and afterwards regions D and F, but not region C and E. A further refinement over the anatomical network that the functional network provides is that it allows assigning directions to the connections between nodes. Activity in region G may frequently follow activity in region F, but activity in region G does not induce activity in region F. However, anatomical connectivity provides an important framework for the study of functional connectivity.

Together, introspection, behavioral experiments, and functional neuroanatomy can individuate the parts of the mind and reveal the connections between them. Evidence from all sources has to be considered, but the biological evidence should be given special consideration. Describing the mind in terms of parts and connections between them instead of describing it in terms of modules does not just mean that "modules" are now called "parts" and connections between the parts are added to the description. Instead, it means that the structure of the mind is described in terms of functionally coupled networks. The parts of the mind are nodes in the network. Nodes are defined by their position within the network. They are points at which connections intersect or branch. None of the criteria that are used to identify modules applies necessarily to all nodes of functionally coupled networks. Informational encapsulation is not a necessary feature of nodes in functionally coupled networks. Each node receives the input that is necessary for it to play its role within the network. Some of these nodes may not receive input from central processes and would therefore be informationally encapsulated modules. Domain-specificity is also not a necessary feature of nodes in a network. In some nodes, only a certain type of information is processed. These are domain-specific nodes with only a single input, like "cognitive process 2" in Figure 13. Other nodes receive many different inputs and are therefore not domain-specific, like "cognitive process 3" in Figure 13. The relation between the functionally coupled networks and modules is therefore that the modules are subsets of the nodes of the functionally coupled networks. Which subset of the nodes can be considered modules depends on the criteria for modularity. Researchers, who find nodes that receive input from only a single source interesting, will define modules in terms of domain-specificity. For those that are more interested in where the nodes' input comes from, informational-encapsulation is the relevant criterion. Both approaches have in common that they illuminate only a very small subset of the entire structure of the mind.

Perhaps I am overly optimistic that a combination of different sources of evidence will reveal the functionally coupled network that constitute the mind. Given the failure of the concept of modularity to capture how our minds are structured, I think that it is a worthwhile attempt. If the approach I proposed here will work, it will reveal a complex structure of the mind with no overarching organizing principles. Different evolutionary pressures at different times throughout the evolution of brains and minds have resulted in a collection of diverse, highly effective, yet inelegant solutions. Functionally coupled networks can overlap; nodes can be part of several networks, like "cognitive process 3" in Figure 13, which is part of both the blue and the black network. A further level of complexity is added by the fact that connections within networks can have different strength (reflected by the different widths of the arrows in Figure 13). All these complications show that the structure of the mind is very complex and much less orderly and elegant than often assumed. It has no resemblance to engineered modular software packages, as the metaphor of "modules of the mind" suggests.

7.2. Olfaction's position in the mind

Two questions about the structure of the mind have received much attention. Is perception influenced by higher cognitive processes? Are the senses separated? These two questions can be addressed using the framework of functionally coupled networks that I have introduced in the previous section. Within this framework, the questions are whether there are connections from cognitive processes to perceptual processes and whether perceptual processes in different modalities are connected. The connections between olfaction and non-perceptual processes that have been discussed in chapter 6 are parts of networks in which information flows from the periphery to the center. In this section, networks in which information flows in the opposite direction or perpendicular to the flow from periphery to center will be discussed.

Cognitive penetration

The effect of cognition on perception has been termed the "cognitive penetration of perception". Examples of cognitive penetration of perceptual systems are counterexamples to the thesis that perceptual systems are informationally encapsulated and therefore to Fodor's proposal that the perceptual systems are modules (defined as informationally encapsulated parts of the mind). The term "cognitive penetration" has been coined by Pylyshyn, who argued that early vision is cognitively impenetrable (Pylyshyn 1999). The most intuitive argument for cognitive impenetrability of early visual perception is that several visual illusions resist cognitive influence. Take for example the Müller-Lyer illusion: a straight line segment with two arrowheads on both ends looks shorter than a line segment of the same length with two arrow tails on both ends. That this illusion persists after the subject understands that it is an illusion is shown by the fact that even after one measures the two line segments to confirm that they have the same length, the line segment with the arrowheads on its ends looks shorter than the one with the arrow tails[32].

Contrary to Pylyshyn, it has been argued that there are convincing examples of cognitive penetration in the visual system. Siegel likes to use the example of a pine tree (Siegel 2006). According to her, the perception of a pine tree changes when the perceiver learns to identify pine trees and distinguish them from other types of trees. Similar examples can be given for other kinds of acquired expertise. To a trained pathologist, a tissue sample under the microscope may look different than it looked to her before she trained as a pathologist. The problem with these examples is that it is easy to simply deny that the perception changed. Macpherson discusses an interesting example of cognitive penetration in which this is more difficult to deny the changes in perception because they are confirmed through performance-based psychophysics (Macpherson 2012). In an experimental setting, subjects were given shapes cut out of orange paper. Some of the shapes were the shapes of objects that are characteristically thought of as red (like a heart) whereas others were of the shapes of objects not characteristically red (like a mushroom). The task was to match each of the shapes to a colored background. The background color that the subjects matched to shapes of characteristically red objects was, on average, redder than the

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[32] It is perhaps an unrealistically high standard for cognitive penetrability to expect additional information to *always* have the expected effect on other cognitive mechanisms. Our knowledge that matter consists mainly of empty space between atoms does not change how a table looks or feels to the touch. I have perhaps read more books on playing squash than most professional players. The fact that I still could not beat a professional player does not show that my motor systems are cognitively impenetrable. The flexibility and plasticity of biological processes is limited. That a cognitive process does not change in the expected way when additional information is provided does not necessarily mean that the information is not available to the process. There are other explanations.

background color that was matched to shapes of objects that are not characteristically red. When the cutout was in the shape of a not characteristically red object, the subjects selected a more yellowish color (remember that the color of the cutouts was orange) (Delk and Fillenbaum 1965). This result provides strong evidence that the belief that a perceiver holds about the characteristic color of the object that is perceived can influence the perceived color.

The discussion of cognitive penetration in the literature is mainly concerned with cognitive penetration in vision. As I have discussed in chapter 6, the connections between perception and cognition evolved differently in each of the modalities. All modalities have to be investigated individually. Olfaction is a good modality for the study of cognitive penetration because introspection and behavioral experiments suggest that olfactory perception is strongly modulated by cognitive processes (for reviews, see (Stevenson and Boakes 2003; Gottfried and Wu 2009; Yeshurun and Sobel 2010). An example of cognitive penetration in olfaction is the influence of verbal labels on perception. The pleasantness of the same stimulus is rated very differently when it is labeled "cheddar cheese" than when it is labeled "body odor". These differences in reported perception are also accompanied by differences in brain activity (de Araujo, Rolls et al. 2005). Anecdotal reports also suggest that odor perception differs between different cultural groups. An impact of culture on perception indicates that beliefs and background information can penetrate perception. Unfortunately, the presumed cross-cultural differences in odor perception have not been studied systematically yet.

Introspective evidence is difficult to defend against skepticism and behavioral experiments cannot discriminate between an influence on perception and an influence on how behaviors are linked to perception. To investigate whether there is cognitive penetration in olfaction, it is therefore helpful to study the brain in an attempt to identify the potential neural correlate of cognitive penetration in the olfactory system. This is the same strategy of investigating the structure of the mind through investigating how it is implemented in the networks of the brain. In this section, this general strategy is applied to the specific question of cognitive penetration in olfaction.

The brain structures in which olfactory information is processed have been identified. If the olfactory brain receives input from cognitive areas and this input alters the processing of olfactory information, then perception is influenced by cognition. Cognitive penetration has to be relativized to processing stage (Lycan 2014). There could be an influence of cognition on the very peripheral sensory neurons, or, at any of the higher levels of olfactory processing. I will investigating the potential neural correlates for cognitive penetration in the olfactory system starting with the olfactory sensory neurons.

Olfactory sensory neurons are the neurons in the nose that bind to odors. In humans, the responses of olfactory sensory neurons to the odors they encounter do not depend on cognitive processes. However, in other species strong influences of the perceiver's state on the activity of these sensory neurons have been described (see for example the dependence of the sensitivity of olfactory sensory neurons on the perceivers' state in many insects discussed in section 5.1.: (Davis 1984; Root, Ko et al. 2011; Saveer, Kromann et al. 2012)). The strategy behind such changes is to perceive only behaviorally relevant stimuli. When stimuli are relevant only in specific situations, they should only be perceived during these situations. Humans have not developed such a system. We do not become smell-blind to food odors after lunch.

In the next step of olfactory processing, the olfactory sensory neurons project to the olfactory bulb, where information about the molecular structure of odorant molecules is processed (Shepherd et al., 2004). In addition to the input from olfactory sensory neurons, the olfactory bulb also receives information through massive and diverse centrifugal fibers. These fibers originate in brain areas including the olfactory cortex, the brain stem, and the basal forebrain (Matsutani and Yamamoto, 2008). The information processing in the olfactory bulb is influenced by activity in all these diverse regions of the brain. Consistent with these anatomical findings, information processing in the olfactory bulb of rodents differs markedly depending on the behavior the animal is engaged in and its prior experiences (Kay and Laurent, 1999). Processing in the olfactory bulb is for example modulated by prior experiences with the perceived odor (Kato et al., 2012). The massive feedback from higher brain areas to the olfactory bulb is the neural correlate of cognitive penetration in human olfaction. Through these connections, memories and mental states can influence how odors are perceived.

As it is the case with other modalities, in some instances olfactory perception appears penetrable whereas in other instances it appears impenetrable. Perhaps overall olfactory perception is more pliable than vision. The suggestion that a "grilled 40-oz. dry-aged porterhouse steak" smells different after one has just consumed such a steak (Gottfried 2007) is more plausible than the suggestion that the way the steak looks depends on whether the perceiver is hungry or satiated. However, this can also be denied. It is difficult to convincingly and reliably differentiate between changes in perception, and changes in the preferences, tastes, or evaluations of the perception. However, a striking fact about olfaction is that the olfactory bulb, the first processing station of olfactory information, receives massive input from central brain structures. Unless these structures are vestigial structures that have lost their function, olfaction is cognitively penetrated.

Crossmodal perception

Behavioral experiments and evidence from introspection show that perception in one modality can influence perception in another modality. One of the most dramatic examples is the McGurk effect, which is a demonstration of how watching the movements of a speaker's lips influences how the sounds they are making with their lips are perceived (McGurk and MacDonald 1976). Subjects report a strong influence of the lip movements on what they hear. Demonstrations of the McGurk effect can be found online. Another example of the influence of perception in one modality on perception in another modality that can easily be experienced first-hand is the dependence of visual perception on the perception of gravity. If you look at the rows in front of you in an airplane before take-off, they seem to be at the same level with you. If you look at them again while the plane is taking-off, they seem to be elevated although the relative position between you and the rows in front of you has not changed. The visual perception changes depending on information about relative position from other modalities.

The influence of perception in other modalities on olfactory perception is very pronounced. There is some evidence that orthonasal olfaction (in which the odor molecules reach the olfactory sensory neurons through the nostrils) can be influenced by perception in other modalities. However, the most dramatic cases of crossmodal perception are found in retronasal olfaction. When smells are perceived retronasally, the odor molecules reach the olfactory sensory neurons through the throat when the odor source is in the mouth. Although retronasal olfaction has the same stimuli and the same sensory organ as orthonasal olfaction, it is not usually referred to as "smell" Instead, it is a component of what is usually called "taste". When a wine taster says that a wine tastes like apple, she is not referring to a perception that is caused by tastants activating taste buds. Instead, she is referring to a perception that is caused by odorous molecules that smell of apple and activate the olfactory sensory neurons. Odorants from wine in the mouth reach the olfactory sensory neurons in the nasal cavity through the pharynx to elicit this aspect of the wine's taste. The scientific term for what is commonly called "taste" is "flavor". Scientists use the word "taste" for the perception that is mediated by the taste buds on the tongue whereas they use the word "flavor" for the multisensory perceptions elicited by food in the oral cavity. Scientists would not say that the wine tastes like apples, but instead that it has an apple flavor. Flavor has been called, maybe paradoxically, a "multisensory modality" (Taylor and Roberts 2004; Shepherd 2011; Small and Green 2012). The chemical senses work together with texture and temperature perception to produce flavor perception.

Taste is the main contributor to flavor. Humans perceive five basic taste qualities: sweetness, sourness, saltiness, bitterness, and umami (a savory taste). Recent research suggests that we also have dedicated sensory neurons for other tastants, like fat (Laugerette, Gaillard et al. 2007) and calcium (Tordoff, Alarcón et al. 2012). Flavor nuances are added to these basic tastes through the contribution of olfaction. When perceived through taste alone, all Jelly Beans have the same flavor: sweet. However, when olfaction is added, some Jelly Beans have coconut flavor whereas others have popcorn flavor. One can experience this difference by pinching the nose shut with two fingers, then starting to chew a Jelly Bean and then opening the nose. The shift in flavor from sweet to sweet pineapple is due to the odorous molecules released by the Jelly Beans that can reach the olfactory epithelium only when air flows from the mouth to the nose through the pharynx. In addition to taste and olfaction, chemesthesis also contributes to perceived flavors. Chemesthesis is the sensitivity to chemicals of areas of the skin or mucous membranes. The mucous membrane of the oral cavity contains many chemesthesis-mediating neurons (Green 2004). The "hotness" of chili peppers and the "coolness" of menthol do not involve temperature perception, but chemesthetic perception of molecules that are sensed by temperature sensors. Similarly, the "tingling" induced by carbonated drinks is not touch but chemesthesis (Green 2004). In addition to the chemical senses, touch, temperature, and other senses also contribute to flavor perception.

"Flavor" is not just a term for the simultaneous occurrence of perceptions in these modalities. Instead, the different modalities involved in flavor perception influence each other. The perceptual qualities experienced when drinking chilled, sweet, fruity Riesling can be different from the sum of the perception of drinking water chilled to the same temperature as the Riesling, tasting a sugar solution of the same concentration as the wine, and smelling the fruity odorants found in it. For reviews of the crossmodal interactions in flavor perception, see (Taylor and Roberts 2004; Shepherd 2011). Examples of intermodal modulation of olfactory perception during flavor perception is that combining a tastant with an odorant can enhance the perceived intensity of the odorant (Green, Nachtigal et al. 2011) as well as its detectability (Dalton, Doolittle et al. 2000).

The principal evidence for crossmodal perception, like the principal evidence for any structure of the mind, comes from introspection and behavioral studies. Such evidence is easily disputed. In fact, some of the top comments on the websites hosting the demonstration video of the McGurk effect are from people reporting to be immune to the influence of the perception of lip movement on their auditory perception. As in the case of cognitive penetration, it becomes therefore important to investigate whether there are neural correlates of crossmodal perception in olfaction. If some neurons connect photoreceptors to olfactory sensory neurons in the human brain, we can conclude that information is exchanged between the two modalities.

Neuroanatomy and functional connectivity can tell us whether the required wiring for crossmodal penetration of perception is present. There are two complication to evaluating whether a neuronal structure should count as a potential neuronal correlate of crossmodal perception. The first complication is that interactions between two modalities may be direct or indirect. In the section of cognitive penetration, I have already discussed the massive feedback from central brain structures to the olfactory system. This feedback could carry information about perception in other modalities, thereby providing the basis for crossmodal perception. The second complication is that the interaction can be at different levels of processing. A neuronal connection between photoreceptors and olfactory sensory neurons would be a very clear indication of information exchange between vision and olfaction. But what about a connection between two modalities at a much higher level of sensory processing?

A review of the wiring at the level of the neocortex has concluded that there are so many interactions that modalities can penetrate each other. In fact, the interactions are so ubiquitous that it is difficult to identify individual modalities (Shimojo and Shams 2001). However, anatomical connections between the olfactory system and the other sensory systems at lower level of processing than the neocortex are sparse. The lowest levels of processing at which visual, gustatory, and olfactory information are thought to converge are the orbitofrontal cortex and the amygdala (Rolls and Baylis 1994; Rolls, Critchley et al. 2009). Despite the lack of direct anatomical connections between olfaction and other sensory systems in the periphery, it has been shown that in rodents piriform cortex neurons are influenced by gustatory stimuli (Maier, Wachowiak et al. 2012). If these findings generalize to the human brain, the feedback neurons that are the substrate of cognitive penetration are also the best candidate for the neural correlate of the strong crossmodal influences on olfactory perception.

7.3. Conclusion: The mind is a collection of functionally coupled networks

Our mind has a complex structure of interconnected parts. A metaphor that reflects this structure much better than that of the modular mind is to consider the mind is a collection of functionally coupled networks. Each of these networks consists of different nodes that are interconnected. Nodes can be shared between networks and the connections between them have different strengths. The structure of the functionally coupled networks does not follow an overarching design principle. Each network followed its own evolutionary trajectory and found its own unique, idiosyncratic solutions to the problem it evolved in response to. The lack of order and homogeneity that has been discovered in our mind prompted Gary Marcus in his book *Kluge: The Haphazard Construction of the Mind*, to call the mind a "kluge" (Marcus 2008). A "kluge" is a solution to a problem that is effective yet inelegant and clumsy.

Discovering the clumsy, inelegant functionally coupled networks that structure the mind requires a combination of different methods. Introspection and behavioral experiments should be supplemented by neuroanatomy and functional neuroanatomy, which provide the neural correlates for the networks of the mind. Because there are no general principles of how the networks are organized, each question has to be addressed individually. There are no general answers about how perception connects to cognition, or if and how different perceptual modalities are connected to each other. Questions such as these have to be addressed case by case. Some sensory processes probably receive very little input from cognitive processes (like "sense 1" in Figure 13), whereas others receive much cognitive input (like "sense 3" in Figure 13). Each sense was shaped through evolution through natural selection by different needs and constraints. The mind needs to be described to be understood.

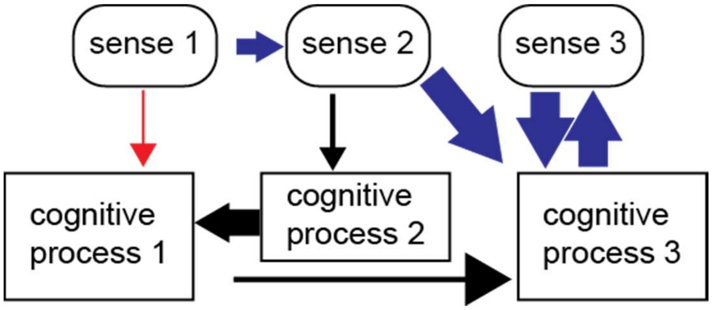

Figure 13: The mind as a collection of overlapping functionally coupled networks. In this hypothetical example, three networks are shown. A red network, which consist of sense 1 and cognitive process1, a blue network, which consists of sense 1, sense 2, cognitive process 3, and sense 3, and a black network, which consists of sense 2, and cognitive processes 1 to 3.

In this chapter, I have described the inputs that olfaction receives from non-perceptual processes, as well as the inputs it receives from other perceptual modalities. Olfaction, probably more so than some other perceptual modalities, is modulated by both types of input. However, from this observation, no general conclusions about cognitive penetration and crossmodal perception can be drawn.

Conclusion: Comparing olfaction and vision

The primacy of vision over other modalities has led to a bias in our understanding of perception. The visuocentrism that dominates our thinking has very deep roots that are reflected in our philosophical vocabulary. We can "glimpse" or "see" the meaning of a proposition. Using a tactile instead of visual metaphor, we can also "grasp" it. After we grasped enough propositions, we will form a certain "view" or "outlook" on the topic. Ideas are talked about as if they are visual objects that are placed before us. They can be "viewed" from certain "angles". Different "positions" can be taken with respect to a certain "view". There are no comparable olfactory metaphors. Undoubtedly, this way of speaking has given vision a special status in philosophy of perception. Philosophy books have titles such as "Seeing and Knowing" (Dretske 1969) or "Philosophy and the Mirror of Nature" (Rorty 1981). Philosophers always have a "point of view", whether it is a logical point of view, a scientific point of view, or the view from nowhere.

I hope that this dissertation will trigger a reexamination of the assumptions about perception that are built into the philosopher's vocabulary. I do not mean to deny that in humans vision is the most important and interesting modality. Humans happen to be active during the day, when the light from the sun allows us to perceive the space around us visually. If humans were active at night, we might have evolved echolocation like bats, to navigate in the dark. The current state of philosophy of perception is in large parts due to the fact that at some point in evolutionary history our ancestors were more likely to be eaten at night than during the day. Once our ancestors become active during the day, it was important to optimize visual perception, even if it meant to reduce further the usefulness of olfaction. The most important evolutionary event that shifted importance from olfactory perception to visual perception was the shift from walking on all fours to walking only on the hind legs. Our head, and with it the sense organs for both vision and olfaction, were moved up from the ground when we became bipedal. This further accelerated the evolution away from an olfactory creature to a visual creature. Close to the ground, down in the bushes, there is much less to see and much more to smell. However, at eyelevel (or noselevel) vision is much more useful than olfaction.

Understanding that the different ways in which humans perceive visual stimuli and odors have been shaped by the unique evolutionary history of our species leads to the realization that there are no differences between how visual stimuli are perceived in all species and how olfactory stimuli are perceived in all species. The differences between the two modalities that I have discussed in this dissertation are differences between how visual perception is implemented in contemporary humans and how olfactory perception is implemented in contemporary humans. Many of the features that are associated with one modality in humans are associated with another modality in other species. In humans, visual perception has spatial structure whereas olfactory perception does not. For us, colors can be, and usually are, arranged in a spatial pattern, while it is not possible for humans to perceive a spatial arrangement of smells. The presence of spatial structure in vision and its absence in olfaction are due to the structure of the human sensory systems. Nothing in the nature of olfactory perceptual qualities prevents them from being spatially arranged. It is easy to imagine an olfactory system that mediates spatially structured olfactory perception. Our whole body could be covered in odor-sensitive cells. We then would experience the smell stronger at the side of our body that is facing the odor source. This is how we perceive heat and why we can tell whether we walk towards or away from the sun based on the pattern of heat perception on our skin. Similarly, we cannot conclude that visual perception is inherently spatial from the fact that human visual perception has spatial structure. Many animal species can perceive visual stimuli, but do not have image-resolving eyes, and therefore do not perceive spatially arranged visual perceptual qualities. The simplest eye consist of only a single photoreceptor (Jékely, Colombelli et al. 2008). With such an eye, all that can be perceived is the level of illumination. A species of marine mollusks has hundreds of small simple eyes distributed over their body surface (Boyle 1969). They perceive a light source in the same way in which humans perceive a heat source.

In the light of this diversity between different perceptual systems, the focus on human vision as a basis for philosophy of perception seems misguided. To make progress, other forms of perception have to be investigated. In this dissertation, I have considered human olfaction. Throughout the rest of this conclusion, I will compare the central findings about olfactory perception with what we know about visual perception to show what kinds of biases one can except when the focus is on a single modality.

At the level of perceptual qualities, olfaction is more complex than other senses. There are more smells than colors or tones. Consequently, arranging the perceptual qualities of olfaction into a similarity space has not been possible yet. For colors or tones, this first step of putting order to perception has been accomplished. However, once the perceptual qualities are individuated, olfaction is much less complicated than vision. What is perceived during olfactory perception in normal cases are individual olfactory perceptual qualities. The olfactory perceptual qualities are not arranged spatially and the temporal structure of odor perception is much impoverished compared to the other senses. This is in contrast with visual perception, which normally is the perception of visual scenes that are arrangements of color qualities in space. A philosophy of perception based on smells would focus heavily on the nature of perceptual qualities rather than on how they are arranged in time and space. As a consequence, entities that consist of spatially and temporally arranged perceptual qualities, like perceptual events and perceptual objects, would not be part of perceptual philosophy if olfaction would be the paradigm sense.

The lack or relative unimportance of spatial and temporal information in odor perception also has consequences for our understanding of the relation between the physical world and our percepts. In vision, space and time are mapped through perception; perception represents the temporal and spatial relations in the physical world. Relative position and distance in the physical are often accurately represented through perception. This is adaptive because when the perceiving organism responds behaviorally to a stimulus, the responses have to be directed and timed based on the spatial and temporal structure of the physical world to have the intended effect on the physical world. This large overlap between similarities in the physical world and similarities in percepts has resulted in the idea of perception as a representation of the physical world. In olfactory perception, perceptual qualities are not arranged in space. When perception without spatial structure is considered, the similarities found in the physical world between stimuli do not appear to be conserved in perception. I have discussed this here for tastants and smells, but it is also apparent in the case of colors, where each perceived color can be the consequence of a very large number of physically very different stimuli[33]. In olfaction, physical similarity between odor molecules is not reliably mapped onto similarities between the perceptual qualities associated

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[33] Different mixtures of light of different wavelengths that result in the same perceptual color are called metamers Rodrigues, A. B. J. and R. Besnoy (1980). "What is metamerism?" Color Research and Application **5**(4): 220-221..

with the stimuli[34]. Because olfactory perception consists of the perception of perceptual qualities with no spatial structure, the relation between similarities in olfactory stimuli and similarities in olfactory perception is weak. If olfaction were the paradigm, the idea that perception represents the physical world would not have the same appeal it has when visual perception is considered. In olfaction, perceptual qualities are closer aligned with appropriate behavioral responses to the stimuli than with the physical features of the molecules. Olfactory perception illustrates that what perception does is not mirroring reality, but guiding behaviors.

Another striking difference between vision and olfaction is that olfaction is more difficult to demarcate than vision. While differentiating vision or audition from other forms of perception, olfaction is in some respects closely related to other chemical senses and involved in the multimodal perception of flavors. Individuating modalities based on representations, phenomenal character, the proximal stimulus, or the sense organs will lead to dramatically different results in the case of the chemical senses, while all four methods largely agree about how to individuate vision or audition. The difficulty of individuating olfaction may have contributed to its relative unpopularity among philosophers of perception. Some apparent disagreements in the philosophy of olfactory perception are a consequence of olfaction being individuated differently by different scholars.

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[34] Of course, it is possible to some degree to predict the perceptual quality of a molecule based on its physical features. Molecules containing a sulphur atom, for example, have a distinct smell. It is also possible that future research will show that the relationship between physical features of molecules and perceptual olfactory qualities is closer than currently appreciated (for a review of structure-odor relationship research, see Rossiter, K. J. (1996). "Structure−Odor Relationships." Chemical Reviews **96**(8): 3201-3240.)

In addition to the more fluid boundaries between olfaction and other sense modalities, olfaction is also difficult to distinguish from non-perceptual processes like emotion processing. Olfactory and emotional processing share the same neuronal substrate and evaluative emotions such as disgust are intricately linked to odor processing. There is also widespread cognitive penetration of the olfactory sensory system. Olfaction illustrates therefore the interconnectedness of the mind better than many other modalities that have a different evolutionary history.

That the different evolutionary histories of the different modalities result in differences in how they are connected to cognitive processes is also reflected by the differential ineffability of the senses. Naming and talking about what is perceived through olfaction is more difficult than naming and talking about what is perceived visually. This also has far-reaching consequences. As speculated above, the perception that is most easy to talk about is the obvious candidate for philosophers to investigate. This may have contributed to the bias towards visual perception in philosophy. The strong connection between vision and language also has methodological consequences for the empirical study of perception. In visual psychophysics, the ability to name a stimulus is often used as a read-out. Often the reliance on verbal report is pushed so far that the absence of a verbal report is interpreted as the absence of perception, or at least the absence of conscious perception. In olfaction, the danger of drawing conclusions about perception based exclusively on verbal reports is less pronounced.

Taken together, an olfaction-based philosophy or perception would be much different from the familiar version based on visual perception. Where to go from here? One possibility is that the account of olfactory perception given here is seen as a supplementing the well-established account of visual perception. The two accounts differ, but the differences between them do not amount to different suggestions about how we should think about perception. Instead, the differences between the account of visual perception and the account of olfactory perception reflect the fact that visual perception in humans is fundamentally different from human olfactory perception. An alternative to embracing the heterogeneity of perception is to try to identify features that are shared by all instances of perception. The differences between the perceptual systems are so pronounced that some are skeptic that a unified account that applies to all types of perception can be developed (Martin 1992). I am more optimistic and believe that enough features are shared between all forms of perception that an interesting general account of perception can be developed. The most striking similarities between olfaction and vision that the analysis presented in this dissertation revealed are that both types of perception involve perceptual qualities and that they both serve to guide behaviors. This, I propose, could be a starting point for a modality-neutral theory of perception.

Bibliography

Aggleton, J. P. and A. E. Young (2000). The enigma of the amygdala: On its contribution to human emotion. Cognitie Neuroscience of Emotion. R. D. Lane and L. Nadel. Oxford, Oxford University Press**:** 106-128.

Akins, K. (1996). "Of sensory systems and the "aboutness" of mental states." The Journal of Philosophy **93**(7): 337-372.

Amoore, J. E. (1967). "Specific anosmia: a clue to the olfactory code." Nature **214**(5093): 1095-1098.

Aristotle (2011). Excerpt from On the Soul (De Anima). The Senses: Classical and Contemporary Philosophical Perspectives. F. Macpherson. New York, Oxford University Press**:** 47-63.

Auffarth, B. (2013). "Understanding smell: the olfactory stimulus problem." Neuroscience and Biobehavioral Reviews **37**(8): 1667-1679.

Aznar, M., R. López, et al. (2001). "Identification and quantification of impact odorants of aged red wines from Rioja. GC-olfactometry, quantitative GC-MS, and odor evaluation of HPLC fractions." Journal of Agricultural and Food Chemistry **49**(6): 2924-2929.

Barwich, A.-S. (2014). "A sense so rare: Measuring olfactory experiences and making a case for a process perspective on sensory perception." Biological Theory **9**(3): 258-268.

Batty, C. (2010). "A representational account of olfactory experience." Canadian Journal of Philosophy **40**(4): 511-538.

Batty, C. (2010). "What the nose doesn't know: Non-veridicality and olfactory experience." Journal of Consciousness Studies **17**: 10-17.

Batty, C. (2011). "Smelling lessons." Philosophical Studies **153**: 161-174.

Batty, C. (2014). "The illusion confusion." Frontiers in Psychology **5**.

Berglund, B. and A. Höglund (2012). Is there a measurement system for odour quality? Olfactory Cognition: From Perception and Memory to Environmental Odours and Neuroscience. G. M. Zucco, R. S. Herz and B. Schaal. Amsterdam, John Benjamins Publishing Company**:** 3-21.

Berlin, B. and P. Kay (1969). Basic Color Terms: Their Universality and Evolution. Berkeley, University of California Press.

Binder, J. R., J. A. Frost, et al. (1997). "Human Brain Language Areas Identified by Functional Magnetic Resonance Imaging." The Journal of Neuroscience **17**(1): 353-362.

Bizley, J. K. and Y. E. Cohen (2013). "The what, where and how of auditory-object perception." Nature Reviews Neuroscience **14**(10): 693-707.

Blauert, J. (1997). Spatial Hearing: The Psychophysics of Human Sound Localization. Cambridge, MIT Press.

Boyle, P. R. (1969). "Rhabdomeric ocellus in a chiton." Nature **222**(5196): 895-&.

Buckner, R. L., F. M. Krienen, et al. (2013). "Opportunities and limitations of intrinsic functional connectivity MRI." Nature Neuroscience **16**(7): 832-837.

Budek, T. and K. Farkas (2014). Which Causes of an Experience Are Also Objects of the Experience? Does Perception Have Content? B. Brogaard. Oxford, Oxford University Press**:** 351-369.

Buller, D. J., Ed. (1999). Function, Selection, and Design. Albany, SUNY Press.

Bushdid, C., M. O. Magnasco, et al. (2014). "Humans can discriminate more than one trillion olfactory stimuli." Science **343**(6177): 1370-1372.

Byrne, A. (2010). "Inverted Qualia." The Stanford Encyclopedia of Philosophy Spring 2010. Retrieved 06/23, 2011, from http://plato.stanford.edu/archives/spr2010/entries/qualia-inverted.

Cain, D. P. and D. Bindra (1972). "Responses of amygdala single units to odors in the rat." Experimental Neurology **35**(1): 98-100.

Carruthers, P. (2006). The Architecture of the Mind. Oxford, Oxford University Press.

Carvalho, F. (2014). "Olfactory objects." Disputatio **6**(38).

Castro, J. B., A. Ramanathan, et al. (2013). "Categorical dimensions of human odor descriptor space revealed by non-negative matrix factorization." PLoS ONE **8**(9): e73289.

Castro, J. B. and W. P. Seeley (2014). "Olfaction, valuation, and action: Reorienting perception." Frontiers in Psychology **5**.

Caterina, M. J., M. A. Schumacher, et al. (1997). "The capsaicin receptor: a heat-activated ion channel in the pain pathway." Nature **389**(6653): 816-824.

Chen, Y. C. and B. Gerber (2014). "Generalization and discrimination tasks yield concordant measures of perceived distance between odours and their binary mixtures in larval Drosophila." Journal of Experimental Biology **217**(12): 2071-2077.

Chobor, K. L. (1992). A neurolinguistic perspective of the study of olfaction. Science of Olfaction. M. J. Serby and K. L. Chobor. New York, Springer-Verlag**:** 355-377.

Chu, S. and J. J. Downes (2000). "Odour-evoked autobiographical memories: Psychological investigations of Proustian phenomena." Chemical Senses **25**(1): 111-116.

Churchland, P. (2005). "Chimerical colors: some phenomenological predictions from cognitive neuroscience." Philosophical Psychology **18**(5): 527-560.

Clark, A. (1993). Sensory Qualities. Cambridge, Cambridge University Press.

Clark, A. (2005). Painfulness is Not a Quale. Pain: New Essays on Its Nature and the Methodology of Its Study. M. Aydede. Cambridge, MIT Press**:** 177-197.

Classen, C., D. Howes, et al. (1994). Aroma: The Cultural History of Smell. London, Routledge.

Cosmides, L. and J. Tooby (1994). Origins of domain specificity: The evolution of functional organization. Mapping the Mind: Domain Specificity in Cognition and Culture. L. A. Hirschfeld and S. A. Gelman. New York, Cambridge University Press**:** 85-116.

Crisinel, A. S. and C. Spence (2011). "A Fruity Note: Crossmodal associations between odors and musical notes." Chemical Senses **37**(2): 151-158.

Croy, I., M. Schulz, et al. (2014). "Human olfactory lateralization requires trigeminal activation." Neuroimage.

Cruse, H., H. Kälberer, et al. (2007). "Sensorimotor supremacy: Investigating conscious and unconscious vision by masked priming." Advances in Cognitive Psychology **3**(1): 257-274.

Cummins, R. (1975). "Functional analysis." The Journal of Philosophy **72**: 741-765.

Dalton, P. (2000). "Psychophysical and behavioral characteristics of olfactory adaptation." Chemical Senses **25**(4): 487-492.

Dalton, P., N. Doolittle, et al. (2000). "The merging of the senses: integration of subthreshold taste and smell." Nature Neuroscience **3**(5): 431-432.

Davis, E. E. (1984). "Regulation of sensitivity in the peripheral chemoreceptor systems for host-seeking behavior by a hemolymph-borne factor in Aedes aegypti." Journal of Insect Physiology **30**: 179-183.

de Araujo, I. E., E. T. Rolls, et al. (2005). "Cognitive modulation of olfactory processing." Neuron **46**(4): 671-679.

Delk, J. L. and S. Fillenbaum (1965). "Differences in perceived colour as a function of characteristic color." The American Journal of Psychology **78**(2): 290-293.

Dennett, D. C. (1991). Consciousness Explained. Boston, Little, Brown and Company.

Deroy, O., A.-S. Crisinel, et al. (2013). "Crossmodal correspondences between odors and contingent features: odors, musical notes, and geometrical shapes." Psychonomic bulletin & review **20**(5): 878-896.

Desor, J. A. and G. K. Beauchamp (1974). "The human capacity to transmit olfactory information." Perception & Psychophysics **16**(3): 551-556.

Dhaka, A., V. Viswanath, et al. (2006). "Trp ion channels and temperature sensation." Annual Review of Neuroscience **29**: 135-161.

Doty, R. L. and E. L. Cameron (2009). "Sex differences and reproductive hormone influences on human odor perception." Physiology & Behavior **97**(2): 213-228.

Dretske, I. F. (1969). Seeing and Knowing. Chicago, University of Chicago Press.

Ehrlichman, H. and L. Bastone (1992). Olfaction and Emotion. Science of Olfaction. M. J. Serby and K. L. Chobor. New York, Springer-Verlag**:** 410-438.

Engen, T. (1982). The Perception of Odors. New York, Academic Press.

Everitt, B. S., S. Landau, et al. (2011). Cluster Analysis, Wiley.

Ferreira, V. (2012). "Revisiting psychophysical work on the quantitative and qualitative odour properties of simple odour mixtures: a flavour chemistry view. Part 1: intensity and detectability. A review." Flavour and Fragrance Journal **27**(2): 124-140.

Ferreira, V. (2012). "Revisiting psychophysical work on the quantitative and qualitative odour properties of simple odour mixtures: a flavour chemistry view. Part 2: qualitative aspects. A review." Flavour and Fragrance Journal **27**(3): 201-215.

Fodor, J. (1983). The Modularity of Mind. Cambridge, MIT Press.

Fodor, J. (2000). The mind doesn't work that way: The scope and limits of computational psychology. Cambridge, MIT Press.

Fodor, J. and E. Lepore (1996). Paul Churchland and State Space Semantics. The Churchlands and their critics. R. N. McCauley. Cambridge, Blackwell Publishing**:** 145-159.

Frasnelli, J., G. Charbonneau, et al. (2008). "Odor localization and sniffing." Chemical Senses **34**(2): 139-144.

Gagliardo, A. (2013). "Forty years of olfactory navigation in birds." Journal of Experimental Biology **216**(12): 2165-2171.

Gallace, A., H. Z. Tan, et al. (2006). "The failure to detect tactile change: a tactile analogue of visual change blindness." Psychonomic bulletin & review **13**: 300-303.

Gibson, J. J. (1966). The Senses Considered as Perceptual Systems. Boston, Houghton Mifflin.

Gilbert, A. N. (2008). What the Nose Knows. New York, Crown Publishers.

Gilbert, A. N. and M. S. Greenberg (1992). Stimulus selection in the design and interpretation of olfactory studies. Science of Olfaction. M. J. Serby and K. L. Chobor. New York, Springer-Verlag**:** 309-334.

Goodman, N. (1951). The Structure of Appearance. Cambridge, Harvard University Press.

Gottfried, J. A. (2007). "What can an orbitofrontal cortex-endowed animal do with smells?" Annals of the New York Academy of Sciences **1121**(1): 102-120.

Gottfried, J. A. and K. N. Wu (2009). "Perceptual and neural pliability of odor objects." Annals of the New York Academy of Sciences **1170**(1): 324-332.

Gottfried, J. A. and C. Zelano (2011). "The value of identity: olfactory notes on orbitofrontal cortex function." Annals of the New York Academy of Sciences **1239**(1): 138-148.

Gould, S. J. and R. C. Lewontin (1979). "The spandrels of San Marco and the Panglossian Paradigm: A critique of the adaptationist programme." Proceedings of the Royal Society of London, Series B **205**(1161): 581-598.

Gray, R. (2013). "Is there a space of sensory modalities?" Erkenntnis **78**: 1259-1273.

Green, B. G. (2004). Oral chemesthesis: an integral component of flavour. Flavor Perception. A. J. Taylor and D. D. Roberts. Oxford, Blackwell Publishing**:** 151-171.

Green, B. G., D. Nachtigal, et al. (2011). "Enhancement of Retronasal Odors by Taste." Chemical Senses **37**(1): 77-86.

Grice, H. P. (1962). Some remarks about the senses. Analytical Philosophy, First Series. R. J. Butler. Oxford, Oxford University Press.

Griffiths, T. D. and J. D. Warren (2004). "What is an auditory object?" Nature Reviews Neuroscience **5**(11): 887-892.

Grosch, W. (1998). "Flavour of coffee." Food/Nahrung **42**(6): 344-350.

Gutiérrez-Castellanos, N., A. Martínez-Marcos, et al. (2010). "Chemosensory function of the amygdala." Vitamins and Hormones **83**: 165-196.

Haddad, R., R. Khan, et al. (2008). "A metric for odorant comparison." Nature Methods **5**(5): 425-429.

Hallett, M. (2007). "Volitional control of movement: The physiology of free will." Clinical Neurophysiology **118**(6): 1179-1192.

Hardin, C. L. (1988). Color for Philosophers. Indianapolis, Hackett Publishing Company.

Henning, H. (1916). Der Geruch. Leipzig, Barth.

Herz, R. S. (2001). "Ah, sweet skunk: Why we like or dislike what we smell." Cerebrum **3**(4): 31-47.

Herz, R. S. (2005). The unique interaction between language and olfactory perception and cognition. Trends in Experimental Psychology Research. New York, Nova Science Publishers, Inc.**:** 91-109.

Herz, R. S. (2007). The Scent of Desire. New York, William Morrow.

Hilbert, D. R. and M. Kalderon (2000). Color and the Inverted Spectrum. Color Perception: Philosophical, Psychological, Artistic, and Computational Perspectives. S. Davis. Oxford, Oxford University Press.

Hinton, P. B. and T. B. Henley (1993). "Cognitive and affective components of stimuli produced in three modes." Bulletin of the Psychonomic Society **31**: 595–598.

Humphrey, N. (2001). "Doing it my way: sensation, perception – and feeling red." Behavioral and Brain Sciences **24**(5): 987.

Jackson, F. (1977). Perception. Cambridge, Cambridge University Press.

Jacobs, G. H. (1981). Comparative Color Vision. New York, Academic Press.

Jacobs, G. H. (2009). "Evolution of colour vision in mammals." Philosophical Transactions of the Royal Society B: Biological Sciences **364**: 2957–2967.

Jacobs, L. F., J. Arter, et al. (2014). "Olfactory navigation in humans: spatial orientation within an odor landscape " AChemS poster.

Jeffery, W. R. (2009). "Regressive evolution in Astyanax cavefish." Annual Review of Genetics **43**(1): 25-47.

Jehl, C., J. P. Royet, et al. (1995). "Odor discrimination and recognition memory as a function of familiarization." Perception and Psychophysics **57**(1002-1011).

Jékely, G., J. Colombelli, et al. (2008). "Mechanism of phototaxis in marine zooplankton." Nature **456**(7220): 395-399.

Jiang, P. H., J. Josue, et al. (2012). "Major taste loss in carnivorous mammals." Proceedings of the National Academy of Sciences **109**(13): 4956-4961.

Johnson, C. J., A. Paivio, et al. (1996). "Cognitive components of picture naming." Psychological Bulletin **120**(1): 113-139.

Jönsson, F. U., A. Tchekhova, et al. (2005). "A metamemory perspective on odor naming and identification." Chemical Senses **30**(4): 353-365.

Kaeppler, K. and F. Mueller (2013). "Odor classification: A review of factors influencing perception-based odor arrangements." Chemical Senses **38**(3): 189-209.

Keeley, B. L. (2002). "Making sense of the senses: Individuating modalities in humans and other animals." The Journal of Philosophy **99**(1): 5-28.

Keller, A., H. Zhuang, et al. (2007). "Genetic variation in a human odorant receptor alters odour perception." Nature **449**(7161): 468-472.

Kemp, S. E. and A. N. Gilbert (1997). "Odor intensity and color lightness are correlated sensory dimensions." The American journal of psychology **110**(1): 35-46.

Khan, R. M., C. H. Luk, et al. (2007). "Predicting odor pleasantness from odorant structure: Pleasantness as a reflection of the physical world." Journal of Neuroscience **27**(37): 10015-10023.

Kleemann, A. M., J. Albrecht, et al. (2009). "Trigeminal perception is necessary to localize odors." Physiology & Behavior **97**(3-4): 401-405.

Köster, E. P. (2002). The specific characteristics of the sense of smell. Olfaction, Taste, and Cognition. C. Rouby, B. Schaal, D. Dubois, R. Gervais and A. Holley. Cambridge, Cambridge University Press**:** 27-44.

Köster, E. P., P. Møller, et al. (2014). "A “Misfit” Theory of Spontaneous Conscious Odor Perception (MITSCOP): reflections on the role and function of odor memory in everyday life." Frontiers in Psychology **5**.

Kraft, P. (2004). Aroma Chemicals IV: Musks. Chemistry and Technology of Flavours and Fragrances. D. Rowe. Oxford, Blackwell.

Kringelbach, M. L. (2005). "The orbitofrontal cortex: Linking reward to hedonic experience." Nature Reviews Neuroscience **6**: 691-702.

Kubovy, M. and D. Van Valkenburg (2001). "Auditory and visual objects." Cognition **80**(1-2): 97-126.

Laing, D. G. (1983). "Natural sniffing gives optimum odour perception for humans." Perception **12**: 99-117.

Lambon Ralph, M. A., K. Sage, et al. (2000). "Classical anomia: A neuropsychological perspective on speech production." Neuropsychologia **38**(2): 186-202.

Laska, M., R. M. Rivas Bautista, et al. (2009). "Gustatory responsiveness to six bitter tastants in three species of nonhuman primates." Journal of Chemical Ecology **35**(5): 560-571.

Laugerette, F., D. Gaillard, et al. (2007). "Do we taste fat?" Biochimie **89**(2): 265-269.

Levinson, S. C. and A. Majid (2014). "Differential ineffability and the senses." Mind & Language **29**(4): 407-427.

Levitan, C. A., J. Ren, et al. (2014). "Cross-cultural color-odor associations." PLoS One **9**(7).

Li, W., L. Lopez, et al. (2010). "Right orbitofrontal cortex mediates conscious olfactory perception." Psychological Science **21**(10): 1454-1463.

Locke, J. (1689/1975). Essay Concerning Human Understanding. Oxford, Oxford University Press.

Lorig, T. S. (1999). "On the similarity of odor and language perception." Neuroscience & Biobehavioral Reviews **23**(3): 391-398.

Lycan, W. G. (2000). The slighting of smell. Of Minds and Molecules: New Philosophical Perspectives on Chemistry. N. Bhushan and S. Rosenfeld. Oxford, Oxford University Press**:** 273–289.

Lycan, W. G. (2014). "The intentionality of smell." Frontiers in Psychology **5**.

Lycan, W. G. (2014). What does vision represent? Does Perception have Content? B. Brogaard. Oxford, Oxford University Press**:** 311-328.

Macpherson, F. (2011). "Taxonomizing the senses." Philosophical Studies **153**: 123-142.

Macpherson, F. (2012). "Cognitive penetration of colour experience: Rethinking the issue in light of an indirect mechanism." Philosophy and Phenomenological Research **84**(1): 24-62.

Macpherson, F. (2015). The space of sensory modalities. Perception and its Modalities. D. Stokes, M. Matthen and S. Biggs. Oxford, Oxford University Press**:** 432-461.

MacRae, A. W., P. Howgate, et al. (1990). "Assessing the similarity of odors by sorting and by triadic comparison." Chemical Senses **15**(6): 691-699.

MacRae, A. W., T. Rawcliffe, et al. (1992). "Patterns of odor similarity among carbonyls and their mixtures." Chemical Senses **17**(2): 119-125.

Maier, J. X., M. Wachowiak, et al. (2012). "Chemosensory convergence on primary olfactory cortex." Journal of Neuroscience **32**(48): 17037-17047.

Mainland, J. and N. Sobel (2006). "The sniff Is part of the olfactory percept." Chemical Senses **31**(2): 181-196.

Mainland, J. D., A. Keller, et al. (2014). "The missense of smell: functional variability in the human odorant receptor repertoire." Nature Neuroscience **17**(1): 114-120.

Marcus, G. (2008). Kluge: The haphazard construction of the mind. Boston, Houghton Mifflin Company.

Marshall, J., T. W. Cronin, et al. (2007). "Stomatopod eye structure and function: A review." Arthropod Structure & Development **36**(4): 420-448.

Martin, G. N. (2013). The Neuropsychology of Smell and Taste. London, Psychology Press.

Martin, M. (1992). Sight and touch. The Contents of Experience. T. Crane. Cambridge, CambridgeUniversity Press.

Matthen, M. (2005). Seeing, Doing, and Knowing. Oxford, Oxford University Press.

Matthen, M. (2010). "On the diversity of auditory objects." Review of Philosophy and Psychology **1**: 63-89.

McAdams, S. and A. Bregman (1979). "Hearing musical streams." Computer Music Journal **3**(4): 26-43.

McBurney, D. H., J. M. Levine, et al. (1977). "Psychophysical and social ratings of human body odor." Personality and Social Psychology Bulletin **3**: 135–138.

McGurk, H. and J. MacDonald (1976). "Hearing lips and seeing voices." Nature **264**(5588): 746-748.

Millikan, R. (1984). Language, Thought, and Other Biological Categories. Cambridge, MIT Press.

Morrot, G., F. Brochet, et al. (2001). "The color of odors." Brain and Language **79**(2): 309-320.

Nagel, T. (2012). Mind & Cosmos: Why the Materialist Neo-Darwinian Conception of Nature is Almost Certainly False. Oxford, Oxford University Press.

Nickerson, D. and S. M. Newhall (1943). "A psychological color solid." Journal of the Optical Society of America **33**(7): 419-422.

Nudds, M. (2010). "What are auditory objects?" Review of Philosophy and Psychology **1**: 105-122.

O'Callaghan, C. (2008). "Object perception: Vision and audition." Philosophy Compass **3**: 803-829.

O'Callaghan, C. (2014). "Auditory Perception." The Stanford Encyclopedia of Philosophy, from http://plato.stanford.edu/archives/sum2014/entries/perception-auditory/.

O'Regan, J. K. and A. Noë (2001). "A sensorimotor account of vision and visual consciousness." Behavioral and Brain Sciences **24**(5): 939-973.

Ohloff, G. (1994). Scent and Fragrances: The Fascination of Odors and their Chemical Perspectives. Berlin, Springer-Verlag.

Olofsson, J. K. (2014). "Time to smell: A cascade model of human olfactory perception based on response-time (RT) measurement." Frontiers in Psychology **5**.

Peacocke, C. (2008). "Sensational properties: Theses to accept and theses to reject." Revue Internationale de Philosophie **62**: 7-24.

Pessoa, L. and R. Adolphs (2010). "Emotion processing and the amygdala: From a 'low road' to 'many roads' of evaluating biological significance." Nature Reviews Neuroscience **11**(11): 773-783.

Phillips, I. "Unconscious perception reconsidered."

Pinker, S. (1997). How the Mind Works. New York, W. W. Norton & Company.

Plato Timaeus.

Pointer, M. R. and G. G. Attridge (1998). "The number of discernible colours." Color Research and Application **23**(1): 52-54.

Porter, J., T. Anand, et al. (2005). "Brain mechanisms for extracting spatial information from smell." Neuron **47**(4): 581-592.

Porter, J., B. Craven, et al. (2007). "Mechanisms of scent-tracking in humans." Nature Neuroscience **10**(1): 27-29.

Price, J. L. (2007). "Definition of the orbital cortex in relation to specific connections with limbic and visceral structures and other cortical regions." Annals of the New York Academy of Sciences **1121**(1): 54-71.

Prinz, J. J. (2006). Is the mind really modular? Contemporary Debates in Cognitive Science. R. Stainton**:** 22–36.

Prinz, J. J. (2009). Is Consciousness Embodied? The Cambridge Handbook of Situated Cognition. P. Robbins and M. Ayede, Cambridge University Press**:** 419-436.

Pylyshyn, Z. (1999). "Is vision continuous with cognition? The case for cognitive impenetrability of visual perception." Behavioral and Brain Sciences **22**: 341-423.

Quine, W. V. (1970). Natural kinds. Essays in Honor of Carl G. Hempel. N. Rescher. Dordrecht, D. Reidel Publishing Company.

Rabin, M. D. (1988). "Experience facilitates olfactory quality discrimination." Perception and Psychophysics **44**: 532-540.

Radil, T. and C. J. Wysocki (1998). "Spatiotemporal masking in pure olfaction." Annals of the New York Academy of Sciences **855**: 641-644.

Rankin, K. M. and L. E. Marks (2000). "Chemosensory context effects: Role of perceived similarity and neural commonality." Chemical Senses **25**(6): 747-759.

Richardson, L. (2011). "Sniffing and smelling." Philosophical Studies **162**(2): 401-419.

Robbins, P. (2010). "Modularity of Mind." The Stanford Encyclopedia of Philosophy Summer 2010. from http://plato.stanford.edu/archives/sum2010/entries/modularity-mind/.

Rodrigues, A. B. J. and R. Besnoy (1980). "What is metamerism?" Color Research and Application **5**(4): 220-221.

Rolls, E. T. and L. L. Baylis (1994). "Gustatory, olfactory, and visual convergence within the primate orbitofrontal cortex." Journal of Neuroscience **14**(9): 5437-5452.

Rolls, E. T., H. D. Critchley, et al. (2009). "The representation of information about taste and odor in the orbitofrontal cortex." Chemosensory Perception **3**(1): 16-33.

Rolls, E. T., M. L. Kringelbach, et al. (2003). "Different representations of pleasant and unpleasant odors in the human brain." European Journal of Neuroscience **18**: 695-703.

Root, Cory M., Kang I. Ko, et al. (2011). "Presynaptic facilitation by neuropeptide signaling mediates odor-driven food search." Cell **145**(1): 133-144.

Rorty, R. (1981). Philosophy and the Mirror of Nature. Princeton, Princeton University Press.

Rorty, R. (1998). Truth and Progress: Philosophical Papers, Volume 3. Cambridge, Cambridge University Press.

Rosenthal, D. (2014). Quality spaces and sensory modalities. The Nature of Phenomenal Qualities: Sense, Perception, and Consciousness. P. Coates and S. Coleman. Oxford, Oxford University Press.

Rosenthal, D. M. (2005). Consciousness and Mind. Oxford, Oxford University Press.

Rosenthal, D. M. (2010). "How to think about mental qualities." Philosophical Issues: Philosophy of Mind **20**: 368-393.

Rosenthal, D. M. (in press). Quality spaces, relocation, and grain. Sellars and His Legacy. J. R. O'Shea. Oxford, Oxford University Press.

Rossiter, K. J. (1996). "Structure−Odor Relationships." Chemical Reviews **96**(8): 3201-3240.

Royet, J. P. and J. Plailly (2004). "Lateralization of olfactory processes." Chemical Senses **29**(8): 731-745.

Salzman, C. D. and S. Fusi (2010). "Emotion, cognition, and mental state representation in amygdala and prefrontal cortex." Annual Review of Neuroscience **33**(1): 173-202.

Samuels, R. (2006). Is the human mind massively modular? Contemporary Debates in Cognitive Science. R. Stainton, Blackwell.

Saveer, A. M., S. H. Kromann, et al. (2012). "Floral to green: mating switches moth olfactory coding and preference." Proceedings of the Royal Society B: Biological Sciences **279**(1737): 2314-2322.

Schwartz, B. L. and J. Metcalfe (2011). "Tip-of-the-tongue (TOT) states: retrieval, behavior, and experience." Memory & cognition **39**(5): 737-749.

Sela, L. and N. Sobel (2010). "Human olfaction: A constant state of change-blindness." Experimental Brain Research **205**(1): 13-29.

Sellars, W. (1965). "The Identity Approach to the Mind-Body Problem." Review of Metaphysics **18**: 430-451.

Shepherd, G. M. (2011). Neurogastronomy: How the Brain Creates Flavor and Why It Matters. New York, Columbia University Press.

Shimojo, S. and L. Shams (2001). "Sensory modalities are not separate modalities: plasticity and interactions." Current Opinion in Neurobiology **11**(4): 505-509.

Siegel, S. (2006). Which properties are represented in perception? Perceptual Experience. T. Szabó Gendler and J. Hawthorne. Oxford, Oxford University Press**:** 481-503.

Simons, D. and R. Rensink (2005). "Change blindness: past, present, and future." Trends in Cognitive Sciences **9**(1): 16-20.

Small, D. M. and B. G. Green (2012). A proposed model of a flavor modality. The Neural Bases of Multisensory Processes. M. M. Murray and M. T. Wallace. Boca Raton, CRC Press.

Smith, A. D. (2002). The Problem of Perception. Cambridge, Harvard University Press.

Smith, K. (2012). "Brain imaging: fMRI 2.0." Nature **484**: 24–26.

Sobel, N., V. Prabhakaran, et al. (1999). "Blind smell: Brain activation induced by an undetected air-borne chemical." Brain **122 (Pt 2)**: 209-217.

Song, C. and B. E. Leonard (2005). "The olfactory bulbectomised rat as a model of depression." Neuroscience and Biobehavioral Reviews **29**(4-5): 627-647.

Sorabji, R. (2011). Aristotle on Demarcating the Five Senses. The Senses: Classical and Contemporary Perspectives. F. Macpherson. New York, Oxford University Press**:** 64-82.

Soudry, Y., C. Lemogne, et al. (2011). "Olfactory system and emotion: common substrates." European Annals of Otorhinolaryngology, Head and Neck Diseases **128**(1): 18-23.

Sperber, D. (1994). The modularity of thought and the epidemiology of representations. Mapping the mind: Domain specificity in cognition and culture. L. A. Hirschfeld and S. A. Gelman. New York, Cambridge University Press.**:** 29-67.

Sperber, D. (2001). In defense of massive modularity. Language, Brain and Cognitive Development: Essays in Honor of Jacques Mehler. E. Dupoux. Cambridge, MIT Press**:** 47-57.

Stevens, S. S. and H. Davis (1938). Hearing, its Psychology and Physiology. New York, John Wiley.

Stevenson, R. J. (2001). "Associative learning and odor quality perception: How sniffing an odor mixture can alter the smell of its parts." Learning and Motivation **32**(2): 154-177.

Stevenson, R. J. (2009). "An initial evaluation of the functions of human olfaction." Chemical Senses **35**(1): 3-20.

Stevenson, R. J. (2009). "Phenomenal and access consciousness in olfaction." Consciousness and Cognition **18**(4): 1004-1017.

Stevenson, R. J. (2014). "Object concepts in the chemical senses." Cognitive Science **38**(7): 1360-1383.

Stevenson, R. J. and R. A. Boakes (2003). "A mnemonic theory of odor perception." Psychological Review **110**(2): 340-364.

Stevenson, R. J., M. J. Oaten, et al. (2010). "Children's response to adult disgust elicitors: development and acquisition." Developmental Psychology **46**(1): 165-177.

Stevenson, R. J. and D. A. Wilson (2007). "Odour perception: an object-recognition approach." Perception **36**: 1821–1833.

Sulmont-Rosse, C. (2005). "Odor naming methodology: Correct identification with multiple-choice versus repeatable identification in a free task." Chemical Senses **30**(1): 23-27.

Taylor, A. J. and D. D. Roberts, Eds. (2004). Flavor Perception. Oxford, Blackwell Publishing.

Thoen, H. H., M. J. How, et al. (2014). "A Different Form of Color Vision in Mantis Shrimp." Science **343**(6169): 411-413.

Tomasello, M. (2008). Origins of Human Communication. Cambridge, MIT Press.

Tomasello, M., M. Carpenter, et al. (2005). "Understanding and sharing intentions: The origins of cultural cognition." Behavioral and Brain Sciences **28**(5): 675-+.

Tordoff, M. G., L. K. Alarcón, et al. (2012). "T1R3: A human calcium taste receptor." Scientific Reports **2**.

Turin, L. (1996). "A spectroscopic mechanism for primary olfactory reception." Chemical Senses **21**(6): 773-791.

Tye, M. (1995). Ten Problems of Consciousness. Cambridge, MIT Press.

Varendi, H. and R. H. Porter (2001). "Breast odour as the only maternal stimulus elicits crawling towards the odour source." Acta Paediatrica **90**(4): 372-375.

Varendi, H., R. H. Porter, et al. (1994). "Does the newborn baby find the nipple by smell." Lancet **344**(8928): 989-990.

Veramendi, M., P. Herencia, et al. (2013). "Perfume odor categorization." Journal of Sensory Studies **28**: 76-89.

Vitevitch, M. S. (2003). "Change deafness: the inability to detect changes between two voices." Journal of Experimental Psychology: Human Perception and Performance **29**: 333-342.

von Békésy, G. (1964). "Olfactory analogue to directional hearing." Journal of Applied Physiology **19**(3): 369-&.

Wallraff, H. G. and M. O. Andreae (2000). "Spatial gradients in ratios of atmospheric trace gases: a study stimulated by experiments on bird navigation." Tellus Series B-Chemical and Physical Meteorology **52**(4): 1138-1157.

Weiss, T., K. Snitz, et al. (2012). "Perceptual convergence of multi-component mixtures in olfaction implies an olfactory white." Proceedings of the National Academy of Sciences **109**(49): 19959-19964.

Weissburg, M. J. (2000). "The fluid dynamical context of chemosensory behavior." Biological Bulletin **198**(2): 188-202.

Whissell-Buechy, D. and J. E. Amoore (1973). "Odour-blindness to musk: simple recessive inheritance." Nature **242**(5395): 271-273.

Wilson, D. and R. J. Stevenson (2006). Learning to Smell: Olfactory Perception from Neurobiology to Behavior. Baltimore, The Johns Hopkins University Press.

Wise, P. M., M. J. Olsson, et al. (2000). "Quantification of odor quality." Chemical Senses **25**(4): 429-443.

Wright, R. H. (1964). The Science of Smell. London, George Allen & Unwin.

Yeshurun, Y. and N. Sobel (2010). "An odor is not worth a thousand words: From multidimensional odors to unidimensional odor objects." Annual Review of Psychology **61**(1): 219-241.

Young, B. D. (2011). Olfaction: Smelling the Content of Consciousness. Philosophy. New York, City University of New York. **PhD**.

Young, B. D. (2014). "Smelling Phenomenal." Frontiers in Psychology **5**: 713.

Young, B. D., A. Keller, et al. (2014). "Qualtiy Space Theory in Olfaction." Frontiers in Psychology **5**(1).

Zald, D. H. and J. V. Pardo (1997). "Emotion, olfaction, and the human amygdala: Amygdala activation during aversive olfactory stimulation." Proceedings of the National Academy of Sciences **94**(8): 4119-4124.

Zald, D. H. and S. Rauch (2008). The Orbitofrontal Cortex. Oxford, Oxford University Press.