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Handedness and Cerebral Lateralization: A Test of the Cerebral Crowding Effect

by

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Abstract

The purpose of this study was to test Levy's (1969) cerebral crowding hypothesis by examining the relationship between functional laterality (verbal versus spatial) and handedness across three handedness groups (Inconsistent Left-handers, Consistent Left-handers and Right-handers) as defined by Peters and Murphy (1992). A total of 89 undergraduate students completed a variety of lateralized and paper-and-pencil verbal and spatial tasks, and three handedness questionnaires. A significant visual field by handedness interaction was found for semantic priming as Inconsistent Left-handers (ILHs) processed verbal information faster and more accurately in their right hemisphere than the other groups. The ILHs also displayed the greatest accuracy on a paper-and-pencil mental rotation test. The prediction that Consistent Left-handers would exhibit the greatest verbal and poorest spatial skills was not met. Overall, this study failed to support the cerebral crowding hypothesis and highlights the need for greater consideration of handedness issues in laterality research.

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Lastly, I would like to thank Andre Paquette for his help in the data collection process, and Reagan Gale for her data entry expertise.

> "If we knew what it was we were doing, it would not be
> called research, would it?"
>
> \- Albert Einstein

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Overview of Lateralization Research

In 1861, Paul Broca made an important discovery about the lateralization of language in the human cortex. A man who had suffered from epilepsy since his youth had been admitted as a patient to the hospice of Bicêtre and though his receptive language was intact, he was unable to respond with any word other than "tan". He was, however, able to express himself through gestures (Broca, 1861). Tan (as he became known) died nearly 30 years after losing the ability to speak and, upon autopsy, Broca discovered that a large portion of Tan's left hemisphere had been destroyed. This finding supported the conclusion that the neural substrates for articulatory language were located in the left hemisphere of the brain in right-handed people. From this he postulated that the right hemisphere must be dominant for articulatory language in left-handers (Broca, 1861), a belief that was not seriously questioned for over a quarter of a century (Chescher, 1936) and not studied empirically until after World War II when systematic studies were carried out on left-handed veterans with unilateral hemispheric lesions (Hécaen, De Agnostini, & Monzon-Montes, 1981).

These studies led to the understanding that the cortical organization of language dominance in the brains of left-handers (LHs) is not necessarily a mirror image of right-handers' (RHs) brains, as previously believed, but rather it is merely different from that of right-handers. If the cerebral organization of left-handers' brains does not, in fact, follow the relatively standard gross functional organization of that of right-handers, then the left-handed brain may organize in normatively uncommon way(s), given the relatively low occurrence of left-handedness. Following basic neurological principles, it is reasonable to hypothesize that the different cortical organization(s) found in left-handers may have functional consequences in terms of efficiencies and inefficiencies in domains of cognitive functioning. This becomes especially important in light of the fact that each hemisphere is (more or less) specialized to perform certain tasks better than others. But what exactly are the cognitive strengths of each hemisphere?

In an attempt to summarize the cognitive capabilities of the two hemispheres in general terms, Levy (1969) concluded that the left hemisphere tends to be characteristically analytic and sequential, whereas the right hemisphere was more spatial and synthetic – nonverbal, in other words. Her work suggested that the two hemispheres develop mutually exclusive functions in order to limit interference, an idea that helped cement the concept of hemispheric lateralization and functional specificity.

While it is widely believed that spatial processing is a right hemisphere function (French & Painter, 1991; Kelley, Chang, Suzuki, Levin, & Reyes-Iglesias, 1993), regardless of handedness, the literature is not as clear-cut as one might think. Furthermore, it is important to keep in mind that while the right hemisphere may be superior in terms of spatial abilities, the left hemisphere is still capable of performing simple spatial tasks (Vogel, Bowers & Vogel, 2003). If the two hemispheres are not clearly delineated in terms of functional lateralization, then any distinctions become further blurred by the addition of handedness issues as both clinical and normal samples suggest that LHs are a more heterogeneous group than right-handers (RHs) for both verbal and possibly for spatial abilities (Levander & Levander, 1990; Laeng & Peters, 1995; Knecht et al., 2000; Hécaen et al., 1981). This makes drawing conclusions about LHs as a group quite difficult as not only is there still much to learn about typical cerebral lateralization (i.e.: that of right-handers), but there is even more still to learn about the lateralization of LHs. Exacerbating matters is the fact that, despite comprising 10% of the population (Perelle & Ehrman, 2005), many researchers exclude LHs from their studies for the very reason that not enough is known about their lateralization.

According to Levy's (1969) crowding hypothesis, LHs have more bilateral representation of language functions and thus their spatial resources in the right hemisphere may be "crowded out" by language, resulting in a decrease in spatial ability. This hypothesis, which was originally devised through work on epilepsy patients, led to the prediction that LHs should have better verbal and poorer spatial skills compared to right-handers (RHs). Levy found initial support for this hypothesis by comparing LHs' and RHs' VIQ and PIQ scores on the Wechsler Adult Intelligence Scale (WAIS) (Wechsler, 1955). She found that while the two groups did not differ in terms of verbal intelligence (LHs = 142, RHs = 138), there was the predicted difference on the performance scale (LHs = 117, RHs = 130) which Levy attributed to the "crowding" of spatial resources by verbal faculties in LHs. Additional support for this hypothesis came from a study on a patient with congenital agenesis of the corpus callosum who had speech in both hemispheres (Sperry, 1968). The author reported that this patient had a verbal intelligence quotient that was above average and while his grades in courses involving language were fair to good, his grades in geography and geometry, the more spatial and nonverbal courses, were comparatively poor. It seemed that with this patient, language in the right hemisphere had developed at the expense of the nonverbal abilities that should have dominated the hemisphere. Bolstering this finding, Lansdell (1969) found language in the right hemisphere in a group of individuals with known neurological or cerebral disorders. In these patients Lansdell concluded that the younger the patient was when brain damage occurred, the more their nonverbal (but not verbal) abilities suffered, supporting the view that the right hemisphere has a greater ability to develop language function in infancy than later in age. It should be noted that many of the researchers who have found support for the cerebral crowding effect (Sperry, 1968; Lansdell, 1969) have used populations with known neurological deficits. It seems likely that if one has neurological damage, fewer resources would already be available, which is why cerebral crowding may be more prevalent in patient populations. Nonetheless, while these (Laeng & Peters, 1995; Levander & Levander, 1990; Tan, 1990; Levy, 1969; McKeever, Rich, Deyo and Conner, 1987) and other researchers using "normal" populations have found support for idea of cerebral crowding, the evidence has been mixed, with some researchers finding no evidence to bolster these notions despite utilizing a wide range of methodologies and populations. For instance, in separate studies looking at handedness differences using the Vandenberg Mental Rotations Test, neither Casey, Brabeck, and Ludlow (1986) nor McGee (1976) found any evidence to support the notion that left-handers have poorer spatial abilities. Similarly, Hardyck, Petrinovich and Goldman (1976) failed to find a relationship between handedness and non-verbal intelligence and figure copying in children. In fact, a series of studies have failed to find any handedness effect on the visual-spatial subtests of the WAIS (Wechsler, 1955), such as Block Design and Object Assembly (Gilbert, 1977) or Block Design and Picture Arrangement (Johnson & Harley, 1980), or on the Block Design subtest of the WISC (Sheehan & Smith, 1986). The fact that researchers come up with contradictory conclusions leads one to wonder what other factors play a role in the spatial and verbal abilities of LHs.

One possible source of confusion in this literature may relate to the assumptions inherent in the cerebral crowding hypothesis. The cerebral crowding hypothesis assumes: 1) that there are limited neural resources available, which in turn assumes that there is replacement, not displacement, of resources; 2) that more complex processing requires more cortical space; and finally 3) that certain functional organizations may be more efficient than others for cognitive processing (e.g., that the majority of us are right-handed because language is largely controlled by the left hemisphere). The validity of these assumptions must be kept in mind when interpreting the apparently inconsistent evidence. In other words, it is possible that displacement of neural resources occurs, not replacement, or that more complex processing does not necessarily require more cortical space. Although a comprehensive review of the literature that may help address these assumptions is beyond the scope of this investigation, the limitations inherent in this theory should best be kept in mind.

Lateralization of Language

Up to the time of Hécaen's research there was merely speculation that left-handers have a different cerebral organization than right-handers (Hécaen et al., 1981). For right-handers, however, it had become widely accepted in neurology that the left hemisphere was the dominant hemisphere, housing language capabilities, while the right hemisphere was deemed the subordinate, non-language hemisphere (Sperry, 1982). In fact, at the time it was even felt that the right hemisphere was entirely incapable of any of the higher cognitive functions responsible for processing language and symbolic information (Sperry, 1982). This view of language lateralization was the predominant neurological theory of language representation for so long that it had nearly reached the status of scientific truth to many.

Though it was not widely accepted, the idea that the right hemisphere contributes to language processing dates back to at least 1836 when the first theory of the interaction between handedness and the lateralization of language was ostensibly put forth by Dax. Dax suggested, as had Broca (1865), that the language lateralization of left-handers was simply the reverse pattern of that known to be true for right-handers. In other words, all non-right-handers had language in their right-hemisphere while all right-handers had language in the left hemisphere (Dax, 1836). Clinical evidence on aphasia began to show, however, that perhaps this was too simplistic a view, as crossed aphasia in non-right-handers seemed to be the rule and not the exception (Hécaen & Sauguet, 1971) and thus a better explanation for language lateralization was needed. In attempting to uncover which hemisphere produced language, John Hughlings-Jackson (1874) postulated that involuntary and automatic word usage in speech was controlled by the right hemisphere whereas the left hemisphere was responsible for voluntary language use. Right hemisphere language was later studied experimentally in split-brain patients (Gazzaniga & Sperry, 1967; Sperry, 1961; Sperry, 1982). Commisurotomy patients surprised researchers by the language capabilities shown in the right hemisphere (Sperry, 1982; Gazzaniga et al., 1967). This raised the issue of why the right hemisphere is able to perform certain cognitive functions after commisurotomy, such as read, that it could not do after a focal lesion to the left hemisphere. Sperry (1982) and colleagues

(Gazzaniga, 1989) advanced the idea that the brain is composed of two halves that operate together as a tightly knit unit such that damage to one half renders the whole system incapable of a given function. After commisurotomy, however, the healthy side is no longer bound to the damaged side and its own remaining function can emerge.

Abstract and conceptual language also appeared to be present in the right hemisphere of such split-brain patients, as well as competence on tasks dealing with semantic information and the ability to determine whether or not a sentence spoken aloud is agrammatical (Gazzaniga, 1989). de Bode and Curtiss (2000) found that right-handed patients who underwent left hemispherectomy had the preserved ability to comprehend speech, and showed signs of recovery of expressive speech (in some cases) after surgery by using their non-dominant right hemisphere. A study by Sperry, Zaidel and Zaidel (1979) found that in commisurotomy patients, appropriate emotional reactions and displays of humour are also under the control of the right hemisphere, a finding that is bolstered by the work of several other researchers (Pell, 2006; Bloom & Borod, 1993; Shamay-Tsoory, Tomer & Aharon-Peretz, 2005).

Theories of Handedness

The high proportion of right-handedness appears to be an evolutionarily long-standing phenomenon. Archaeological evidence has shown that our earliest ancestors used weapons to kill their prey and the fact that it is the left side of the skulls that are crushed suggests that the right hand was used to execute the blow (Dart, 1949). From this it seems that one thing at least is certain: since our earliest times in history, humans have shown a greater preference for using the right hand to perform most tasks.

While it is still not known why the majority of humans are right-handed, there are several theories as to what makes people left-handed. One such theory is Satz's (1972; 1973) model of pathological left-handedness, which suggests that left-handedness is a result of early (before age 6) cerebral insult in natural right-handers. This theory assumes that lesions are equally likely to occur in either hemisphere but that because the left hemisphere begins to develop earlier it is more susceptible to damage. Thus, if a natural right-hander suffers an insult early on to their left hemisphere, hemihypoplesia likely occurs, their right hand will become weaker and they will switch handedness as a result. Silva and Satz (1979) stress that it is actually the *potentially* preferred hand that switches as most insults occur pre- or perinatally (i.e.: before any strong lateralization has occurred). This theory of the pathological left-hander may explain why certain groups, such as mentally retarded and/or epileptic populations, have a much higher incidence of left-handedness than is found in the general population (approximately 17% vs. 8%, respectively) (Satz, 1973). However, results of this study also suggest that even if one suffers from a mild brain injury at an early age (i.e.: before the age of 6), there may be no clinical sequelae later on, meaning that factors other than genetic or cultural influences continue to obscure the causes of natural left-handedness (Satz, 1973). Lastly, it is also important to note that while this theory may apply to exceptional groups, it does not necessarily apply to "normal" populations who have not sustained a cerebral insult that could result in their switching handedness.

Regardless, for the majority of the population, hand dominance is contralateral to the hemisphere dominant for language (i.e.: left hemisphere), meaning that surgery on this hemisphere at any stage in life could affect both handedness and verbal ability.

Historically, one of the most accurate methods of discerning cerebral dominance is through the use of sodium amobarbital injections into one of the carotid arteries. This procedure, sometimes known as the Wada test, enables clinicians to determine if the main components of speech for a given individual are in the right or left hemisphere because it produces a transitory loss of function in the hemisphere ipsilateral to the injection. Due to the dangers of undergoing the procedures, the Wada test is mainly used with patients suffering from intractable epilepsy who must undergo surgery and for whom speech localization is of great importance to ensure that following the surgery they are able to both produce and understand speech. Using this technique, Rasmussen and Milner (1977) looked at factors that may influence the alteration of hemispheric language dominance following early injury. Based on their results, they posit that the critical factor in deciding whether hemispheric language dominance will switch after early cerebral insult is the location of the lesion, with injury to the left peri-Sylvian regions being associated with language and speech dominance either switching to the right hemisphere or becoming bilateral, findings that bolster those of Penfield and Roberts (1959). They go on to state that “an early lesion that does not modify hand preference is on the whole unlikely to change the side of speech representation” (Rasmussen & Milner, 1977, p. 359).

Annett (1972; 1978b; 1998) has put forth a different model for lateralization. Her right shift (RS) theory (Annett, 1972; 1978b; 1998) states that left-handers with a family history of sinistrality (left-handedness) failed to inherit the basic tendency for left hemispheric speech and therefore they are more likely to have speech and language in the right hemisphere. This theory, which assumes that right-handedness is a universal norm of humanity (Annett & Alexander, 1996), posits that a single gene (RS+) is responsible for producing left-hemisphere language dominance (thus giving a slight advantage to the right hand) and that without this gene (i.e.: the presence of the RS- gene), hemispheric dominance is left to chance factors (Annett, 1985). Along a similar vein, Levy and Nagylaki (1972) claim that there are two genes used to determine handedness and language dominance: the L gene (L and l) determines which is the language-dominant hemisphere, while the C gene (C and c) determines whether or not hand control is ipsilateral or contralateral to the language-dominant hemisphere. In this model, L and C are the dominant genes, where L results in left hemisphere language dominance and C results in contralateral (to the dominant hemisphere) hand control. Thus, inheritance of the L-l gene results in left hemisphere language dominance because the L-allele overpowers the l-allele, resulting in higher rates of left hemisphere dominance for language in the general population. Therefore, the C-c gene, which determines which hand will be dominant, is dependent on the L-l deciding which pathway is dominant before it can determine if hand dominance will be ipsilateral or contralateral.

More recent studies looking at X-linked genes have found support for a so-called ‘maternal effect’ for left-handedness. For instance, when using writing hand as the sole criterion for determining handedness, McKeever (2000) found that more left-handed sons than daughters were born of left-handed mothers while left-handed fathers showed the opposite pattern, producing more daughters who are left-handed than sons. This study also showed that left-handed fathers produce no more left-handed sons than do right-handed fathers and that when both the mother and the father were left-handed, more left-handed children were produced (regardless of sex) as compared to when both parents were right-handed. The results supporting these theories have been mixed with some researchers finding little support for a genetic influence on handedness (Bishop, 2001).

Using same-sex monozygotic and dizygotic twin samples, Bishop found that cultural transmission was the model that best fit any similarity between parent-child handedness, and that genetic models did not provide a better fit to the data than theories of handedness that excluded genetic factors. A genetic basis for handedness has also run into difficulties with adoption studies, such as that by Saudino and McManus (1998) using the Colorado Adoption Project (CAP). In this study, the authors failed to find any evidence of genetic influence on handedness, or for that matter on footedness, eyedness and earedness. Further, they concluded that results from initial studies touting genetic links to handedness in adopted children lacked sufficient statistical power to differentiate genetic from environmental influences. Despite the fact that their study had great power, Saudino and McManus failed to replicate the findings of earlier adoption research, leading them to conclude that no such familial link exists. Nonetheless, whether or not there really is a gene for determining handedness, it must be kept in mind that none of these theories are entirely without fault as they all make major assumptions about the basic nature of human cerebral organization and none can completely account for all of the factors known to be related to handedness (e.g.: age, sex, family sinistrality, etc.).

Assessment of Handedness

It has been suggested (Brown, Roy, Rohr, Snider & Bryden, 2004; Eisenman, 1993; Cavill & Bryden, 2003; Peters, 1992; Peters, 1998; Steenhuis & Bryden, 1999) that the methods used to assess handedness – questionnaires (hand preference) vs.

performance measures – may be at least in part responsible for the disproportionate number of recorded RHs in the general population. For instance, there are many different handedness questionnaires, the most common of which is the Edinburgh Handedness Questionnaire (Oldfield, 1971), as well as performance measures, all of which have different cut-off points for determining handedness and all of which use different scales. Some researchers have also used a classification scheme wherein participants are deemed "right-" or "non-right-handed" (Nalçaci, Kalaycioğlu, Çiçek & Genç, 2001), a method that clumps left-handers as well as ambidextrous participants together.

In an effort to tackle this problem, Peters and Murphy (1992) administered the 60-item Waterloo Handedness Questionnaire (Steenhuis & Bryden, 1989) and a modified 14-item version of the Edinburgh Handedness Questionnaire (Oldfield, 1971). A cluster analysis of 645 undergraduate participants found five handedness groups emerged for the Waterloo questionnaire and three handedness groups emerged for the modified Edinburgh questionnaire when examined separately. When combined, they found a three cluster solution, which they labelled as follows: Consistent Left-handers (CLHs; those who consistently prefer to use their left hand for all activities), Inconsistent Left-handers (ILHs; those who tend to use their left hand to write and their right hand to throw) and Right-handers (RHs; those who prefer to use their right hand for all activities). Using this method, they found that 47% of their sample was classified as ILHs while in a similar study, Gilbert and Wysock (1992) found that ILHs comprised 30% of their sample. Together these studies illustrate once again that LHs truly are a heterogeneous group and for this reason they must not be lumped together into one group.

Relationship of Handedness with Verbal and Spatial Abilities

In terms of human evolution, it is generally accepted that our preference for right-hand dominance predates our ability to communicate using language (Perelle & Ehrman, 2005; Corballis, 1999; Corballis, 1999b), suggesting that our hand-dominance likely played a role in our language dominance. It makes sense from an efficiency standpoint that the neural substrates of language would be strategically located near the dominant hand representation for gesturing and writing. Thus, at least from an evolutionary, neuroanatomical perspective, it is likely that most people are right-handed and have language in the left hemisphere because the neural mechanisms responsible for language developed in close proximity to those responsible for our already-established dominant hand.

However, this begs the question: What about LHs? Using functional MRI (fMRI), Pujol, Deus, Losilla and Capdevila (1999) found that the degree of left-handedness is related to the incidence of right language dominance as determined by the pattern of activated areas. Further, they found that right hemisphere participation of LHs while performing a silent word generation task is quite common, with 10% of their LH sample ($n = 50$) showing right hemisphere activation. These results are comparable to those reported by Rasmussen and Milner (1977), who cite an occurrence of right hemisphere speech in 15% of LHs. These findings are bolstered by the work of Knecht et al. (2000) who also found, using functional transcranial Doppler sonography (fTCD), that the strongest incidence of right hemisphere language dominance (as determined by a silent word generation task) is evident in those who are strongly left-handed. The authors concluded that the more right-handed their participants were, the less right hemisphere language they had. Conversely, they found that strong LHs were 7 times more likely to have right hemisphere language dominance. In addition, a separate fTCD study by Basic et al., (2004) found that 93.3% of the RHs showed an increase in blood flow velocity in the left middle cerebral artery, while 77.3% of the LHs showed an increase in blood flow velocity in the right middle cerebral artery during a word generation task. The findings of both these fTCD studies should be interpreted with caution, however, as a PET study by Bookheimer, Zeffiro, Blaxton, Gaillard and Theodore (1995) found an increase in regional blood flow during separate silent reading and word generation tasks but not when these tasks were done aloud. In addition, Pujol et al. reported that out of 50 normal LHs used in their study, only 1 showed strong right hemisphere language lateralization. Furthermore, they found that 76% of the LHs exhibited increased activation in the left hemisphere, 14% showed bilateral activation, and 10% had right hemisphere activation. It should be noted, however, that only a small region of the brain was imaged in this study, suggesting that the proportion of right hemisphere language may increase if more areas were included. Nonetheless, if language is more likely to be processed in the right hemisphere in LHs than in RHs, as is evidenced by the increase in blood flow and the activation of both hemispheres during a verbal task (Bulla-Hellwig, Vollmer, Götzen & Skreczek, 1996), what about spatial processing? Is it also largely mediated by the right hemisphere as with right-handers, or is the cerebral organization of left-handers opposite to that of right-handers?

The literature seems to suggest that the right hemisphere is also dominant for spatial processing in left-handers. For instance, a study by Reio, Czarnolewski and Eliot (2004) found that the Cube Perspective Test (a 3-D mental rotation test) was indicative of greater right hemisphere "brain organisation", a finding supported by Hellige (1993). Further, they also found that greater left-handedness than right-handedness was related to spatial ability, meaning that higher scores were attained by the LHs on Maze-Tracing, Hidden Figures and Cube Perspective Tests.

Although most of the research that examines spatial abilities includes only RH participants (Fischer & Pellegrino 1988; French & Painter, 1991; Kelley, et. al., 1993), Vogel et al., (2003) examined the relationship between handedness in general and spatial ability using meta-analysis. Drawing on studies from computerized databases, Vogel et al. found that overall the right hemisphere is most involved in spatial tasks. However, the type of study is also key in interpreting findings as handedness studies suggest that spatial ability has a slight advantage when housed in the left hemisphere (although the authors caution that this finding may be due to low reliability). They also found that those who have good spatial skills fail to show a hemispheric advantage for spatial ability, whereas those who are poor at spatial tasks show a strong right hemisphere advantage. In terms of handedness itself, RHs have a strong right hemisphere advantage for spatial ability, while LHs do not seem to show a preference. The same is true for females, who show no hemispheric advantage, whereas males in general show a right hemisphere advantage. Lastly, on a task of spatial visualization (a mental rotation task), they found that neither hemisphere showed an advantage, suggesting that mental rotation may be a task that draws upon both hemispheres for successful completion, as suggested earlier by Fischer and Pellegrino (1988) and more recently by Chabris and Kosslyn (1998). In fact, Chabris and Kosslyn suggest that the left hemisphere does in fact process spatial information, but it is the *type* of spatial information that differs, a notion bolstered by Laeng and Peters

(1995) and Servos and Peters (1990). According to this model, the left hemisphere is thought to be better at encoding and using categorical spatial relations (i.e.: above/blow, left/right distinctions), while the right-hemisphere is better at encoding and utilizing coordinate spatial information (i.e.: those that deal with precise locations such as those needed for navigation).

Regardless, if left-hander's lateralization does not mirror that of right-handers, then it must be determined if there are any functional effects of bilateral representation or of having both verbal and visual spatial abilities processed in the same hemisphere. This is important because if left-handers are purposefully excluded from research for the reason that not enough is known about their lateralization, then finding evidence about the lateralization of LHs' verbal and spatial abilities will spur researchers to start including them in future research. Further, if there are functional effects of having both verbal and spatial abilities processed in the same hemisphere, we can begin to gain a better understanding of the costs and benefits of particular functional anatomical organizations. Such knowledge may aid in the understanding of individual differences in cognitive abilities as they relate to handedness and in turn improve our understanding of the neuropsychology of non-right-handed subgroups.

Factors such as gender, age, intelligence, test stimuli used for assessment and family sinistrality have all be found to be associated with both hemispheric asymmetries in cognitive function and handedness. In terms of familial sinistrality, Snyder and Harris (1993) found that CLHs performed worse than the ILHs and the RHs on a 2-dimensional spatial task and that performance was further worsened by being FS+. Similarly, O'Boyle and Benbow found that FS+ had a negative effect on spatial abilities, especially for LHs. So it seems that the role of FS interacts with handedness, such that those who are FS+LH fare the worst on spatial tasks. The question remains: Why is this so? Is it due to cerebral crowding, as Levy (1969) suggests?

The purpose of the current study was to compare the lateralization of verbal and spatial processing of LHs with that of RHs in order to test the cerebral crowding hypothesis. Through the use of several handedness questionnaires, participants were divided into naturally occurring groups (i.e.: CLHs, ILHs, or RHs) based on the 3 factor model proposed by Peters and Murphy (1992). They also completed several tasks that assessed their verbal and spatial capabilities. Based on Levy's (1969) cerebral crowing hypothesis, it was expected that left-handers as a group would obtain the lowest score on tasks of spatial ability as compared to right-handers because the resources that would normally be available to process spatial information were being "crowded out" and occupied by verbal facilities. More specifically, it was predicted that the spatial abilities of the CLHs would be significantly lower than those of the ILHs or the RHs as they would have fewer spatial resources. Overall, the ILHs were expected to perform much like the RHs on both verbal and spatial tasks because they should largely be left hemisphere dominant for language, as it is with the RHs, and thus little or no "crowding" was expected. It was also predicted that there would be a visual field by group interaction such that the ILHs and the RHs would exhibit a relative weakness in processing verbal stimuli that was presented to the left visual field (right hemisphere) and to show a relative weakness in spatial ability when geometric stimuli were presented to the right visual field (left hemisphere). On the other hand, it was expected that the verbal abilities of CLHs would be superior to those of the ILHs and RHs, regardless of the visual field to which the stimuli were presented, because they have more resources available overall for the processing of verbal information. It was hypothesized that there would not be the expected right hemisphere advantage for spatial processing that is typically seen in RHs, as presumably the CLH's spatial resources have been "crowded out" by their verbal resources present in that hemisphere. It was felt that if these predictions were met, it will show that the degree of handedness plays a role in the degree of spatial and verbal processing taking place in the right hemisphere and that there is in fact a crowding affect for CLHs.

Method

Participants

A total of 97 undergraduate students (66 female, 23 male) enrolled in a psychology course at the University of Windsor participated in this study in exchange for extra credit toward their course. Ethics approval was gained by the University of Windsor Research Ethics Board and informed consent was obtained from all participants before taking part in the study. Participants were recruited based upon self-reported handedness (i.e.: left- or right-handed) and inclusion in a specific subgroup was determined after completion of all three handedness questionnaires. This method resulted in unequal sample sizes among the three handedness groups. A total of 8 participants were excluded from the analysis for the following reasons: did not have English as their first language (n = 5); were above the age-limit for this study (n = 1); had a neurological deficit (n = 1); or were trilingual (n = 1). Thus, the total sample (n = 89) consisted of 32 right-handed (RH) (26 female, 6 male), 33 consistently left-handed (CLH) (28 female, 5 male) and 24 inconsistently left-handed (ILH) (12 female, 12 male) participants as classified by the handedness questionnaires. Participants had normal or corrected-to-normal vision.

Stimuli

For the semantic priming task, stimuli consisted of 48 semantically and categorically related word pairs (e.g.: "sofa" and "chair"), 48 semantically and categorically unrelated word pairs (e.g.: "key" and "horse"), and 96 unrelated non-word pairs, for a total of 192 pairs. The non-words, which were created by replacing one letter of an English word, served as the targets and were always preceded by a prime real word that did not exist elsewhere in the word list (e.g.: "heart" is the prime, and "wone" is the target). The non-word primes were drawn from a high-frequency noun pool (http://memory.psych.upenn.edu/wordpools.php) (Sederberg, et. al., 2007) and the targets were drawn from a larger pool of non-words (Hutchinson, Whitman, Abeare, & Raiter, 2003). Prime words range in length from three to six letters, while target words range from three to five letters in length. The related and unrelated word pairs were those used by Chiarello, Liu, Shears, Quan and Kacinik (2003) and Chiarello, Burgess, Richards and Pollock (1990). All the words used (primes and targets for related, unrelated, and non-word pairs) had high frequency values (Chiarello et al., 1990) and were in white type on a black background. As in Chiarello et al., (2003), two different stimulus onset asynchronies (SOAs) were used in order to assess automatic (150ms) and controlled (800ms) processing of the stimuli (see Appendix A for word pair lists).

The spatial stimuli consisted of a set of 12 random shapes selected from Vanderplas and Garvin (1959): Number of points (Shape number), 6 (28), 6 (29), 6 (30), 8 (27), 8 (29), 8 (30), 12 (28), 12 (30), 16 (29), 16 (30), 24 (29), 24 (30) (see Appendix B). These shapes were selected from the larger set as they have been found to have the lowest association values (Vanderplas & Garvin, 1959) indicating that it is less likely that participants will use verbal mediation to aid in the encoding of the shapes. The shapes were white on a black background.

Participants completed the North American Adult Reading Test (NAART) (Blair & Spreen, 1989), a list-reading task, and the Revised Mental Rotation Test (MRT-A, Peters et al., 1995), a visual spatial test requiring the mental rotation of cubed geometric designs. These tests were administered in order to provide a baseline measure of verbal and spatial abilities. Further, the NAART ensured that participants had an adequate reading level to enable their completion of the lateralized semantic priming task.

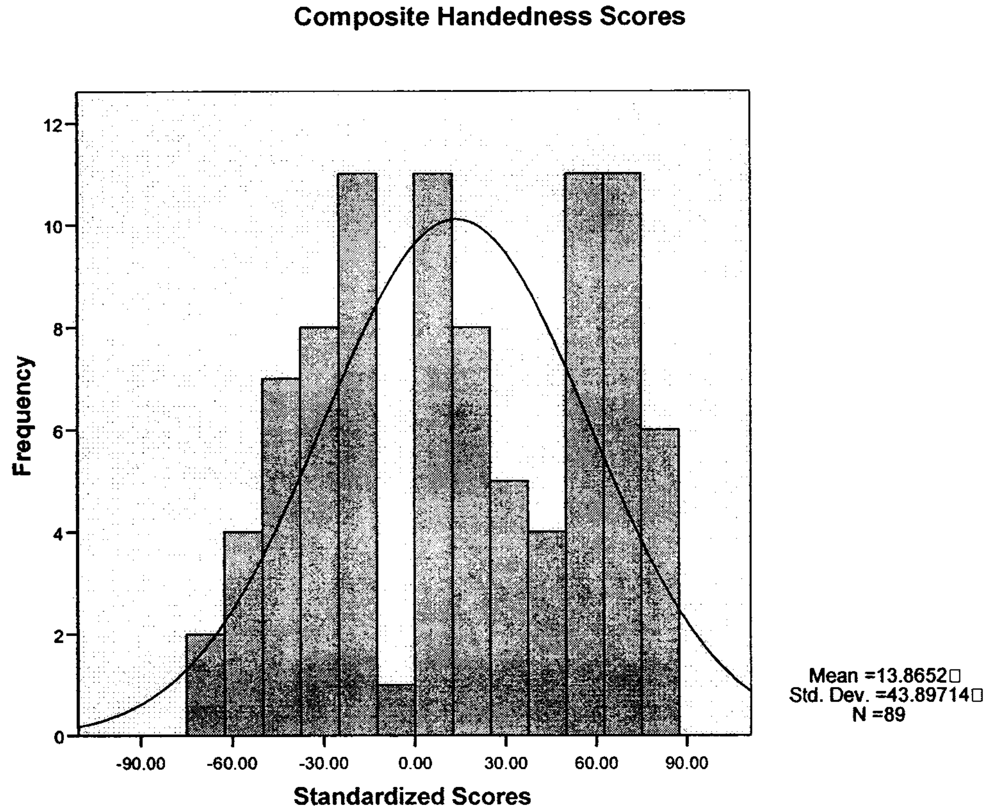
Apparatus

The lateralized semantic priming and mental rotation tasks were done on a Dell computer using Direct RT software. Participants used a chin rest to help keep their eyes at the fixed distance of 20" from the screen in order to ensure that the laterally presented stimuli fell within the desired visual field. The visual angle of the presented stimuli was 2° and participants responded via key-press on the keyboard.

Design and Procedure

Each participant completed a total of three handedness questionnaires at set intervals throughout the testing session: a modified version of the Edinburgh Handedness Questionnaire (Oldfield, 1971), the MNI Handedness Questionnaire (Crovitz & Zener, 1962), and the 36-item Waterloo Handedness Questionnaire – Revised (Steenhuis & Bryden, 1989). These questionnaires were used to determine to which handedness group participants belonged. Since little research has distinguished between the two subgroups of left-handers, exploratory analyses were used to arrive at our distinctions. To do this, the scales for each handedness questionnaire were standardized along a 5-point Likert scale where a score of -2 meant for an item meant "Always Use Left Hand", a score of -1 meant "Normally Use Left Hand", a score of "0" meant "No Preference", a score of +1 meant "Normally Use Right Hand" and a score of +2 meant "Always Use Right Hand". Participants scores for each handedness questionnaire where then added together to get a composite score. These composite scores were then plotted to yield a pattern of naturally occurring groupings in the data that enabled us to divide the participants into their appropriate handedness categories (see Figure 1). A score of -100 to -6 meant one was a CLH, a score of -5 to 35 meant one was an ILH, and a score of 36 or above meant one was a RH. As defined by our composite measure, CLHs had a mean of -34.70 (*SD* = 15.63), the ILHs had a mean of 14.75 (*SD* = 9.52) and the RHs had a mean of 63.28 (*SD* = 10.92).

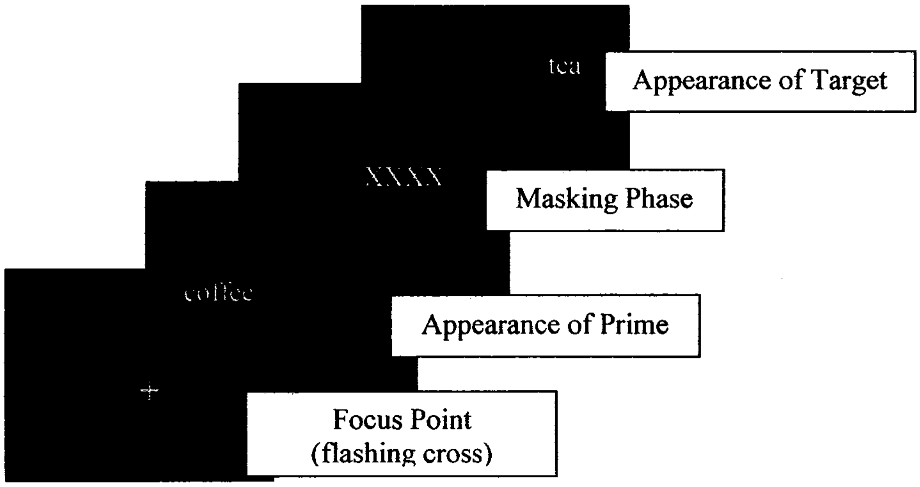
Figure 1. Composite Handedness Scores Showing Naturally Occurring Handedness Groupings



The testing session began with participants completing one of the handedness questionnaires, after which they completed the first of two lateralization tasks (the order of task administration was counterbalanced). Upon completion, they filled out a second handedness questionnaire followed by the second lateralized task. The final handedness questionnaire was then completed. Lastly, the NAART (Blair & Spreen, 1989) and the MRT-A (Peters et al., 1995) were administered in counterbalanced order and participants were debriefed. Thus, the order in which the handedness questionnaires, the lateralized tasks and the paper-and-pencil tasks were administered was randomized so as to control for order effects. Further, the NAART (Blair & Spreen, 1989) and the MRT-A (Peters et al., 1995) were always administered after completion of all the handedness questionnaires and the two lateralized tasks so as to not affect the lateralized tasks, in which the dependent measure (reaction time) is highly sensitive. Each participant was randomly assigned to an SOA of either 150ms or 800ms for both the semantic priming and the mental rotation computer tests independently.

In the semantic priming task, the word pairs were chosen at random from the larger set of semantically related, unrelated and non-word pairs such that for each trial, there was a 50% chance that the target would be a non-word. All trials began with the presentation of a flickering red "+" (cross) in the center of the screen that was designed to attract the participants' attention. Following the cross, the prime was randomly presented to either the right or left visual field for 100ms and was immediately followed by a masking pattern (a series of XXXXs presented in the middle of the screen). After the pattern mask, the target randomly appeared in either visual field for a total of 115ms, and the participant had to decide if it was a word or a non-word (see Figure 2). If it was a word, the participant pressed the 'Y' key (covered in green tape) on the keyboard, and if the target was not a word, the participant pressed the 'H' key (covered in red tape) on the keyboard. The next trial began after a response had been made.

Figure 2. Example of Semantic Priming Task



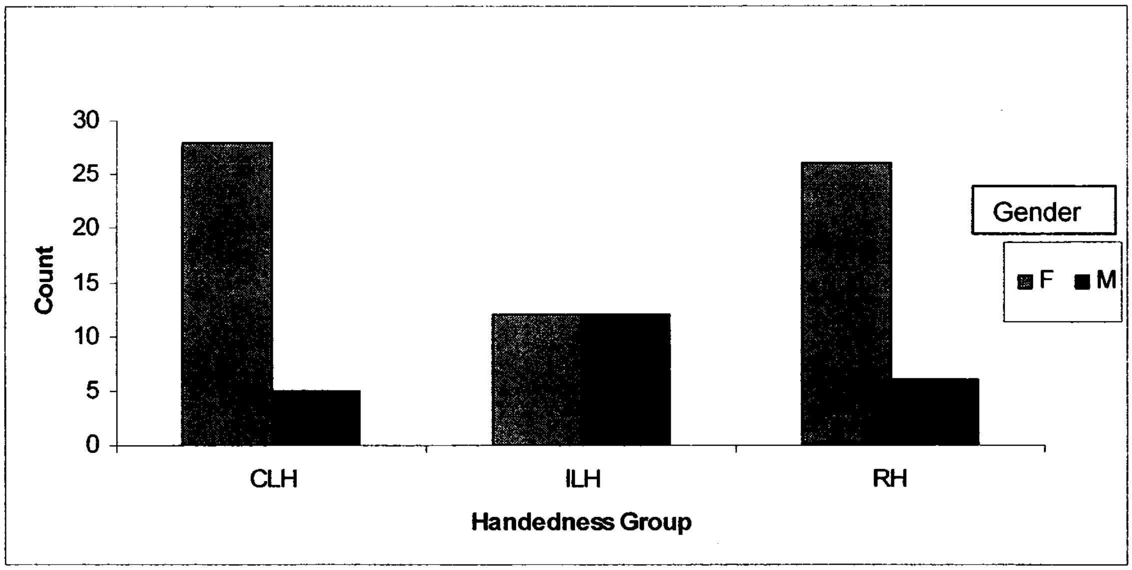
The same design was used for the mental rotation task, with each trial beginning with the flickering red "+" at center screen. The prime shape, which was chosen randomly from the larger set, was then presented at random to either visual field for 100 ms. Following the presentation of the prime, a masking pattern (a series of XXXXs presented in the middle of the screen) immediately appeared and lasted for 50 ms. Following the masking pattern, a target was then presented randomly to either visual field for 115ms and the participant decided if the target was the same stimulus as the prime. A stimulus was deemed the same as long as it was the same shape as the prime; if it was a rotated version of the prime shape, it was still deemed "the same". As in the semantic priming task, participants responded via key press. If it was a match, the participant pressed the 'Y' key (covered in green tape). If the target was not a match, the participant pressed the 'H' key (covered in red tape). The next trial began after a response had been made.

For both the verbal and the spatial tasks, participants used their dominant hand (i.e.: whichever hand they used most consistently when performing single-handed tasks on a computer) to respond, thus avoiding potentially slowed response times caused by using the non-dominant hand. Participants completed practice trials for each task (32 for the mental rotation task and 30 for the semantic priming task) before commencement of the test session to ensure that participants were clear on what they were to do and to allow for any questions or uncertainties to be addressed. Reaction time and response accuracy was recorded during both tasks; no feedback was given as to correct responses.

Results

A chi-square analysis was run in order to determine whether gender had to be taken into account as a contributing factor to the overall handedness results. With an alpha level of .05, the effect of gender was statistically significant $[\chi^2(2, N = 89) = 10.12, p < .01, \varphi c = .006]$ (see Figure 3). This result is primarily due to a disproportionately large number of males in the ILH group (50%) compared to the CLH and RH groups which have 15% and 18%, respectively. For this reason, subsequent analyses controlled for gender effects by entering gender as a covariate. The remaining results will be presented in three parts. The spatial processing data will be discussed first, followed by the verbal processing data. Lastly, overall spatial and verbal processing data by handedness group will be discussed.

Figure 3. Interaction Between Handedness and Gender



Spatial Processing

It was predicted that the overall spatial abilities of the CLHs would be significantly lower than those of the ILHs or the RHs as they will have fewer spatial resources available due to the "crowding out" of spatial resources by verbal abilities. In order to investigate overall spatial ability, a composite score was devised for each participant by summing the standardized accuracy scores of the MRT-A (paper-and-pencil task) and the lateralized MRT task, resulting in a single score. A oneway ANCOVA was run to compare the three handedness groups on the spatial composite, with gender entered as a covariate. No significant relationship was found between handedness group and overall spatial ability [$F(2, 84) = .53, p > .05$], suggesting that, overall, the three handedness groups were comparable in terms of spatial ability. Gender was not a significant covariate [$F(1,84) = 2.46, p > .05$].

Further analyses were conducted looking at each spatial task separately. A one-way ANCOVA on MRT-A scores by handedness group, with gender as a covariate, revealed gender as a significant covariate [$F(1, 85) = 6.31, p < .05, r = .26$]. Closer inspection revealed that males had higher overall scores on the MRT-A ($M = 11.52, SD = 5.06$) than did females ($M = 8.02, SD = 4.39$) [$F(1, 87) = 10.04, p < .005, r = .32$]. In addition, there was a significant difference between ILHs and RHs [$t(85) = 2.04, p < .05, r = .21$], but not between CLHs and RHs [$t(85) = 1.24, p > .05, r = .13$]. There was no significant difference between CLHs and ILHs on MRT-A scores (see Table 1).

Table 1. Lateralized MRT Mean Accuracy Scores Between Handedness Groups

Handedness Group	M	SE
CLHr	9.10	.80
ILHr	10.30*	.96
RHr	7.71*	.80

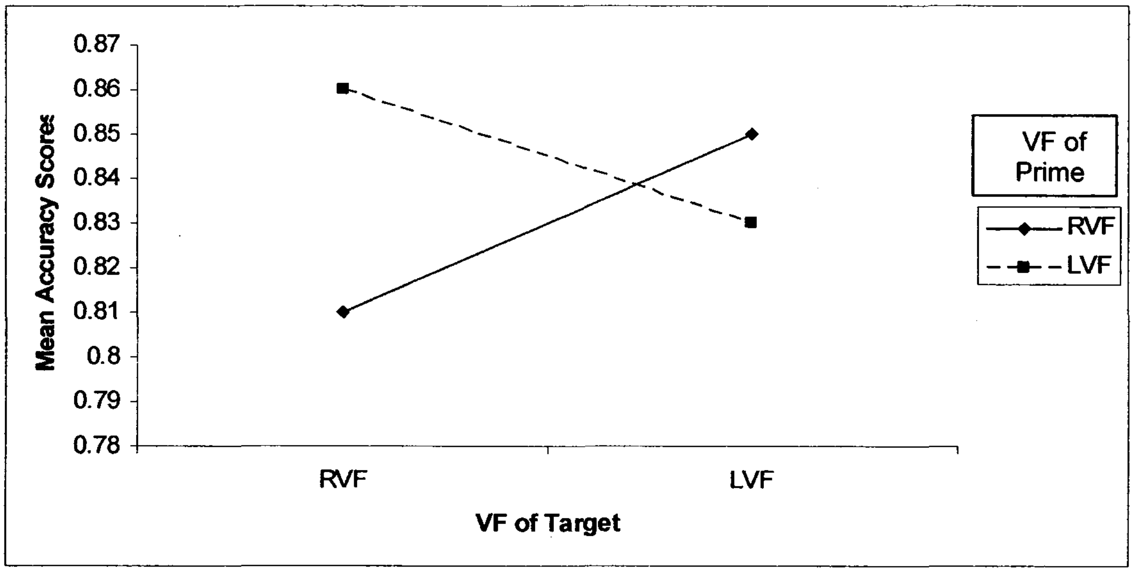
n = 89
*Only significant difference, $p < .05$

A lateralized MRT accuracy score was calculated by averaging the accuracy scores across visual field conditions. A oneway ANCOVA on lateralized MRT accuracy scores by handedness group, with gender entered as a covariate, found no significant effect of handedness [$F(2, 84) = .48, p > .05$]. Gender was not a significant covariate [$F(1,84) = 1.23, p > .05$].

Visual Field Effects

It was also predicted that there would be a Visual Field x Handedness Group interaction such that the ILHs and the RHs would presumably exhibit a relative weakness in spatial ability (i.e.: be less accurate) when geometric stimuli are presented to the right visual field (left hemisphere). In order to test this prediction, a mixed factorial ANCOVA was run on Visual Field of the prime (VFprime) (2) x Visual Field of the target (VFtarget) (2) x Handedness Group (3) on lateralized MRT accuracy scores, with gender as a covariate. Gender was not a significant covariate [$F(1,84) = 1.23, p > .05$]. No significant relationship was found between handedness, VFtarget and lateralized MRT accuracy scores [$F(2,84) = .45, p > .05$]. There was, however, a significant interaction between the VFprime and the VFtarget [$F(1,84) = 5.15, p < .05, r = 0.24$]. When the prime was presented to the right VF (RVF), participants (regardless of handedness) were more accurate when the target was then presented to the left VF (LVF) (i.e.: right hemisphere) than to the RVF (i.e.: left hemisphere). When the prime was presented to the LVF, greater accuracy was seen when the target was presented to the RVF than when it was presented to the LVF (see Figure 4). It should be noted that the assumption of normal distribution for one of the lateralized MRT conditions was violated [$F(2,85) = 3.97, p > .05$]. In trying to resolve this violation, logarithmic, square root and reciprocal transformations were conducted, but none were able to fix the positive skew. For this reason, analyses were performed on the non-transformed data.

Figure 4. Interaction Between VFprime and VFtarget, Collapsed Across Handedness Group



In terms of response time (RT) on the lateralized MRT task, an identical VFprime (2) x VFtarget (2) x Handedness Group (3) mixed factorial ANOVCA, with gender as a covariate, was run and several significant findings emerged. There was a significant effect for VFprime [$F(1, 84) = 8.76, p < .005, r = 0.31$]. Further examination revealed that participants were faster to respond when the prime was presented to the LVF ($M = 654.43$, $SE = 14.16$) than when the prime was present to the RVF ($M = 667.44$, $SE = 14.22$). No main effect of gender was found [F(1,84) = 2.56, p>.05]. There was, however, a significant interaction between the VFprime and gender, [$F(1, 84) = 3.98, p < .05, r = 0.21$], indicating that females were faster when the prime was presented to the LVF (M = 649.21, SE = 16.01) than to the RVF (M = 661.29, SE = 16.34), while males showed no difference in response time to either VF (see Table 2).

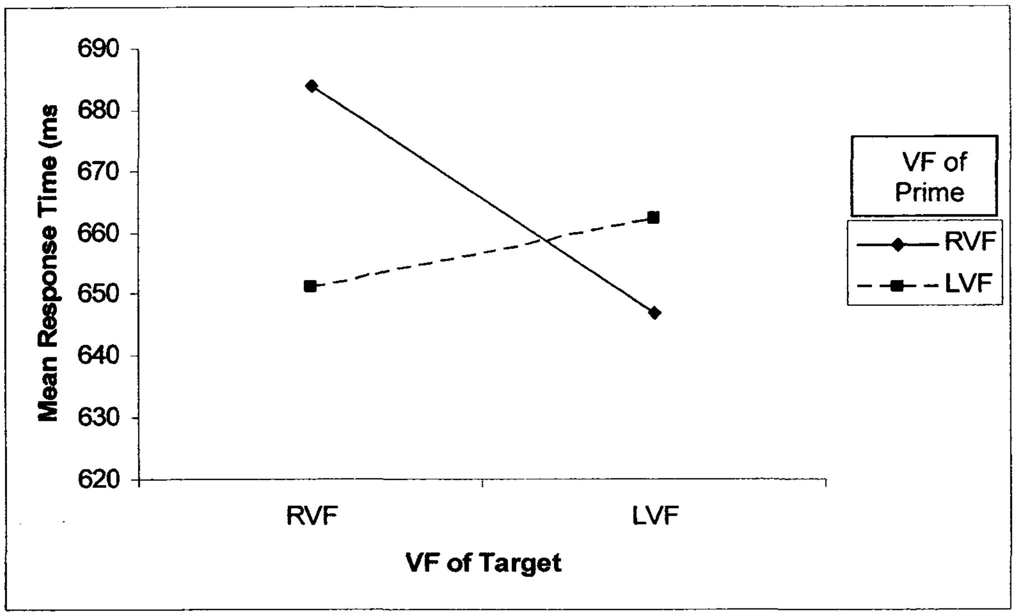
Table 2. Interaction Between Gender and VFprime on Lateralized MRT Response Time (ms)

	VFprime			
	RVF		LVF	
Gender	M	SE	M	SE
Female	661.29	16.34	645.30*	16.34
Male	693.26	27.47	691.26	27.46

**p* < .05

Even when gender was taken into account, a significant interaction remained between VFprime and VFtarget [$F(1,84) = 3.94, p > .05, r = 0.21$], showing the same pattern of faster response times for targets presented contralaterally to the prime. When the prime and target were presented to the RVF, the mean response time was 683.82 ms ($SE = 15.20$), while it fell to 651.06ms ($SE = 13.90$) when the prime was to the RVF but the target was to the LVF. Conversely, when the prime and target were both to the LVF, the mean response time was 662.04 ms ($SE = 14.51$), while it was 646.81 ms ($SE = 14.39$) when the prime was to the LVF and the target was to the RVF (see Figure 5).

Figure 5. Interaction Between VFprime and VFtarget on Lateralized MRT Response Times (ms), Collapsed Across Gender



There was no significant interaction between handedness groups, VFtarget and lateralized MRT response times [$F(2,84) = .170, p > .84$].

A repeated-measures, VFprime (2) x VFtarget (2) ANCOVA was run on MRT response times for RHs, with gender as a covariate. A significant interaction was found [$F(1,30) = 7.94, p <. 05, r = 0.46$] indicating faster processing in the LVF (right hemisphere) than in the RVF (left hemisphere) for RHs. Gender was not significant [$F(1,30) = 2.92, p <.05$]. Similar repeated-measures VFprime (2) x VFtarget (2) ANCOVAs on MRT response times, with gender as a covariate, were run on the CLH and ILH groups. No significant interaction was found between VFprime and VFtarget on MRT response times for either CLHs [$F(1,30) = 2.63, p >.05$], or for ILHs [$F(1,22) = .003, p >.05$] (see Table 3). Gender was not a significant factor for the CLHs [$F(1,30) = .202, p >.05$] or for the ILHs [$F(1, 22) = .120, p >.05$].

Table 3. Interaction Between VF, Lateralized MRT Response Times (ms), and Handedness Groups

	VF			
	RVF		LVF	
Handedness	*M*	*SE*	*M*	*SE*
CLH	704.30	25.37	680.45	24.03
ILH	669.72	26.50	642.83	20.95
RH	679.98	26.37	666.42*	26.80

*$p < .05$

Verbal Processing

It was predicted that ILHs would perform like RHs on verbal tasks. In order to investigate overall verbal abilities, separate verbal composite scores were calculated for each participant. This score was derived by taking the mean of the summation of the standardized accuracy scores of the NAART and of the computer semantic priming task, resulting in a single score that was used to measure overall verbal ability. A oneway ANCOVA on verbal composite scores by handedness group, with gender as a covariate, revealed no significant relationship [$F(2,85) = 2.40, p > .05$]. Gender was not significant [$F(1, 85) = 1.73, p > .05$].

Further oneway ANCOVAs were conducted looking at each verbal task separately. A oneway ANCOVA on NAART scores by handedness group, with gender as a covariate, was not significant [$F(2, 85) = .59, p > .05$]. There was no main effect for gender [$F(1,85) = 1.73, p > .05$]. Semantic accuracy composite scores were calculated by averaging the total accuracy scores for the semantic priming task, collapsing over relatedness. A oneway ANCOVA on semantic accuracy composite scores by handedness group, with gender as covariate, similarly failed to find a significant effect of handedness [$F(2,85) = 2.02, p > .05$]. There was no significant effect for gender [$F(1,85) = 1,03, p > .05$].

Visual Field Effects

It was also predicted that there would be a Visual Field x Handedness Group interaction such that the ILHs and the RHs will presumably exhibit a relative weakness in verbal ability when verbal stimuli are presented to the LVF (right hemisphere). Again, it should be noted that only the VFtarget was included in these analyses as the target is the stimuli to which participants responded. A mixed factorial ANCOVA on Relatedness (2) x VFprime (2) x VFtarget (2) x Handedness (3), with gender as a covariate, was utilized to investigate effects on semantic accuracy. A significant interaction was found between VFtarget and handedness group [$F(2,85) = 4.78, p <.05$], indicating that both CLHs and ILHs were less accurate than RHs when responding to verbal information presented to the RVF. When verbal information was presented to the LVF, ILHs were more accurate than either the CLHs or the RHs (see Table 4). Gender was not significant [$F(1, 85) = 1.03, p >.05$].

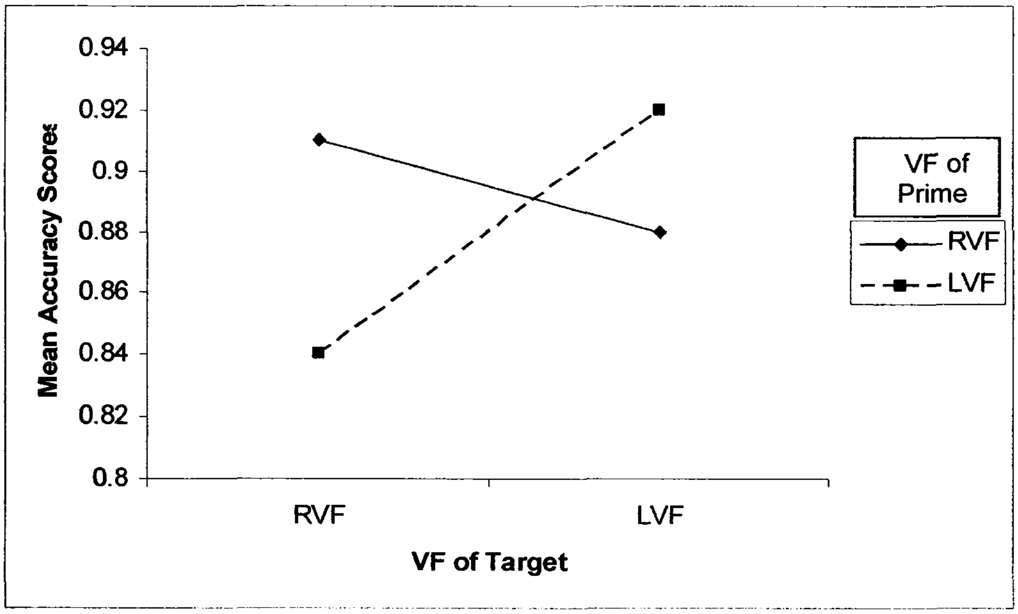
Table 4. Interaction Between VFtarget and Handedness Group on Semantic Accuracy Scores

	VFtarget			
	RVF		LVF	
Handedness	*M*	*SE*	*M*	*SE*
CLH	.87	.01	.87	.02
ILH	.90	.02	.91*	.02
RH	.92*	.01	.86	.02

*$p < .05$

There was also a significant interaction between the VFprime and the VFtarget on semantic accuracy scores [$F(1,85) = 5.61, p < .05, r = 0.25$], indicating that participants responded with the greatest accuracy when both the prime and the target were presented to the same VF, regardless of handedness. When both the prime and the target were presented to the RVF, mean accuracy scores were 0.91 (*SE* = .01), while they fell to 0.84 (*SE* = .01) when the prime was sent to the RVF and the target was sent to the LVF. Similarly, mean accuracy scores were 0.92 (*SE* = .01) when both the prime and the target were sent to the LVF, but they fell to 0.88 (*SE* = .01) when the prime was to the LVF and the target was to the RVF (see Figure 6).

Figure 6. Interaction Between VFprime and VFtarget on Semantic Accuracy Scores, Collapsed Across Handedness Groups



In terms of response time, an identical mixed factorial ANCOVA on Relatedness (2) x VFprime (2) x VFtarget (2) x Handedness (3) was run with gender as a covariate. A significant effect was found for VFtarget [$F(1,85) = 7.09, p <.05, r = 0.28$], indicating that participants were faster to respond when the target was presented to the RVF (M = 677.93, SE = 15.88) as compared to the LVF (M = 668.47, SE = 16.23). A main effect of gender was found, with females being faster to respond than males, regardless to which VF the target was presented. A significant VFtarget x Gender interaction [$F(1,85) = 6.22, p <.05, r = 0.26$] revealed that females had slower response times when the target was presented to the LVF than to the RVF. Males, on the other hand, showed the opposite pattern, being faster to respond when the target was presented to the RVF than to the LVF (see Table 5).

Table 5. Interaction Between Gender and VFtarget on Semantic Priming Response Time (ms)

	VFprime			
	RVF		LVF	
Gender	M	SE	M	SE
Female	671.32	18.19	654.93*	18.78
Male	702.91*	30.82	724.44	31.81

*$p < .05$

A significant interaction was also found between the VFtarget and handedness groups [$F(2,85) = 5.96$, $p < .005$], indicating that CLHs are slower to respond than ILHs or RHs when verbal information is presented to the RVF. Further, it showed that ILHs are faster to respond than CLHs or RHs when verbal information is presented to the LVF (see Table 6).

Table 6. Interaction Between VFtarget and Handedness Group on Semantic Response Time (ms)

	VFtarget			
	RVF		LVF	
Handedness	*M*	*SE*	*M*	*SE*
CLH	705.85	26.11	687.33	26.67
ILH	664.11	31.61	621.61*	32.28
RH	663.83	26.32	696.46	26.89

*$p < .05$

A three-way interaction was also found between semantic relatedness, VFtarget and gender on semantic response times [$F(1, 85) = 6.71, p <.05, r = 0.27$]. Closer examination revealed that females were faster to respond to both related and unrelated word pair targets than were males, regardless of which VF the stimuli were presented. Also note that between word pair types, females responded faster to related word pair targets than to unrelated word pair targets. Further, within the related word pairs, females were much faster to respond when the targets were presented to the LVF than to the RVF, a pattern that repeated itself on the unrelated word pair trials. Males were also faster to respond to related than to unrelated word pair targets. Within the related word pairs, males were faster to respond when targets were presented to the LVF than to the RVF, but showed the opposite pattern on the unrelated word pairs, responding much faster to targets that were presented to the RVF than to the LVF (a difference of 62.53 ms) (see Table 7).

Table 7. Semantic Relatedness x VFtarget x Gender Interaction on Semantic Response Time (ms)

	VFtarget			
	RVF		LVF	
Gender	*M*	*SD*	*M*	*SD*
	Related Word Pairs			
Females	657.67	138.17	641.74	146.05
Males	710.26	174.56	690.78	194.73
	Unrelated Word Pairs			
Females	684.97	156.62	668.12	140.30
Males	695.57	161.98	758.10	204.05

Priming Effects

Semantic priming effects were also analyzed in order to investigate any differences between handedness groups. It should be noted at this point that the assumption of normal distribution for one of the priming conditions (RVFprime/RVFtarget) has been violated [$F(2,86) = 4.15, p < .05$]. Logarithmic, square root and reciprocal transformations were conducted in an attempt to resolve this violation, but none were able to correct the distribution. For this reason, analyses were performed on non-transformed data. A mixed factorial ANCOVA on handedness groups and semantic priming, with gender as a covariate, revealed no significant priming effects between handedness and VFtarget [$F(2,85) = .06, p > .05$]. However, a significant priming effect was found for VFtarget and gender [$F(1,85) = 6.71, p <.05, r = 0.27$].

Closer examination revealed that while females displayed little difference in semantic priming in either VF, males showed a much larger priming effect in the LVF than in the RVF (see Table 8).

Table 8. Differences in Priming Effect Between Gender and VFtarget

	VFtarget			
	RVF		LVF	
Gender	M	SE	M	SE
Female	27.30	9.92	26.38	11.32
Male	-14.70	16.80	67.17*	19.17

*$p < .05$

Left-handers vs. Right-handers

It was predicted that left-handers (LHs), as a whole, would obtain the lowest scores on tasks of spatial processing as compared to RHs because the resources that would normally be available to process spatial information were being "crowded out" by verbal faculties. In order to test this hypothesis, ILHs and CLHs were combined together to create a single LH group to enable comparisons to be made with previous studies. A oneway ANCOVA on spatial composite scores by handedness group (LH vs. RH), with gender as the covariate, was calculated and found to be nonsignificant [$F(1,85) = .02, p > .05$]. Each spatial task was then looked at independently. There was a main effect of gender on MRT-A scores [$F(1, 86) = 8.79, p < .005, r = 0.30$]. In order to investigate this relationship, a oneway ANOVA was utilized looking at scores on the MRT-A for LHs and RHs of each gender separately. This analysis not only revealed that LH males scored significantly higher than RH males [$F(1,21) = 8.76, p < .05, r = 0.5$), but also that female accuracy rates for LHs did not differ significantly from those of RHs [*F*(1,64) = .35, *p* >.05] (see Table 9).

Table 9. Interaction Between Left-handedness, Gender and MRT-A Scores

	Handedness			
	LH		RH	
Gender	M	SE	M	SE
Female	8.28	.70	7.62	.86
Male	13.12*	1.07	7.00	1.80

$*p < .05$

Overall, LH participants scored higher on the MRT-A (M = 9.72, SE = .62) than did RHs (M = 7.50, SE = .83) [$F(1,87) = 4.56, p <.05, r = .22$). It should be noted that the assumption of normal distribution for the lateralized MRT condition was violated [$F(1,87) = .342, p > .05$]. In trying to resolve this violation, logarithmic, square root and reciprocal transformations were conducted, but none were able to fix the positive skew. For this reason, analyses were performed on the non-transformed data.

A oneway ANCOVA on lateralized MRT accuracy scores by handedness group (LH vs. RH), with gender as a covariate, revealed no significant effect of handedness on accuracy scores [$F(1, 85) = .15, p >.05$]. Gender was not significant [$F(1,85) = 2.15, p >.05$].

On the verbal tasks, a oneway ANCOVA was carried out on verbal composite scores by handedness (LH vs. RH) and revealed no significant effect of handedness on the verbal composite scores [$F(1,85) = .37, p > .50$], nor of gender [$F(1,86) = .45, p$

$>.05$]. Similarly, a oneway ANCOVA on NAART scores by handedness (LH vs. RH), with gender as a covariate, failed to reach significance [$F(1,85) = .001, p > .05$], as did gender [$F(1,86) = 1.04, p > .05$]. Lastly, a oneway ANCOVA on semantic accuracy scores by handedness (LH vs. RH), with gender as a covariate, was not significant [$F(1,85) = .211, p > .05$]. Gender was not significant [$F(1,86) = .17, p > .05$].

Discussion

The purpose of this study was to examine Levy's (1969) "cerebral crowding" hypothesis in light of one's handedness to see whether or not verbal capabilities "crowd out" spatial resources in the right hemisphere in those with presumed right hemisphere (i.e.: atypical) language dominance. It was predicted that, overall, the left-handers (i.e.: both CLHs and ILHs) would obtain the lowest scores on tasks of spatial ability and that CLHs would exhibit significantly poorer spatial skills than the other two groups. Furthermore, based on the research of both Laeng and Peters (1995) and Knecht et al. (2000), it was predicted that ILHs would perform like RHs on spatial and verbal tasks, respectively. It was also expected that CLHs would have superior verbal abilities as compared to the other groups, but that they would fail to exhibit the left visual field (LVF) / right hemisphere spatial advantage that is typically seen in RHs. Visual-field effects were also predicted, with the expectation that ILHs and RHs would exhibit a relative weakness in processing verbal stimuli presented to the LVF, and a relative weakness in processing spatial information presented to the RVF. Of these predictions, only some were met with significant findings. Furthermore, several other significant interactions were found and for this reason, each will be discussed separately in the following discussion, beginning with spatial abilities and then progressing to verbal abilities.

Spatial Abilities

The prediction that LHs, as an overall group, would obtain the lowest scores on tasks of spatial ability as compared to RHs was not supported. Additionally, the prediction that CLHs would exhibit the poorest spatial abilities of all three groups, was also not supported as there were no differences between handedness groups on the measure of overall spatial ability as calculated by the spatial composite. These predictions were based on Levy's (1969) cerebral crowing hypothesis, which states that the resources that would normally be available to process spatial information are being "crowded out" and occupied by verbal facilities in left-handers. As discussed earlier in this paper, the support for this hypothesis has been mixed and thus it comes as little surprise that the present study failed to find any overall evidence of a "crowding effect" on spatial abilities between handedness groups.

However, both gender and handedness effects were found on the MRT-A. The main effect of gender revealed that males were more accurate than females. This finding is in line with the known gender effects of the MRT-A (Peters et al., 1995). The main effect of handedness revealed that ILHs were more accurate than the RHs. In addition, no significant difference was found between either CLHs and RHs, or between ILHs and CLHs. Furthermore, the fact that ILHs differ from RHs on this task goes against the prediction of the current study, based on Laeng and Peters (1995), that these two groups would perform similarly on spatial tasks.

In order to see if this pattern held for other spatial tasks, the lateralized MRT task was also examined. Here it was found that the RHs, but not the ILHs or CLHs, showed the typical right hemisphere advantage for processing spatial information, thereby providing evidence that LHs are not lateralized in the same way as RHs. Further, this result supports the prediction that CLHs would show no VF disadvantage in terms of speed of response on the lateralized MRT, regardless of which VF the target was presented. Taken together, these findings bolster the idea that perhaps LHs, regardless of the degree of left-handedness, are not as strongly lateralized as RHs, a notion that is generally agreed upon in the literature (Hécaen & Sauguet, 1971; Oldfield, 1971; Laeng & Peters, 1995; Perelle & Ehrman, 2005; Knecht et al., 2000). It also provides evidence that LHs are not as homogeneous a group as RHs are generally found to be (Levander & Levander, 1990).

Collapsing across handedness groups, several other significant findings emerged. On the lateralized MRT task, an effect was found between the VFprime and the VFtarget such that when the prime was presented to the RVF, participants were more accurate when the target was then presented to the LVF. When the prime was presented to the LVF, greater accuracy was seen when the target was presented to the RVF. This is presumably due to the fact that the information entering the visual field crosses to the contralateral hemisphere via the optic chiasm, meaning that the information from the prime is already “in” the hemisphere responsible for processing and responding to the stimuli. It is possible that this finding emerged because the stimuli were not presented long enough so that when both the prime and the target were presented to the same VF, they masked each other, making accurate processing more difficult. A more likely explanation, however, is that bihemispheric activation occurred such that both hemispheres took part in actively rotating (and thus processing) the MRT shapes. In fact, this is the very notion put forth by Cook, Fruh, Mehr, Regard, and Landis (1994) who state that when two shapes must be rotated into congruence with each other, the greatest performance is demonstrated when the reference shape is maintained by the right hemisphere and the rotation is performed by the left hemisphere (i.e.: the two hemispheres work together). Further evidence to support the notion that both hemispheres may be differentially involved in mental rotation is that practice effects have been shown capable of cancelling (or at least lessening) a strictly right-hemispheric dominance (Hannay, Dee, Burns, & Masek, 1981). What is more, increased task complexity has been found to result in increased left-hemispheric input, presumably in recruitment of verbal functions (McGuinness & Bartell, 1982). For these reasons, it makes sense that contralateral presentation of the VF primes and targets results in bilateral hemispheric activation, regardless of handedness.

It was also found that the presentation of the VFprime itself affected response times as participants, regardless of handedness, were faster to respond when the prime was presented to the LVF than when the prime was present to the RVF. Again, speaking in neuroanatomical terms, this makes sense as the typical cerebral organization places spatial abilities in the right hemisphere, and thus if spatial information is presented to the LVF it is already automatically sent to the right hemisphere, resulting in faster response times. Of interest, the VF to which the target itself was presented had no effect on response times, suggesting that speed of responding was not affected by the VF presentation of the target stimuli per se, but rather by the interaction between the VF of the prime and the target.

There has been a great deal of research looking at mental rotation abilities between both gender and handedness groups, the results of which are not always complimentary. For instance, Bulla-Hellwig et al., (1996) found no hemispheric differences on a cube comparison mental rotation task, leading to the conclusion that, at least for RHs, mental rotation does not have a reliably dominant hemisphere, the same conclusion reached by Cohen and Polich (1989) using letters and polygons. Conversely, Fischer and Pellegrino (1988) found that the RVF was in fact superior to the LVF on mental rotation. They do, however, purport that the left hemisphere contributes nonspatial resources, suggesting that while mental rotation is a spatial task, its successful performance does not rely solely on spatial components. It should be pointed out that this study was comprised of only 20 participants, all of whom were right-handed males, a point worth noting since superior mental rotation abilities of males have been widely documented (Linn & Petersen, 1985; Lewis & Harris, 1990). In addition, Corballis and Manalo (1993) found that spatial attention affected the speed of mental rotation such that speed was slowest when both attention and stimulus presentation were shifted to the RVF, while it was fastest when attention was shifted to the LVF. Taken together, these studies, in conjunction with the present research, illustrate how the inconsistencies in the MRT literature, and indeed within much of the laterality literature, are at least in part due to the fact that different studies use different populations and different measures or methods of testing (French & Painter, 1991), making it difficult to compare studies and find a reliable pattern of findings. The question remains: which hemisphere is dominant for spatial processing?

Recall the earlier discussion that mental rotation, as suggested by Fischer and Pellegrino (1988), and more recently by Chabris and Kosslyn (1998), may be a task that draws upon both hemispheres for successful completion. In fact, Chabris and Kosslyn suggest that the left hemisphere does in fact process spatial information, but it is the *type* of spatial information that differs, a concept bolstered by Laeng and Peters (1995) and Servos and Peters (1990). According to this model, the left hemisphere is thought to be better at encoding and using categorical spatial relations (i.e.: above/blow, left/right distinctions), while the right-hemisphere is better at encoding and utilizing coordinate spatial information (i.e.: those that deal with precise locations such as those needed for navigation).

A slightly different interpretation of the differences in hemispheric spatial processing was put forth by Yoshizaki, Weissman and Banich (2007). In a series of studies that required participants to mentally rotate two capital letters that were presented either to the same or to the opposite hemisphere, the researchers found that the more complex the task, the greater the across-field advantage became, consistent with Goldberg and Costa (1981). In other words, the greater the number of degrees the letters had to be rotated to reach an upright position, the more each hemisphere "helped out". This model of hemispheric interaction suggests that if the cognitive load to each hemisphere is not equal (i.e.: if the letter presented to one hemisphere has to be rotated more than the other) then the hemisphere to which more information is presented will take the lead in processing the perceptual information, while the other hemisphere will take the lead in deciding on a response. If this is true, it may at least in part explain why the present study failed to find any hemispheric differences between the left-handed groups for processing spatial information using MRT tasks. Recall that in the present study, the random shapes were rotated by increments of 45°, meaning that before participants could decide if the prime and target were the same shape, they had to rotate each stimulus to its upright position. As suggested by Yoshizaki et al., it could be that as the discrepancy between the degree of rotation increased, the likelihood one hemisphere taking the lead over the other in processing the information also increased. Thus, while the RHs displayed the expected right hemisphere advantage, the LHs (who are not as strongly lateralized) were more adept at utilizing both hemispheres on MRT tasks, resulting in neither hemisphere being "dominant" for any stage of the processing. Further investigation will be needed before any conclusions can be drawn on this matter.

Lastly, when interpreting these results in light of past research which has found support for a cerebral crowding effect, it is important to keep in mind that the present study utilized samples from a "normal" population (undergraduate university student). Participants with any neurological disorders were not included in this study which puts it at odds with the findings of others who have reported crowding effects when looking at mentally retarded and/or epileptic populations. As mentioned earlier, it is possible that crowding is found in those with cerebral damage because such patients are already more likely to show atypical cerebral organization and/or lateralization.

Verbal Abilities

In terms of verbal capabilities, it was predicted that ILHs would perform like RHs on verbal tasks and thus little or no "crowding" would be expected. This prediction was based on Knecht et al. (2000) who stated that the more right-handed one is, the less right-hemisphere language one should have. Since ILHs are less left-handed than CLHs, it would make sense to expect ILHs to have more of a "right-handed brain" (i.e.: left hemispheric language dominance) than CLHs. This prediction was in fact supported by the present study as there were no differences between any of the handedness groups on an overall composite measure of verbal ability, enabling the conclusion that ILHs did in fact perform like RHs on verbal tasks. As a reminder, our composite verbal score was comprised of the summation of the semantic priming task accuracy scores (collapsed across relatedness) and total scores on the NAART. Finding no difference in overall verbal capabilities between handedness groups is not a completely unexpected finding as Annett (1982) stated that LHs in general are apt to show no hemisphere differences at all, and if they do it is likely to be the same advantage as is seen in RHs (i.e.: verbal processing in the left hemisphere). It is always possible, however, that in the present study no effect of handedness was found on the verbal composite score because the measures that comprised it were not sensitive enough to any between-group differences when combined into a single score or because of inadequate sampling from the domain of verbal abilities. Therefore, in order to determine if there were any differences between handedness groups across the different verbal tasks, each subtest was looked at separately. Both the NAART and the semantic priming accuracy composite failed to show any effect of handedness. Taken together, these findings suggest that there was no difference in overall gross verbal ability between the different handedness groups. Furthermore, these results also fail to provide support for the idea put forth by Levy (1969) that spatial resources get "crowded out" and occupied by verbal facilities in left-handers, a notion which suggests that there would be increased resources available for processing verbal information as a result. If this were true, one would expect greater verbal skills in those who are in fact "crowding out" the spatial abilities in their right hemisphere. The lack of differences in overall verbal ability found in the present study suggests that neither displacement nor replacement of resources occurs. Rather, it suggests that the neurocognitive resources available for verbal processing are comparable for most neurologically intact people.

On the semantic priming task, an interaction was found between handedness groups and the VFtarget. Recall that it was predicted that ILHs and RHs would exhibit a relative weakness in processing verbal stimuli that is presented to the LVF (i.e.: right hemisphere) on the semantic priming task. It turns out, however, that even when gender effects are controlled for, ILHs are not only the most accurate, but they are also the fastest of the handedness groups at responding to verbal information that is presented to the LVF. Conversely, when verbal information is presented to the RVF (left hemisphere), CLHs and ILHs are less accurate than RHs, and CLHs are the slowest of the three groups. This provides some limited evidence of a reversal of the typical pattern of verbal dominance, with ILHs having better verbal abilities in the right hemisphere than in the left. This difference disappears, however, when ILHs and CLHs are pooled together into a single LH group without regard to VF presentation, as no significant findings emerged for the LH group on any of the verbal tasks. Thus, it seems likely that the verbal abilities of ILHs are sufficiently divergent from those of CLHs that if they are not investigated separately, those differences are unable to emerge. Reconciling this finding with the literature, however, is somewhat difficult due to the fact that most studies do not parcel out the subtypes of left-handedness, and those that do often arrive at different conclusions. Either way, these inconsistencies within the literature underscore the difficulties discussed earlier regarding differing methods and populations leading to different conclusions.

It was also predicted that CLHs would be superior to both ILHs and RHs for processing verbal information, regardless to which hemisphere it is presented, because it was believed that CLHs would have a greater amount of verbal resources upon which to draw. This prediction was not supported by the data, suggesting that CLHs do not possess more verbal resources than ILHs or RHs. A possible (and likely) explanation for why this prediction was not met is that perhaps verbal and spatial resources are relatively static, meaning that regardless of one's handedness, human cerebral organization only provides us with a certain fixed allotment of each. Thus, no matter if one was a LH or a RH, each would have a comparable amount of verbal and spatial resources available assuming no cerebral insult has occurred.

Summary

The present study failed to find support for the cerebral crowding effect as hypothesized by Levy (1969). There are several reason why this may be so. First of all, Levy's hypothesis originated through work with epilepsy patients whose neocortical commissures had been surgically separated to control seizure activity. This population cannot be expected to show the normal cerebral organization by the very fact that atypical development has led to the condition (epilepsy) in the first place. Nonetheless, she did support her hypothesis by showing that normal LHs ($n = 10$) performed more poorly on the performance measures of the WAIS (Wechsler, 1955) than did the RHs ($n = 15$). However, her sample of LHs, in addition to being relatively small, did not parcel out the different types of LHs. The present study showed that the ILHs out-performed the CLHs and the RHs on the paper-and-pencil MRT-A task, obtaining higher scores than the other two groups.

The current findings call into question the assumptions inherent in the cerebral crowding hypothesis. Addressing each one in turn, the first assumption states that there are limited neural resources available, which in turn assumes that there is replacement, not displacement, of resources. It is entirely possible that displacement of neural resources occurs, which would in part explain why CLHs in the present study did not exhibit greater verbal skills based on the prediction that they would have greater verbal resources available resulting from having replaced spatial resources. This is especially likely among neurologically impaired populations for whom there may be a higher likelihood for atypical cerebral organization. In such cases, the brain reorganizes itself in light of insult and such reorganization would likely result in displacement as opposed to replacement of resources. Secondly, the hypothesis assumes that more complex processing requires more cortical space. It is instead possible that the amount of cortical space required for simple processing is the same as that needed for complex processing. Perhaps the only difference between simple and complex processing is the degree to which other areas of the brain are recruited for a given task, given the hierarchical arrangement of constituent cognitive processes. For instance, it has been shown that women exhibit more bilateral activation when completing a spatial task and it has been suggested that the reason for this is that women are more likely than men to recruit verbal resources to help "talk it through" (McGlone & Kertesz, 1973). Such recruitment is also more likely for neurological groups who may already have a deficit of a given type of cognitive resource(s). Finally, the hypothesis assumes that certain functional organizations may be more efficient than others for cognitive processing (e.g.: that the majority of us are right-handed because language is largely controlled by the left hemisphere). While this assumption makes sense in light of the known neuroanatomical organization of the human brain, it does a poor job at explaining why approximately 10% of the population is left-handed, a figure that has changed little throughout history (Perelle & Ehrman, 2005). Furthermore, many studies have found that the corpus callosum of LHs is larger than that found in RHs, suggesting that LHs have neuroanatomical predispositions for greater interhemispheric connectivity than RHs (Witelson, 1985). What is more, the greater prevalence of left-handedness in neurologically impaired populations does not fit with the model of right-handedness resulting from left-hemisphere language. The end result of all this is that Levy's hypothesis makes some fairly large assumptions that cannot easily be reconciled with the data. Many of the studies that have found support for her hypothesis have used neurologically impaired populations; those who have not used patient populations have had difficulty replicating her results, as in the case of the present study.

The results of the current study suggest that LHs are a much more heterogeneous group than previously suspected and whose abilities cannot easily be described unless the different subtypes are parcelled out. Overall, LHs were not found to be faster or more accurate on verbal task than RHs. Breaking the LH group into subtypes, however, illustrated that ILHs are significantly different than both CLHs and RHs in terms of verbal abilities. It was found that ILHs demonstrate a greater propensity for right hemisphere language than either CLHs or RHs based on their greater accuracy and faster response times for verbal information presented to the LVF as opposed to the RVF. Inconsistent left-handers were also more accurate on the MRT-A, which probably explains why LHs on the whole were found to be more accurate on this task than RHs. For this reason, researchers should be more conscientious of handedness issues and should make a concerted effort to clarify, and include, members of the three different handedness groups in their research on laterality issues. If this is done, it is felt that the field of laterality research could make great leaps not only in terms of discovering the different ways in which the human brain is lateralized, but also in terms of producing research with greater generalizability to the population at large.

Future research into this area should focus on further elucidating the differences between the two hemispheres across handedness groups, as research has shown that each hemisphere contributes differentially in the processing of distinct types of verbal and spatial information. Thus, examining the subcomponents of verbal and visuospatial processing in relation to handedness would enable a greater understanding of the ways in which the two hemispheres process information. Additional data collected during this study that can be analyzed include differences in speed and accuracy of responses across the two SOAs (150 ms vs. 800 ms), as well as progressions over time (i.e.: any changes in response patterns across trials). Additionally, examining handedness effects utilizing a more extensive and comprehensive assessment of the various cognitive domains will make this research more applicable to clinical practice in terms of assessing language deficits in light of traumatic or organic brain injury. The ultimate goal of this line of research is to help inform clinicians of quick and effective ways of evaluating handedness in order to inform their assessment and treatment of individuals of different handedness groups with known neurocognitive deficits.

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Appendix A

Word Pairs

Related Prime-target word pairs

ale	beer	steel	iron	pot	pan	uncle	aunt	brush	comb
sofa	chair	sword	knife	ounce	pound	butter	bread	nickel	dime
jacket	coat	army	navy	figure	shape	mint	candy	silver	gold
wolf	dog	doctor	nurse	boot	shoe	dog	cat	coat	hat
inch	foot	sea	ocean	coffee	tea	mouse	rat	arm	leg
moth	fly	oven	stove	cotton	wool	shirt	tie	tiger	lion
road	path	string	rope	ball	bat	queen	king	frown	smile
pepper	salt	brandy	wine	lotion	cream	engine	motor	man	woman
basin	sink	lizard	snake	knife	fork	dirt	mud		
blouse	skirt	sleet	snow	jelly	jam	tack	nail		

Unrelated Prime-target word pairs

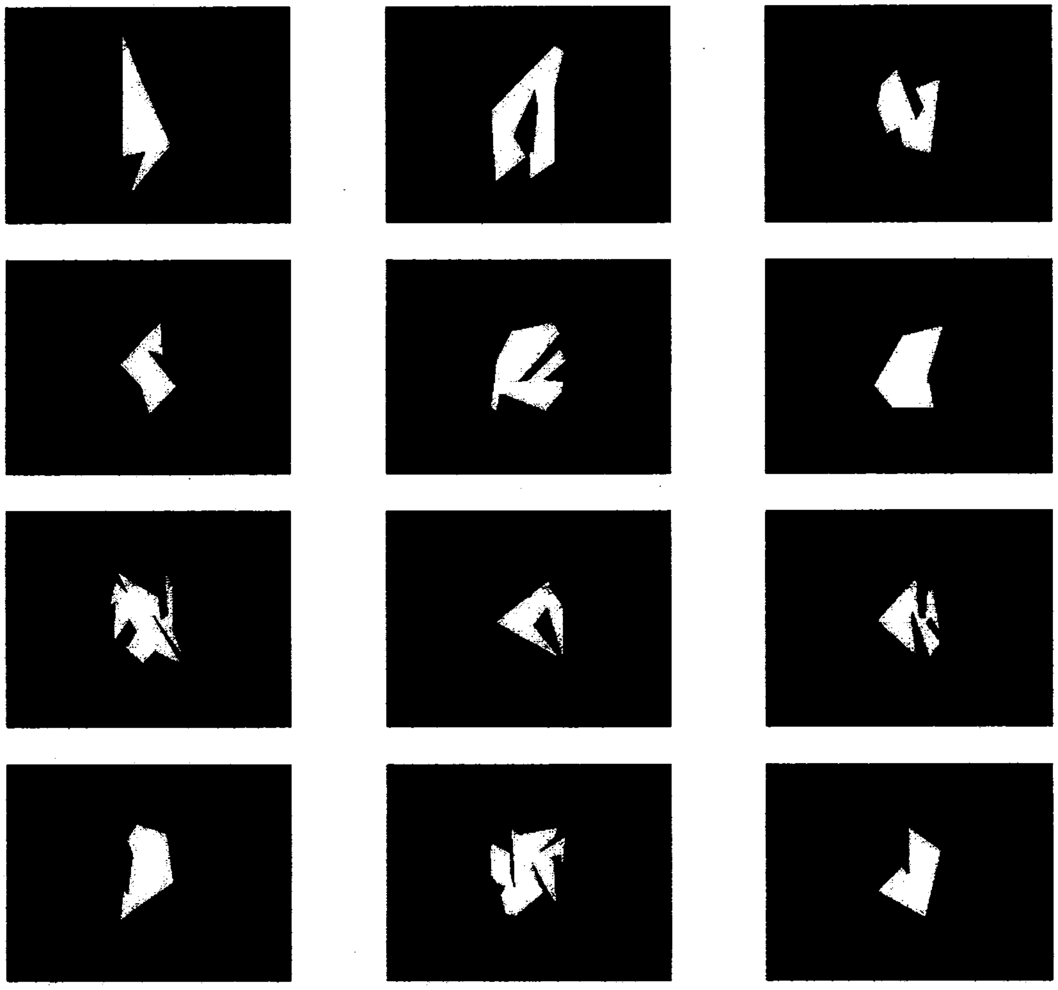
cradle	milk	onion	hump	crew	dress	apple	sea	book	tree
waist	bird	spider	clown	rubber	track	fish	stool	table	movie
alley	door	sheep	jug	train	water	harbor	belt	shell	boat
circus	sky	nest	wool	hermit	page	bacon	ship	house	daisy
miner	bed	key	horse	gallon	peach	banana	paint	grocer	fur
cloth	web	candle	tire	cow	maple	deer	plow	bear	baby
decoy	ice	bee	flame	crater	pony	desk	plane	music	cabin
rug	leaf	camel	duck	usher	moon	oak	art	tulip	honey
hockey	cat	artist	coal	pilot	store	hair	floor		
rake	cow	farmer	steak	star	cave	fox	tears		

Nonword Prime-target word pairs

ant	rance	jeep	inkle	sock	madage	rain	ordan	grass	taple
axe	ploud	lamb	ulk	soup	moul	spring	sive	heart	wone
bag	sish	mail	thay	spark	noidy	sword	squade	hen	mool
barn	jull	maze	onk	spear	octacle	pond	clof	hill	lidy
bean	frow	mole	shide	sponge	pibble	phone	conute	seed	heaning
bench	loy	mouth	aborn	stair	pletant	cow	freelig	sheet	indinite
bowl	kump	mug	buvy	stone	priek	clay	stuple	ski	jubiter
brick	atep	net	cafin	street	raniator	truck	baid	slush	lown
broom	dag	oar	chog	suit	revorse	foam	chope	chalk	delial
bush	bainy	palm	claid	tape	sandine	shield	demiver	van	finter
crane	fouse	park	cood	toast	shoder	sky	grafe	tool	hufor
crow	ure	paste	deveat	toe	spinder	foot	haben	seat	miment
cube	cenny	pea	drame	wall	stunch	tent	invury	hand	plare
cup	blay	purse	emect	whale	takern	cart	breag	tree	quabum
egg	crint	rib	exapt	wheel	thenapy	stove	juby	lamp	resilve
fog	chely	rock	fove	wood	tronch	pig	kiffer	vest	throt
frog	vose	room	fluis	yard	unip	badge	livit	cloud	opruss
glass	hea	root	gallip	geese	verpict	pool	mazor	band	wilch
glove	gerve	school	gont	shoe	whame	cage	nurrify	seal	greep
goat	ning								

Appendix B

Mental Rotation Shapes



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