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Evolutionary advantages of human hemispheric asymmetries

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Durham University, Psychology Department

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Declaration

I confirm that no part of the material offered has previously been submitted by me for a degree in this or in any other University. If material has been generated through joint work, my independent contribution has been clearly indicated. In all other cases material from the work of others has been acknowledged and quotations and paraphrases suitably indicated.

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Diese Doktorarbeit widme ich meinem Großvater Fritz Hirnstein, der kaum Englisch kann, aber in diesem Moment sicher von irgendwo da oben herunterschaut und ein wenig lächelt.

Abstract

Hemispheric asymmetries are a basic principle of human brain organization. Once thought to be unique to humans, hemispheric asymmetries have meanwhile been documented in a wide range of species, suggesting they contain an evolutionary advantage. However, there are a few theories as to why asymmetry confers such an advantage and, moreover, there is a paucity of empirical work which is chiefly limited to a small number of animal studies. The present thesis is concerned with directly testing theories about potential evolutionary advantages in humans.

Because it is widely believed that hemispheric asymmetries generally enhance cognitive processing, the first study investigated the general relationship between functional lateralization and cognitive performance using two visual half-field paradigms. The second study employed the same paradigms to test the notion that hemispheric asymmetries specifically enhance parallel processing. The final study tested the notion that high degrees of lateralization (determined with a dichotic listening test) are associated with enhanced left-right discrimination. It was hypothesized that in all studies highly lateralized participants would outperform less lateralized participants.

In contrast to our hypotheses however, highly lateralized participants were consistently outperformed by less lateralized participants. Less lateralized participants showed higher cognitive performance and excelled at parallel processing and left-right discrimination. The results of the present thesis thus challenge a) the general notion that high degrees of lateralization are associated with enhanced cognitive processing, b) the specific notions that lateralization enhances parallel processing and left-right discrimination and c) the idea that hemispheric asymmetries are advantageous for cognitive processing *per se*. Taken together with previous studies, it is argued that advantages of hemispheric asymmetries depend on the degree of lateralization and situational requirements. That is, high, low and intermediate degrees of lateralization of the brain are each associated with distinct advantages (and disadvantages), depending on the demands placed upon it.

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Chapter I

Introduction

At first glance, the two halves of the human brain look fairly similar. And indeed, they serve to control a body that is bilaterally symmetrical: Movements of our right limbs are initiated primarily by the left hemisphere and sensations on the right side of our body are projected primarily to the left hemisphere (with the notable exception of the olfactory system). Conversely, the right hemisphere controls and receives input from the left side of our body. It has been suggested that the crossing of all efferent and afferent connections has originated in the crossed pathways of the visual system. That is, since the right visual field projects to the left hemisphere and the left visual field to the right hemisphere an organism can readily respond with its right side of the body to events in the right visual field and vice versa (Young, 1962). However, the symmetrical organization of the brain is superimposed by a marked asymmetry. A closer look at the two halves of the human brain reveals that there are several differences between the left and right hemispheres. These differences cannot be accounted for by random natural fluctuations, but are consistently shared by the vast majority of people. For instance, the right hemisphere is usually larger and heavier than the left (Kertesz et al., 1992; LeMay, 1976) and protrudes beyond the left hemisphere in the frontal region, while the left hemisphere protrudes beyond the right hemisphere in the occipital region (Bradshaw & Nettleton, 1983). More specifically, the Sylvian fissure curls upward more in the left than in the right hemisphere and the planum temporale is up to ten times larger in the left hemisphere. In contrast, Heschl's gyrus is larger on the right side and there are often two Heschl's gyri in the right hemisphere and only one in the left (Chi, Dooling & Gilles, 1977). Apart from these anatomical asymmetries, both hemispheres also differ in terms of cytoarchitecture and neurochemistry. For instance, the left hemisphere contains up to 186 million neurons more than the right hemisphere (Pakkenberg & Gundersen, 1997) and neurotransmitters such as acetylcholine, GABA, dopamine and noradrenaline are distributed unevenly across the two sides of the brain. For example, dopamine is more prevalent in the left hemisphere (Glick, Ross & Hough, 1982) and noradrenaline more prevalent in the right (Oke et al., 1978). These anatomical, cytoarchitectural and neurochemical differences are finally the basis for functional cerebral asymmetries, the phenomenon that both hemispheres contribute differentially to several functions and abilities. The two most common functional hemispheric asymmetries are (right-) handedness and language, which both reflect a left-hemispheric dominance. Specifically, there is a left hemisphere advantage for the production and perception of phonetic information, reading and writing, verbal memory, but also complex and fine motor skills as well as numeric operations. The right hemisphere, on the other hand, is dominant for a variety of visuospatial tasks including navigation (Burgess, Maguire & O'Keefe, 2002) and mental rotation (Corballis, 1997) as well as for processing geometrical patterns and faces (Dien, 2009), music and prosody of language (Griffiths et al., 1997). Emotions are also lateralized, although the exact relationship between hemispheric asymmetries and emotions is still unclear to date. While an older model proposed that only the right hemisphere processes emotions (Ley & Bryden, 1982), more recent models assume that positive emotions are processed by the left and negative emotions by the right hemisphere (Tucker, 1981) or that an activation of the left hemisphere leads to approach behavior while an activation of the right hemisphere leads to withdrawal behavior (Davidson, 1995). Taken together, hemispheric asymmetries can be found in virtually all higher cognitive functions including language, memory, learning, perception, spatial processing, attention, (fine) motor skills and emotions (for a short overview of functional hemispheric asymmetries see Figure 1). Hemispheric asymmetries thus constitute a basic principle of human brain organization.

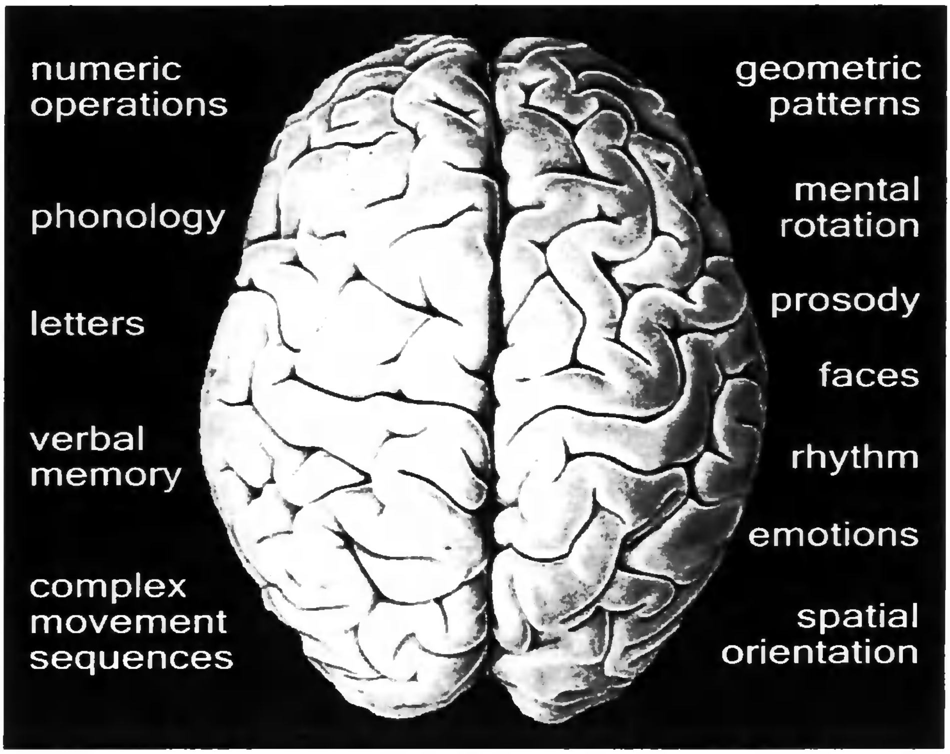

Figure 1. Overview of functional hemispheric asymmetries in the human brain.

Paul Broca set a milestone for lateralization research by claiming that right-handedness and language are both under the control of the left hemisphere (Broca, 1865). Since then many scientists believed that hemispheric asymmetries are unique to humans and separate us from the animal kingdom, because language and handedness were, and are, often regarded as human trademarks. This in turn led them to believe that the evolutionary origins of hemispheric asymmetries would lie in the development of language and intelligence. This belief was further strengthened by failed attempts to demonstrate handedness in animals and, if handedness was found, the ‘evidence’ was usually *based* on anecdotes or semi-scientific single case observations (e.g. Cunningham, 1921), which did not reveal a profound basis for a population bias as in humans (Güntürkün, in press). Hence, until the early and mid 90s of the last century scientists argued that hemispheric asymmetries are evolutionary advantageous, because they gave rise to our superior verbal and intellectual skills (Corballis, 1991), culminating in the view that the development of hemispheric asymmetries was the speciation event for Homo sapiens (Crow, 2002).

Hemispheric asymmetries in animals

Meanwhile however, it has become clear that hemispheric asymmetries are by no means unique to humans and exist in a wide range of species. As Güntürkün (in press) noted: "Non-human animals have asymmetries of brain and behavior at the population level. [...] this has been shown in ca. 1000 scientific publications that were conducted in more than 50 different species." Hemispheric symmetries can not only be found in our closest relatives the great apes (Hopkins, Russell & Cantalupo, 2007; Hopkins, 2006), and other mammals (e.g. Lippolis et al., 2005), but also in virtually all vertebrate classes including birds (Güntürkün, 1997), reptiles, amphibians and fish (Bisazza, Rogers & Vallortigara, 1998; Vallortigara, Rogers & Bisazza, 1999; for review Vallortigara & Rogers, 2005; Halpern et al., 2005; Rogers & Andrew, 2002). Recently, lateralization has even been demonstrated in invertebrates such as octopuses (Byrne et al., 2006), spiders (Ades & Ramires, 2002), fruit-flies (Pascual et al., 2004), bumblebees (Kells & Goulson, 2001) and honey-bees (Letzkus et al., 2006; Letzkus et al. 2008; Rogers & Vallortigara, 2008).

Obviously, the fact that animals also possess lateralized brains has considerable implications for the evolutionary origins of lateralization. If, for instance, hemispheric asymmetries in animals and humans are based on common ancestry (homology), the long-held view that evolutionary origins of lateralization lie in the development of our superior verbal and intellectual skills would have to be revised, because apparently animals have a lateralized brain but lack those high cognitive abilities. However, if lateralization has evolved independently in animals and humans (homoplasy), it might be possible that we developed hemispheric asymmetries for different reasons than animals, namely language and intelligence. A common method to differentiate between homology and homoplasy is to look for similar characteristics, that is, do hemispheric asymmetries in humans and animals follow a similar pattern (homology) or are they entirely unrelated to each other (homoplasy)? As we will see, the empirical evidence strongly suggests that hemispheric asymmetries are based on common ancestry. Hence, we will have to abandon the idea that hemispheric asymmetries evolved to enable humans to develop their superior verbal and intellectual skills.

A common pattern of hemispheric asymmetries across species

One of the most common hemispheric asymmetries in humans is (right-) handedness. Handedness has long been considered a unique human trait, largely as a result of the influential work of Collins (1968; 1969) on mice, which indicated that each animal has a preferred side but that there is no population bias (i.e. half of the population was left- and half was right-pawed) and even selective breeding of left-pawedness did not change this pattern. Similarly, some researchers failed to find a population bias for handedness in great apes (Finch, 1941; Annett & Annett, 1991). However, a problem with these studies is that very basic behavior has been observed, in which lateralization often does not become apparent. It has been argued that in humans simple tasks like reaching are under the control of a neural system which does not seem to be lateralized whereas complex, intricate activities like throwing require finer motor skills which tend to be lateralized (Healy, Liederman & Geschwind, 1986). Taking this distinction into account, Hopkins et al. indeed found right-handedness for complex activities in great apes (Hopkins, 2006; Hopkins & Leavens, 1998; Hopkins et al., 2005a; see Figure 2). To rule out that right-handedness was not merely adopted from (mostly right-handed) human keepers, it has not only been observed in chimpanzees in captivity but also in the wild (Lonsdorf & Hopkins, 2005). Accordingly, a right hand bias for extracting food from a narrow tube has been shown in capuchin monkeys (Spinozzi, Castornina & Truppa, 1998) and olive baboons (Meguerditchian & Vauclair, 2006). Moreover in birds, a population bias for 'handedness' also seems to exist, albeit that it is a right hemispheric bias (Güntürkün, in press): For instance, according to the early work of Friedman and Davis (1938) parrots preferentially pick up food with their left foot. Finally, some toads have a preference for their right hand for removing a sticking paper from their mouth or righting when they were overturned on their back (Bisazza et al., 1998; see also Figure 2). However, although there is plenty of evidence for a population bias of handed- /footed- or pawedness in animals, this bias is usually far lower than the 90% rate of right-handedness in humans, namely around 65% (but see Hopkins et al., 2005a for great apes). This is probably a result of humans having their hands entirely free while animals, such as monkeys, also use their hands for walking and might therefore simply lack the opportunity to develop a stronger lateralization (Corballis, 2008).

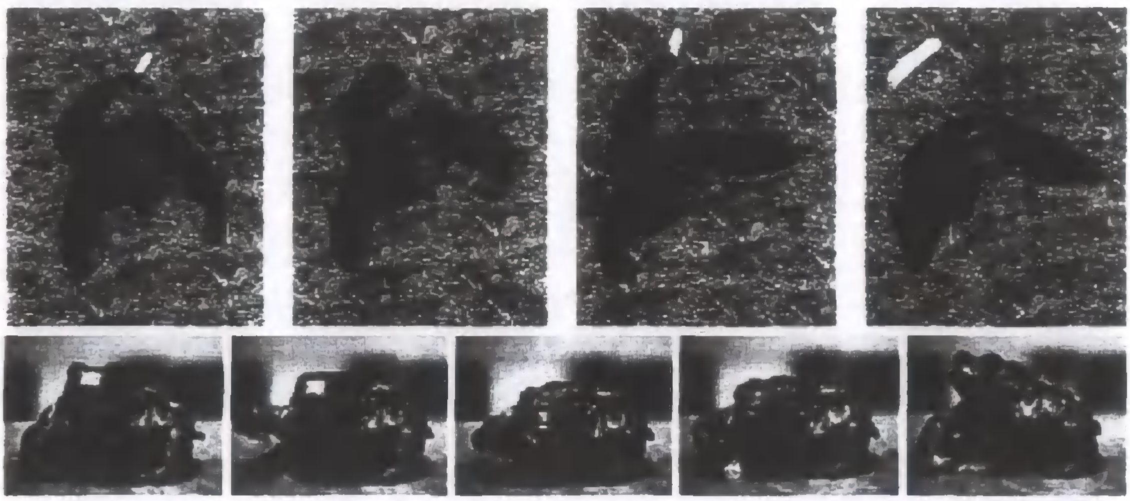

Figure 2. Chimpanzees (Pan troglodytes) have a right hand preference for complex actions like throwing a tube (upper picture sequence, courtesy of William D. Hopkins). Below: Toads (bufo bufo) have a right hand preference for removing a sticky tape from their snout (courtesy of Giorgio Vallortigara).

Although animals do not possess the advanced language abilities of humans, they nevertheless communicate and there is evidence that particularly the left hemisphere is involved – as in humans. In primates for example, species-specific vocalizations are preferentially processed by the right ear/left hemisphere (for Japanese macaques see Petersen et al., 1978; for rhesus monkeys see Hauser & Andersson, 1994) and impairments in the perception of these sounds are more severe after lesions of the left hemisphere. Chimpanzees, like humans, use their right hand more often for gestures than the left hand, particularly when those gestures are accompanied by vocalizations (Hopkins et al., 2005b; Losin et al., 2008), and their left planum temporale is also larger than the right planum temporale (Gannon et al., 1998). Accordingly, the equivalent of Broca's area is enlarged in chimpanzees, bonobos and gorillas (Cantalupo & Hopkins, 2001). In song birds, both the production (Nottebohm, 1977) and the perception of vocalizations (Okanoya et al., 2001) seem to rely more on the left than on the right hemisphere. For instance, lesions of the left hemisphere or sections of the left hypoglossal nerve (which connects the brain to the syrinx) resulted in greater song impairments than lesions or sections of the right. Similarly, when vocalizations in frogs are induced by clasping them behind the forelimbs, the number of vocalizations is significantly more reduced after lesions to the left hemisphere than after lesions of the right hemisphere (Bauer, 1993).

The evidence for a consistent pattern across species is probably weakest in spatial abilities. Although hemispheric asymmetries in the (visuo-) spatial domain can be found in a variety of primates, mammals and birds, it is not necessarily the right hemisphere that is dominant (Güntürkün, in press). This inconsistency may partly result from the fact that spatial abilities are less well-defined than language abilities and refer to a large number of distinct subcomponents. Therefore, different subcomponents might be investigated across different species, which makes the data difficult to compare and lead to inconsistent results.

Emotions or processing basic “fight or flight”-responses on the other hand seem to follow a similar pattern across different species in an obvious manner. For instance, cats, rats, dunnarts, chicks, frog tadpoles, toads and fish detect predators faster, and show escape responses more frequently and more rapidly, if the predator is presented in the left visual field (which as a result of the retino-cortical pathways corresponds to the right hemisphere) than in the right visual field (Rogers & Andrew, 2002). Accordingly, monkeys and apes exhibit a right hemispheric dominance for avoidance and withdrawal behavior and in humans fear is commonly regarded as being lateralized to the right (Vallortigara & Rogers, 2005). Aggressive responses also seem to be processed preferentially by the right hemisphere in monkeys, chicks, toads and lizards (Vallortigara & Rogers, 2005), which corresponds to a right hemispheric bias in humans (Bayer, 2008; Boes et al., 2008). On the other hand, prey discrimination, approach and manipulation of objects, as well as inhibition of aggressive behavior, have been associated with the left hemisphere in humans, monkeys, apes, chicks, toads and fish (Vallortigara & Rogers, 2005).

The lateralization of those functions listed above is certainly more complex than the brief overviews provided here might imply. In humans, for example, there are different views whether *all* emotions are preferentially processed by the right hemisphere or only *'negative'* emotions like anger, grief, fear and aggression (Bayer, 2008). However, the fact that similar functions are lateralized in a similar pattern across all those different species, particularly in communication, is unlikely to be mere coincidence. It rather suggests a common ancestry of hemispheric asymmetries and argues against an independent development of lateralization. Depending on whether only mammalian and avian species are taken into account or whether amphibians are also included, hemispheric asymmetries seem to have a history of at least 250 to 280 Mio years or 350 Mio years, respectively (Güntürkün, in press). As outlined above, this also implies that the evolutionary origins of hemispheric asymmetries most likely do not lie in the development of our language skills and our intelligence.

However, hemispheric asymmetries are still likely to be evolutionary advantageous (i.e. they contain a selection advantage over a non-lateralized brain), given they have existed for such a long period of time and are so widespread across different species. But despite the long and rich history of research on lateralization, potential evolutionary advantages other than our language skills and intelligence have hardly been investigated before. The reason probably lies within the long-held view that hemispheric asymmetries were unique to humans and separated us from the animal kingdom. Hence, potential advantages of hemispheric asymmetries were scarcely examined before the rather late discovery of lateralization in animals. As a consequence, this is a relatively recent research field and few of the putative advantages of hemispheric asymmetry that have been proposed have been tested empirically.

De-duplication of space

One of the first ideas comes from Levy (1969; 1974; 1977) who suggested that hemispheric asymmetries enable a more efficient use of anatomically limited brain space. Instead of having two hemispheres, which are equally capable of processing, for example, visuospatial abilities, the brain would double its cognitive resources, if only a single hemisphere conducted visuospatial processing. The other half of the brain would then be free to adopt additional functions, hence the term 'de-duplication'. Levy further argued that the gain of additional functions would outweigh the costs of motor and perceptual biases and the loss of a safety circuit in humans. In animals, however, the motor and perceptual biases would be too detrimental to compensate for the gain of cognitive power. Although her latter point was based on the incorrect view that hemispheric asymmetries are unique to humans, the idea of saving neural space by a de-duplication of function might still hold true. Although Levy's theory seems reasonable, it also has two major weaknesses. First, it does not explain why lateralization is necessary to save neural space: Instead of one hemisphere losing a certain function entirely, the brain would save as much space if each hemisphere lost similar portions of the function. Second, to test Levy's theory directly, one would have to examine whether an organism (be it human or not) adopted a new function after its brain became lateralized, which is difficult to test empirically with hindsight.

Elimination of interhemispheric conflict

Another reason for the emergence of hemispheric asymmetries might be the elimination of interhemispheric conflict (Corballis, 1991; Vallortigara, 2000). For example, interhemispheric conflict about medial organs like the tongue might arise if the control of these organs were represented equally in the left and right hemisphere. Moreover, a completely symmetrical brain might be very costly for animals like birds or amphibians with laterally placed eyes and no bilateral input into both hemispheres. If such an animal were to detect a predator on the left side with its left eye, the right hemisphere (as a result in the complete decussation of the optic tract) would precipitate a flight response, while the left hemisphere would literally 'see' no reason for escape, since it receives input from the right eye only. The consequence might be a conflict between hemispheres and a delay in the initiation of the response. There is only indirect evidence for this theory, coming from studies on toads (Vallortigara et al., 1998) and dogs (Quaranta, Siniscalchi & Vallortigara, 2007), in which sometimes the left and sometimes the right hemisphere takes control of the tongue (toads) or the tail (dogs), depending on the emotional content of the stimuli presented. But although this theory may sound convincing for animals with laterally placed eyes, it becomes more difficult for species such as humans and most mammals with a large overlap of the visual fields or structures that connect both hemispheres via commissural pathways such as the corpus callosum. In humans and most mammals each hemisphere receives input from both eyes (unless a stimulus is perceived in the extreme lateral monocular field) and information about one side is rapidly transferred between the hemispheres, hence interhemispheric conflict is unlikely to occur.

Preventing interhemispheric incompatibility

Akin to the idea of preventing interhemispheric conflict, Vallortigara et al. (1999) put forward the idea that hemispheric asymmetries may overcome the problem of functional incompatibility. Functional incompatibility is supposed to arise when an organism has to assess a novel stimulus/event. On the one hand, the organism needs to recognize, extract and categorize familiar features and ignore new, idiosyncratic features in order to initiate an appropriate, familiar response. On the other hand, it has to pay attention to these unique features in order to recognize their novelty and, at the same time, memorize them for future events. According to Vallortigara et al. (1999), the left hemisphere might be responsible for the categorization of novel stimuli while the right hemisphere might be in charge of detecting novelty. This assumption is based on the idea that the left hemisphere is dominant with processing local cues and the right hemisphere dominant with processing global cues and categorization is supposed to rely more on local features and detecting novelty on global features. Although there are studies on chicks showing that their left hemisphere is dominant for selecting single property cues (thus local information) to assign stimuli to certain categories (Andrew, 1991), support for this theory is rather indirect at best. Alternatively, the advantage of a lateralized brain may not rest on functional incompatibility itself. As will be seen, there are proponents of the view that lateralization enhances simultaneous, parallel processing (Deacon, 1997; Dunaif-Hattis, 1984). Simultaneous, parallel processing is a crucial feature of functional incompatibility, namely processing categorization and detection of novelty at the same time. Therefore the beneficial effects of parallel processing might be superimposed on preventing functional incompatibility.

Avoiding interhemispheric transfer time loss

Ringo et al. (1994) reasoned that hemispheric asymmetries might have arisen because they prevent time-consuming interhemispheric transfer. After calculating the conduction time (based on the diameter of myelinated and unmyelinated fibers of the corpus callosum in humans), they came to the conclusion that the interhemispheric delay for a single transmission from one temporal lobe to another would be on average greater than 15ms. If one takes into account that information constantly needs to be send back and forth between the two hemispheres (e.g. Schmidt, 2008), it would take considerably more time to process information between two hemispheres than just simply within a single hemisphere. Again, the empirical evidence is rather indirect and limited to very few studies. For example, it has been shown that fast large-diameter callosal fibers are more prevalent in brain areas devoted to primary sensory analysis, whereas higher-order areas are interconnected via slow small-diameter fibers (Aboitiz et al., 1992; Aboitiz, Lopez & Montiel, 2003). However, higher-order areas in particular require a constant flow of information between hemispheres (Varela et al., 2001) and thus the time loss would be particularly high. Furthermore, a study which compared the relationship between the size of the brain, the size of the corpus callosum and neuroanatomical asymmetries in humans, great apes and monkeys revealed that larger left-hemispheric asymmetries were associated with a smaller ratio of corpus callosum size/brain volume size (Rilling & Insel, 1999). In accordance with the notion of a reduced transfer time loss, this might imply that as the brain size increased, the interhemispheric connectivity decreased and as a consequence hemispheric asymmetries evolved or increased. The notion that hemispheric asymmetries avoid a transfer time loss is one that is readily testable. Following the rationale of Ringo et al. (1994) one would predict, for example, that animals with extremely large brains like elephants and big cetaceans would also have an extremely asymmetric brain, because of the immense transfer time loss. However, studies on very large animals are obviously difficult to conduct and expensive. Therefore, it is not surprising that so far only one such study indicates that elephants might have side preferences for their trunk during feeding behavior (Martin & Niemitz, 2003). Here, however, only individual biases but no population bias were found and it is unclear whether this is actually based on a hemispheric asymmetry. Conversely, in very small animals like insects there would be no need for an asymmetric brain, because the relative time gain of *intra-* vs. *inter*hemispheric processing would be virtually zero. Still, brain asymmetries have been reported in fruit flies (Pascual et al., 2004), bumble- and honey bees (Kells & Goulson, 2001; Letzkus et al., 2008; Letzkus et al., 2006; Rogers & Vallortigara, 2008) arguing against the notion of Ringo et al. (1994).

Enhanced parallel processing

Similar to the notion of de-duplication, that is, that lateralization might save neural space by leaving the other hemisphere free for complementary cognitive processes (Levy 1969, 1977), it has been proposed that lateralization might enhance parallel processing (e.g. Deacon, 1997; Dunaif-Hattis, 1984). According to this view however, the remaining hemisphere is not freed to adopt a new function but it is able to perform an additional task simultaneously while the other hemisphere is already occupied with another task. The concept that the two hemispheres can process different information simultaneously has been developed earlier and independently of hemispheric asymmetries. Dimond (1972) argued that since each hemisphere had the capacity to perceive, remember and learn independently of each other, the bihemispheric structure of the brain would enable parallel processing with the two hemispheres acting as two separate channels. He further suggested that when information is distributed between both hemispheres (instead of using only a single hemisphere) the overall capacity of the brain would be increased (Dimond & Beaumont, 1971). This idea is supported by a number of studies (e.g. Davis & Schmit; 1971, 1973; Guiard & Requin, 1977; Beaton, 1979; for review see Beaton, 1985). While parallel processing has been suggested to be the consequence of a bihemispheric structure, irrespective of hemispheric asymmetries, it is tempting to assume that parallel processing would be most efficient if tasks were carried out by the hemisphere that is specialized to this task. Indeed, the theory that hemispheric asymmetries enhance parallel processing is currently the most promising explanation for the emergence of lateralization, because there is direct empirical evidence coming from at least two species. Rogers, Zucca and Vallortigara (2004) tested chicks in two different conditions. In the first condition, chicks only had to perform a single task, namely discriminating small pebbles from grain. Here, a right eye/left-hemispheric advantage is usually found (Güntürkün & Kesch, 1987; Rogers, 1990). In another condition, chicks had to perform the grit/grain-discrimination task and simultaneously had to hide from a predator (a silhouette of a hawk circled over their head) for which a left eye/right hemispheric advantage exists (Vallortigara & Rogers, 2005). In chicks the trigger for lateralization is light stimulation during the last days before hatching (Rogers, 1990). The light stimulates the retina of only the right eye through the egg shell (the left eye is occluded by the body), which leads to a cascade of neural events finally resulting in a functionally and anatomically lateralized brain. If light stimulation is absent, chicks do not develop hemispheric asymmetries. Hence, Rogers et al. (2004) were able to compare the performance of light-incubated (lateralized) with dark-incubated (non-lateralized) chicks. In accordance with the notion of enhanced parallel processing, the light-incubated chicks learned faster than dark-incubated chicks to handle both the grit-grain discrimination and predator-avoidance tasks at the same time, while no differences were observed in the single-task condition. These findings were replicated in fish (Dadda & Bisazza, 2006). Lateralized and non-lateralized goldbelly topminnows (obtained by selective breeding) were placed in a water tank and had access to a feeding zone, where brine shrimps were released. Another water tank just behind the feeding zone was either empty (control condition) or contained a living predator (experimental condition). Similar to the experiments with chicks, no differences were found between lateralized and non-lateralized fish in the control condition. But when a potential predator was present, lateralized fish were twice as fast at catching shrimps as non-lateralized fish. Finally, there is a hint of a similar pattern in marmosets. The greater the degree of hand strength, as a potential sign for higher laterality, the shorter the latencies to detect a predator when they had just obtained food. But when they had not received food just prior to the introduction of a predator, no such correlation emerged (Rogers, 2006). A potential challenge to this theory, however, is that enhanced parallel processing cannot be seen as a general rule because it is limited to functions which are located in opposite hemispheres. In humans, for example, one might expect enhanced performance for simultaneous spatial (right hemisphere) and verbal (left hemisphere) processing but not for spatial and emotional processing (both right hemisphere). On the contrary, one would rather expect interferences between both processes. It is therefore difficult to see why functions became lateralized if the outcome in terms of parallel processing is sometimes reduced and sometimes enhanced, depending on the combination of the lateralized functions. On the other hand, it is possible that in the beginning of the development of hemispheric asymmetries two rather basic antagonistic functions became lateralized and further functions were grouped and aligned alongside these primal asymmetries (see also Vallortigara & Rogers, 2005). Foraging and predator avoidance as tested by Rogers et al. (2004) and Dadda and Bisazza (2006) might possibly be such basic antagonistic functions.

Distinction between advantages on individual and populational level

One major flaw is present in all theories described above. None of them can explain why hemispheric asymmetries are aligned in a consistent pattern across most individuals in certain species. In other words, given hemispheric asymmetries have evolved to enhance parallel processing (or to avoid transfer time loss, or to prevent interhemispheric conflict etc.), why does the vast majority of humans, for example, reveal a left hemispheric advantage for language? Why are not half of them lateralized to the left and the other half to the right? Vallortigara and Rogers (2005) have pointed out the distinction between evolutionary advantages of lateralization on an individual level and evolutionary advantages of the alignment of lateralization on a populational level. For instance, as outlined above, a number of species has a left visual-field/right-hemispheric dominance for detecting predators or initiating flight responses. If all individuals had the same bias, this could be easily exploited by predators which only had to approach these organisms from the 'right' side to raise their success rate. However, this could be easily avoided, if half of the population had a left- and half had a right hemispheric bias. In such a scenario, the benefits of a yet-unknown processing advantage would be maximal and at the same time, the costs of being predictable and therefore exploitable would be minimal. Yet, there are hemispheric asymmetries on a populational level. According to Vallortigara and Rogers (2005) there are social constraints for the alignment of hemispheric asymmetries. Specifically, they argued that the alignment of hemispheric asymmetries evolved as an evolutionary stable strategy (Maynard Smith, 1982), because "individually asymmetric organisms must coordinate their behavior with the behavior of other asymmetrically organisms of the same or different species" (Vallortigara & Rogers, 2005, p. 575). In other words, there is a delicate balance between the number of left- and right-lateralized organisms and deviations from this balance are punished by a negative outcome in fitness. For instance, if a group of animals were hunted by a predator, the chances of an individual getting caught are low if it followed the vast majority (say to the right). Concomitantly, if a small group of animals turned to the left, they would have a higher chance of survival, too, because the predator would probably chase after the larger group. However, the left turn advantage could only be maintained as long as the group size is small. Alternatively, based on the right-shift theory proposed by Annett (1995), Corballis (2005;

2006) suggested that the populational alignment of hemispheric asymmetries might be the result of one allele coding for a bias towards a specific side and one allele coding for a lack of any bias (leaving lateralization to any side at chance). If both alleles were maintained in the population, individuals with two 'lack of bias' alleles would randomly become either left- or right-lateralized, while individuals with one 'directional bias' allele would become lateralized to a specific side, eventually resulting in a majority lateralized to a specific side. Regardless of which of the two explanations (if any) is correct, this discussion emphasizes how important it is to distinguish between potential evolutionary advantages of lateralization for an individual and potential advantages for an alignment of lateralization on a populational level. The present thesis focuses solely on the question as to whether hemispheric asymmetries are evolutionarily advantageous for individuals.

Aims of the present thesis

To date none of the aforementioned theories can fully account for the potential evolutionary advantages of hemispheric asymmetries at an individual level. First, there are not enough studies available to evaluate those theories. Second, the predictions made by those theories are sometimes difficult to test empirically. Another problem is a profound lack of studies on humans. Many aspects of lateralization have been investigated extensively in humans, but the evolutionary origins of lateralization have not, probably because it was believed for a long time that hemispheric asymmetries were unique to humans and the evolutionary advantage would be language and intelligence. Since the discovery of lateralization in animals however, evolutionary advantages of hemispheric asymmetries have been investigated, but only in animals. Without doubt, animal research is of crucial importance to establish potential evolutionary advantages of lateralization, especially because hemispheric asymmetries seem to have developed in animals first. But it is questionable as to whether data from animal models (with e.g. laterally placed eyes and no corpus callosum) can be adopted without any adjustments. Hence, the present thesis investigates potential evolutionary advantages of lateralization in humans with the aim of a) providing us with *direct* insights about the origins of a fundamental principle of human brain organization and b) adding further evidence to the existing literature, mostly based on animals.

The few existing theories and notions about evolutionary advantages of hemispheric asymmetries share the general idea that lateralization ultimately enhances cognitive processing. Thus in the first study, the general relationship between lateralization and cognitive performance was examined (chapter II). More specifically, we investigated whether a more asymmetric brain is associated with higher performance in cognitive tasks than a less asymmetric brain. In two further studies specific theories and notions about potential advantages of hemispheric asymmetries were tested. Despite the caveats described above, the theory of enhanced parallel processing has arguably received the most empirical support so far. Chapter III thus describes a study which investigated whether this theory does not only hold true for fish and chicks but also applies to humans. Chapter IV finally deals with left-right discrimination, a cognitive ability that supposedly relies on, and is enhanced by, hemispheric asymmetries (Corballis & Beale, 1970, 1976). We therefore tested the hypothesis that high degrees of lateralization are associated with enhanced left-right discrimination.

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Chapter II

Although there is a consistent pattern of hemispheric asymmetries across the majority of people, there are large interindividual differences regarding the strength of lateralization, that is, the extent to which an individual is lateralized varies immensely between humans. Some people, for example, have a very pronounced left-hemispheric advantage for language processing, while others are more evenly organized and yet others have a right-hemispheric advantage.

All those theories that are supposed to explain evolutionary advantages of lateralization more or less imply that hemispheric asymmetries have arisen to enhance cognitive processing. A further inherent assumption is that the higher the degree of lateralization in a specific domain, the higher should be the cognitive performance in a task testing this domain. If lateralization were advantageous *per se* and if higher lateralization led to enhanced cognitive performances, one would expect an evolutionary race for a highly lateralized brain. However, there are still many individuals, who are not highly lateralized for specific brain functions. This seeming paradox led us to investigate the relationship between hemispheric asymmetries and cognitive performance more thoroughly.

Brain and Cognition, submitted

Disentangling the relationship between lateralization and performance

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Abstract

It is widely believed that advantages of hemispheric asymmetries originated in better cognitive processing, hence it is often implied that the relationship between hemispheric asymmetry and cognitive performance is linearly positive: The higher the degree of lateralization in a specific cognitive domain, the better the performance in a corresponding task. Yet, the empirical evidence for this notion is mixed and the statistical methods to analyze this relationship have been criticized. The present study therefore investigated the relationship between hemispheric asymmetries and cognitive performance in two behavioral tasks (a left-lateralized word-matching task and a right-lateralized face-decision task) in 230 participants (140 women, 90 men) by using a traditional, but problematic method *and* an alternative approach. Both methods correspondingly revealed that a relationship between hemispheric asymmetries and cognitive performance does exist. Contrary to a positive (linear) relationship however, the data could be best described by an inverted U-shaped curve. Although the optimal degree of lateralization seemed to be task-specific, a slight or moderate degree of hemispheric asymmetry achieved best cognitive performance in all tasks. Moreover, performances deteriorated towards extreme ends of lateralization (i.e. participants with either extreme left or right hemispheric biases). Taken together, the present study provides evidence against the notion that higher lateralization is related to enhanced cognitive performance. Rather, excessive degrees of lateralization seem to be detrimental for cognitive performance.

Introduction

For more than 100 years now, hemispheric asymmetries are known to be a basic principle of human brain organization. Particularly in the last decade, however, hemispheric asymmetries have also been reported in many other species, comprising vertebrates such as mammals, birds, reptiles, amphibians and fish (Güntürkün, 1997; Hopkins, 2006; Vallortigara, Rogers & Bisazza, 1999); for review see (Hellige, 1993; Rogers & Andrew, 2002; Vallortigara & Rogers, 2005) and invertebrates such as insects (Letzkus et al., 2006; Pascual et al., 2004) and octopuses (Byrne et al., 2006). Since lateralization is such a wide-spread phenomenon it likely contains a selection advantage over a symmetric brain. For example, it has been suggested that a lateralized brain prevents conflicts between the two hemispheres (Vallortigara, 2000), eliminates functional incompatibility between processing familiar events and producing novel behavior (Vallortigara et al., 1999) or leads to a 'de-duplication' of functions and increasing neural capacity (Levy, 1969, 1974, 1977). Moreover, lateralization is supposed to enhance parallel processing. While one hemisphere is occupied with a certain task, the other hemisphere can simultaneously perform an additional process (Dunaif-Hattis, 1984; Rogers, 2006). Taken together, most of those theories suggest that hemispheric asymmetries emerged because its development led to enhanced cognitive processing. Taking interindividual differences in the degree of lateralization into account, it is widely believed that a positive relationship between the degree of lateralization and cognitive performance exists (Güntürkün et al., 2000). That is, the higher the degree of lateralization in a specific cognitive domain, or in other words, the more a cognitive domain is lateralized to a particular hemisphere relative to the other hemisphere, the better is the cognitive performance in a corresponding task.

However, empirical evidence for this notion is rather patchy with some studies showing the exact opposite. For example, more lateralized participants were outperformed by less lateralized participants on a single task (Ladavas & Umilta, 1983) and also when performing two tasks simultaneously (Hirnstein, Hausmann & Güntürkün, 2008). Furthermore, mathematically gifted participants exhibit a more symmetrical activation of brain regions than those of average math ability (O'Boyle et al., 2005). On the other hand, a recent study (Chiarello et al., in press) found positive correlations between visual field asymmetries and reading performance, but only in young adults with strong and consistent hand preferences and less so in mixed handers. The probably most extensive study dealing with the relationship between hemispheric asymmetry and cognitive performance was conducted by Boles, Barth and Merrill (2008) who reanalyzed data from nearly 800 participants on various dichotic-listening and visual half-field (VHF) tasks by correlating the *mean* of left and right hemispheric performances with a *laterality index* which was also derived from left (LH) and right hemispheric (RH) performances. For the majority of these tasks, the analyses revealed significant linear relationships between both measures. However, about half of those significant correlations were positive and the other half were negative. Similar ambiguous results have been reported by others (Birkett, 1977; Bryden & Sprott, 1981; Springer & Searleman, 1978), suggesting that the relationship between the degree of lateralization and cognitive performance depends on the specific task used. According to (Boles et al., 2008), the crucial factor that determines whether the relationship is positive or negative is the age, in which a particular cognitive function becomes lateralized. The relationship between hemispheric asymmetries and cognitive performance is said to be positive, when the cognitive function lateralizes early (≤ 5 years of age) or relatively late (> 14 years of age) during ontogenesis, whereas negative relationships should emerge, if lateralization in cognitive functions is established between the age of five and eleven years.

Other studies investigated the relationship between the strength of handedness (as an indicator of hemispheric asymmetry) and performance on different manual tasks (e.g. Annett & Manning, 1990a, 1990b). However, Leask and Crow (2006; see also Leask, 2003) have criticized the statistical approach that was used in those studies and this criticism also applies to the study of Boles et al. (2008). The main problem is that the two correlated variables are statistically dependent. The degree of lateralization in those studies is typically derived from accuracy and reaction times of the left (LH) and right hemisphere (RH) by simply calculating the difference between LH and RH performances or by calculating a lateralization index which additionally takes the overall performance into account. This lateralization measure is then correlated with either the LH or RH performance or a mean/sum from LH and RH performances. That means the lateralization- and the cognitive performance-measures are correlated with each other, although they were both calculated from the same LH and RH performances which often correlate with each other. As (Leask & Crow, 2006) conclude:" [...] presentations of such data, in which one variable is the function of the other, are vulnerable to misinterpretation." (p. 222). To avoid this problem, one could determine the degree of lateralization with a certain task and measure cognitive performance in a different but related task (Leask & Crow, 2001). However, in previous studies (e.g. Boles et al., 2008) such independent but related tasks were not always available. Alternatively, (Leask & Crow, 1997, 2006) offered a seminal solution for the problem of dependent lateralization/cognitive performance measures. The authors used data from more than 10,000 school children (10-11 years of age) and plotted the degree of lateralization (measured as hand dominance in a box-marking or match-picking task) against the mean performance in those tasks (and also against an independent verbal and nonverbal task). In addition, empirical data were used to generate reference plots, in which any correlation between LH and RH performance was removed. These plots served as reference lines for the empirical plots and revealed an inverted U-shape relationship between the degree of lateralization and the mean performance. That is, participants with a single, mild degree of lateralization performed best and performance deteriorated towards extremely left- or right-lateralized participants.

Taken together, research on the relationship between hemispheric asymmetries and cognitive performance is inconclusive. One reason might be that different studies used different statistical approaches and some of the methods chosen were questionable. The present study therefore sought to combine the rather 'traditional' approach of calculating correlations (Annett & Manning, 1990a, 1990b; Boles et al., 2008) with the recently proposed 'alternative' approach (Leask & Crow, 2006). The traditional approach has the inherent problem that the relationship between hemispheric asymmetries and cognitive performance might be confounded by the correlation of left and right performances. The 'alternative' approach however has the inherent problem that it is purely descriptive. Furthermore, rather selective samples were investigated so far. The most extensive study using the traditional approach (Boles et al., 2008) tested only male students, while the alternative approach was only applied to ten- and eleven-year old school children (Leask & Crow, 2006). Thus, in the present study, both the traditional and the alternative approach were applied to a relatively large sample of adult males and females. The major aims of the present study were three-fold: (1) To investigate whether a significant relationship between hemispheric asymmetries and cognitive performance exists, (2) to clarify whether this relationship is indeed positively linear, as it is commonly believed, and (3) to compare the outcomes of the traditional with the alternative approach.

Moreover, several studies revealed individual differences in the degree of lateralization. In general, women, for example, seem to be less lateralized than men (Halpern, 2000; Hiscock et al., 1994; Hiscock et al., 1995). We were thus additionally interested in whether the relationship between hemispheric asymmetries and cognitive performance differs between men and women. One previous study (Boles, 2005; Leask & Crow, 2001) failed to find a substantial sex difference.

Methods

Participants

Overall, 140 women and 90 men were included in the present study. The data was partly taken from previous studies (Hausmann et al., 2002; Hausmann & Güntürkün, 1999, 2000; Hausmann, Güntürkün & Corballis, 2003). All participants completed the Edinburgh Handedness Inventory (Oldfield, 1971). The laterality-quotient (LQ), provided by this test is calculated by [(R-L)/(R+L)] × 100, resulting in values between -100 and +100. Positive values indicate a preference for the right hand, while negative values indicate left handedness. Women had a mean LQ of 91.18 (SD = 15.7, range: 18 – 100), while the LQ for men was 89.18 (SD = 17.47, range: 9 – 100). Although the majority of participants were university students, also older adults were included (women: M = 36.96, SD = 16.27, range 19 – 80; men: M = 36.18, SD = 16.72, range 19 – 70). The large age-range suggests a rather representative sample compared to previous studies (Boles et al., 2008; Leask & Crow, 2006) allowing for more general conclusions about the relationship between degree of lateralization and cognitive performance.

Visual half-field tasks

Two VHF-tasks were used in the present study, the word-matching task and the face-decision task. In both tasks, participants were asked to place their head on a chin rest in front of a computer screen and keep their head and body still during the whole experiment. This ensured that the stimulus presentation was more than 2° visual angle to the left or right of a central fixation cross. In both tasks, participants completed 70 trials (10 practice trials and 30 experimental trials with each hand) and reaction times and frequency of correct responses in percent were recorded.

Word-matching task

After presentation of a fixation cross, a German noun was presented for 200ms at the centre of the computer screen. The nouns were selected for a high degree of abstraction to maximize the left-hemispheric advantage (Baschek et al., 1977) and consisted of at least four and no more than seven letters. Subsequently, a word was presented for 185ms to either the left (LVF) or right visual half-field (RVF) while an empty frame appeared on the contralateral side. Participants were asked to indicate via button press whether the laterally presented word matched the previously presented word or not (for details see (Hausmann & Güntürkün, 1999).

Face-decision task

Participants were presented either normal or 'distorted' non-faces in one VHF while an empty frame was shown on the contralateral side (stimulus time 185ms). Photographs for the faces were taken from a U.S. college album of the 1950s. The students on these pictures were all male, clean shaven, short-haired and without glasses. To avoid further nonfacial characteristics, all photographs were framed with an ovoid overlay which covered the background and the clothes. The distorted faces were generated by translocating some facial characteristics, like swapping the mouth and one eye or deleting the eyes. Participants were asked to indicate via button press whether a picture showed a normal or a 'distorted' face as quickly and as accurately as possible.

Both VHF-tasks revealed the expected VHF-differences in previous studies. The word-matching task consistently showed a RVF/left hemisphere advantage, whereas the face-decision task showed a robust LVF/right hemisphere advantage (Hausmann et al., 2002; Hausmann & Güntürkün, 1999, 2000; Hausmann et al., 2003). Further support for a RVF/left-hemispheric advantage for the word-matching and a LVF/right hemisphere advantage for face-processing in VHF-tasks comes from recent magnetic resonance imaging studies (Weis et al., 2008; Yovel, Tambini, & Brandman, 2008).

Data analysis

Traditional approach

According to (Boles et al., 2008), the easiest and most common way to determine the degree of lateralization in accuracy and reaction times is a laterality index (LI) calculated as [(RVF–LVF)/(RVF+LVF)]*100. In terms of accuracy, a negative index thus indicates a LVF/RH and a positive index a RVF/LH advantage. Conversely, in terms of reaction times, a negative index indicates a RVF/LH and a positive index a LVF/RH advantage. The LI for each task (word-matching and face-decision) and each dependent variable (accuracy and reaction time) was then correlated with the mean LVF/RH and RVF/LH performance. This was done for negative and positive LIs, indicating the direction of the bias (hence termed directional LIs) and absolute LIs (i.e., the degree of lateralization irrespective of its direction). In addition to Boles et al. (2008) however, not only linear regressions but also a quadratic regressions were calculated, because both the data of Leask and Crow (2006) and the regression figures in the study of Boles et al. (2008) imply a U-shaped relationship between the degree of lateralization and overall cognitive performance when directional LIs were considered.

Alternative approach

The alternative approach was adopted from Leask and Crow (2006). To prevent confounding effects of correlations between LVF and RVF performances, the relationship between the degree in lateralization and cognitive performance was derived from comparing the real data with reference data which share the same mean and standard deviation as the real data, but rely on uncorrelated LVF and RVF performances. A plot of the real data (correlation between the degree of lateralization and mean performance) was then compared to the reference plot, and the relationship between degree of lateralization and performance was simply shown by the difference between these plots. A detailed description of the procedure is given below.

To obtain the real data plot, the LI and the mean performance of RVF and LVF for both accuracy and reaction times were calculated and plotted against each other. Then, LI and mean performance were smoothed using locally weighted scatterplot smoothing (LOESS). LOESS is a modern smoothing method, which "[...] can be seen as a type of moving average, where the value of a 'y' for a given 'x' consists of the average of all the 'local' y-values, cubically weighted by their distance each side of x. This 'smoothing kernel' moves along the x-axis, calculating a mean value for y, with data further away contributing less and less" (Leask & Crow, 2006, p. 222). In contrast to simple regressions, LOESS does not make any presuppositions about the relationship between two variables and can therefore detect any linear and non-linear relationship between LI and mean performance.

After smoothing the empirical data, reference lines were obtained by creating reference plots based on uncorrelated LVF and RVF performances. Reference data were created "by displacing the column of observation on one side 'vertically' with respect to the other, by one or more rows, matching observations on one side effectively at random with those on the other" (Leask & Crow, 2006, p. 222). Thus, reference data share the same mean and standard-variation as the real data. For comparison with the real data only reference datasets with very low correlations between LVF and RVF performances ($r < .05$) were used. Subsequently, for each reference dataset the LI and the mean performance of LVF and RVF were plotted against each other and smoothed using LOESS, resulting in the actual reference lines. The relationship between degree of lateralization and mean performance is then revealed by the difference between real and reference lines (real line minus reference lines).

Results

Hemispheric asymmetries

A mixed 2×2 ANOVA with VHF (LVF vs. RVF) as within- and sex as between-participants factor was calculated for both tasks and for both accuracy and reaction times. The effect size is given as the (partial) proportion of variance accounted for (partial η^2) throughout. Mean accuracies, response times and LIs across both tasks and both sexes are shown in Table 1.

Word-matching task

Accuracy: Participants responded more accurately in the RVF (92.1% ± SE = .62) than in the LVF (86.6% ± .83) as indicated by a significant main effect of VHF ($F(1,227) = 68.66$, $p < .001$, $\eta^2 = .23$). Moreover, a significant interaction between sex and VHF emerged ($F(1,227) = 4.93$, $p = .027$, $\eta^2 = .02$) with the rightward bias being more pronounced for women (RVF: 92.0% ± .77, LVF: 85.0% ± 1.04) than men (RVF: 92.3% ±.97, LVF: 88.2% ± 1.30). The main effect sex did not reach significance ($F(1,227) = 1.75$, $p = .187$, $\eta^2 = .01$). *Reaction times:* The analysis revealed neither any significant main effect nor interaction for response times (all $F(1,227) < 1.93$, $p > .166$, $\eta^2 < .01$)

Face-decision task

Accuracy: Participants responded more accurately in the LVF (80.5% ± .73) than in the RVF (74.3% ± .72; $F(1,227) = 80.35$, $p < .001$, $\eta^2 = .26$) indicating a strong right-hemispheric advantage. Neither the main effect of sex nor the interaction between sex and VHF became significant (all $F(1,227) \leq .32$, $p \geq .565$, $\eta^2 \leq .001$). *Reaction times:* Participants responded faster in the LVF (967.4ms ± 15.7) than in the RVF (1006.8ms ± 15.7; $F(1,227) = 27.79$, $p < .001$, $\eta^2 = .11$), again indicating a strong RH advantage. The main effect of sex ($F(1,227) = .49$, $p = .485$, $\eta^2 = .002$) and the interaction between sex and VHF ($F(1,227) = 3.59$, $p = .06$, $\eta^2 = .016$) failed to reach significance.

Taken together, both tasks revealed robust hemispheric asymmetries in the expected direction. Moreover, women demonstrated a slightly more pronounced asymmetry than men in the word-matching task, albeit the effect size was very small ($\eta^2 = .02$).

Table 1

	Word-matching task						Face-decision task					
	Women (N = 140)			Men (N = 89)			Women (N = 140)			Men (N = 89)		
	LVF	RVF	LI	LVF	RVF	LI	LVF	RVF	LI	LVF	RVF	LI
Accuracy [%]	**84.98**	**92.02**	**4.30**	**88.19**	**92.26**	**2.50**	**80.35**	**73.81**	**-4.31**	**80.75**	**74.88**	**-3.75**
	(12.71)	(9.54)	(6.24)	(11.48)	(8.47)	(5.84)	(10.39)	(10.53)	(7.02)	(11.43)	(10.91)	(6.44)
Reaction times [ms]	**1010.9**	**1014.1**	**.23**	**957.8**	**974.0**	**.92**	**998.8**	**1033.0**	**1.68**	**936.0**	**980.6**	**2.47**
	(256.3)	(247.4)	(4.72)	(287.6)	(283.6)	(5.46)	(229.4)	(235.0)	(4.84)	(233.4)	(224.3)	(5.39)

Mean accuracy, mean reaction times and corresponding mean laterality indices (LIs) in both the word-matching and face-decision task across both sexes and both visual half fields (SD in brackets). Accuracy: Positive LIs indicate a RVF/LH advantage, negative LIs a LVF/RH advantage. Reaction times: Positive LIs indicate a LVF/RH advantage, negative LIs a RVF/LH advantage.

Relationship between laterality index and mean performance

Traditional approach

Correlation coefficients between LI and mean performance are shown in Table 2. The p-level was adjusted to p < .01 because of the relatively high number of regression analyses. In sum, five principal findings were found:

1. *Relationship between degree of lateralization and mean performance does exist*

Regression analyses revealed significant relationships particularly for the word-matching task in accuracy (only), which were almost identical for males and females. Only one significant relationship was found in the face-decision task (response times), indicating a significant quadratic relationship between the degree in lateralization and overall reaction time in this task for men.

2. *(Extremely) High degrees of lateralization are detrimental*

All significant relationships for the word-matching task in accuracy were negative, suggesting an increased overall performance when the RVF/LH advantage in this task was low. Significant quadratic regressions in the word-matching task revealed that optimal cognitive performance was achieved with rather low negative LIs (females: optimum at LI = -0.01, range -9.88 to 21.72, mean = 4.30; males: optimum at LI = -1.32, range -7.67 to 21.77, mean = 2.50). The quadratic regression in the face-decision task also revealed an optimal performance at an LI=4.85 nearby the mean (mean = 2.47, range -9.29 to 19.21). Overall, the analyses suggest that extremely large LIs (negative or positive) are related to lower performance.

3. *Quadratic or linear relationship*

The relationship between degree of lateralization and mean performance slightly favored a quadratic model, at least when directional asymmetries were considered. Across all conditions/measures, correlation coefficients for quadratic regressions were consistently higher than those for directional, linear regressions, as indicated by a Wilcoxon-test across all correlation coefficients in quadratic and linear regressions ($Z = 2.37$, $p = .018$). Also, in the face-decision task (reaction times in males), it was only the quadratic regression which revealed significance. These differences however seem to disappear when absolute, linear regressions were compared to directional, quadratic regressions (Z = 1.26, p = .21; equal number of significant relationships).

4. *The optimal degree of lateralization*

The existence of a quadratic model implies that a task-specific optimum in the degree of lateralization exists. Surprisingly, the optimal degree of lateralization was always related to a small RH advantage in both tasks (note that negative LIs in accuracy and positive LIs in reaction times are related to a LVF/RH advantage). This observation was particularly unexpected for the word-matching task, because the vast majority of participants had a RVF/LH advantage in the word-matching task. This finding, however, might be similar to the linear analyses, which localize the optimum in the degree of lateralization close to an LI = 0.

5. *Sex difference*

Although previous studies (and the present study) revealed a sex difference in the degree of lateralization, the relationship between degree in lateralization and mean performance was very similar between males and females. The only exception occurred in the face-decision task (response times), in which the quadratic regression was significant in males but not in females.

Table 2

Regression Coefficient *r*			**Accuracy**		**Reaction Times**	
			Word-matching (Max/Min LQ)	Face-decision (Max/Min LQ)	Word-matching (Max/Min LQ)	Face-decision (Max/Min LQ)
Directional	Linear	Women (N=140)	**-.45*****	.08	-.07	-.002
		Men (N=89)	**-.35****	.01	-.05	-.12
	Quadratic	Women	**-.56*****	-.20	.07	.17
		(N=140)	(-.01)	(-1.25)	(-2.21)	(2.14)
		Men	**-.41*****	-.22	.07	**.32****
		(N=89)	(-1.32)	(-4.55)	(4.50)	(4.85)
Absolute	Linear	Women (N=140)	**-.59*****	-.18	.003	.13
		Men (N=89)	**-.49*****	-.17	.002	.19

Linear and quadratic regressions between LI (absolute and directional) and mean performance (measured with accuracy or reaction times) in the word-matching and face-decision task across both sexes. Positive values in quadratic regressions indicate a U-shaped, negative values an inverted U-shaped curve. The values in brackets in quadratic regressions indicate the best/worst LI. For accuracy: Positive LIs indicate a RVF/left-hemisphere advantage and negative LIs a LVF/right-hemisphere advantage. For reaction times: Conversely, positive LIs indicate a LVF/right-hemisphere advantage and negative LIs a RVF/left-hemisphere advantage.

Alternative approach

The results can be found in Figure 1. In terms of clarity, a single mean line (black) was calculated across all subtractions of real and reference lines (grey). Performance peaks and lows refer to this mean line.

Word-matching task

Accuracy: In line with the traditional approach, males and females showed optimal mean performance (compared with reference lines) when the degree of lateralization was low (and slightly shifted towards the RH, men: LI = 0; women: LI = –1.68). Mean performance drops with increasing degrees in lateralization. For men only, an additional drop in performance occurred at around LI = 5.21.

Reaction times: An optimal degree of lateralization for men was at LI = –4.82. Higher negative LIs and lower negative LIs led to slower responses. At an LI = 0.92, mean performances briefly improved with increasing positive LIs (LVF/right hemisphere advantage), before eventually dropping again at around LI > 6.52. Women with extremely high negative LIs (RVF/LH advantage), however, responded faster than the reference lines imply. With increasing LIs, they responded more slowly until a mean performance minimum was reached at LI = –7.94. Then mean performance improved again before it finally deteriorated at around LI = 1.45.

Face-decision task

Accuracy: Highly negative LIs (LVF/RH advantage) were associated with poor accuracy in men and women. But while men also showed low accuracy with highly positive LIs (RVF/LH advantage) and an optimum at LI = –2.02, women in fact showed an upswing at around LI = 5.00. There were marginal differences between real data and reference lines between both LIs, indicating no specific relationship with mean performance within this LI range.

Reaction times: Men had a single mean performance optimum at LI = 4.68, while women had two optima at LI = 1.19 and LI = 13.61. Mean performances between both peaks were indifferent (i.e., only marginal differences between real and reference lines). Highly positive (LVF/RH advantage) and negative LIs (RVF/LH advantage) resulted in a steady mean performance decline.

Summary of the main findings

1. *Relationship between degree of lateralization and mean performance does exist*

Similar to the traditional approach, the alternative approach suggests that there is a relationship between degree of lateralization and mean performance. The empirical data differed considerably from the reference lines in all conditions.

2. *(Extremely) High degrees of lateralization are detrimental*

The vast majority of plots suggest that the mean performance did not enhance with an increasing degree of lateralization (for exceptions see Point 4 below). On the contrary, participants with extremely high positive or negative LIs usually revealed lowest performances.

3. *Quadratic or linear relationship*

In accordance with the directional quadratic models in the traditional approach, the LOESS procedure led in most cases to lines which came closest to an inverted U-shaped curve (for accuracy; U-shaped curve for response times). In fact, none of the other plots suggest a linear relationship between LI and mean performance except for women's accuracy in the face-decision task.

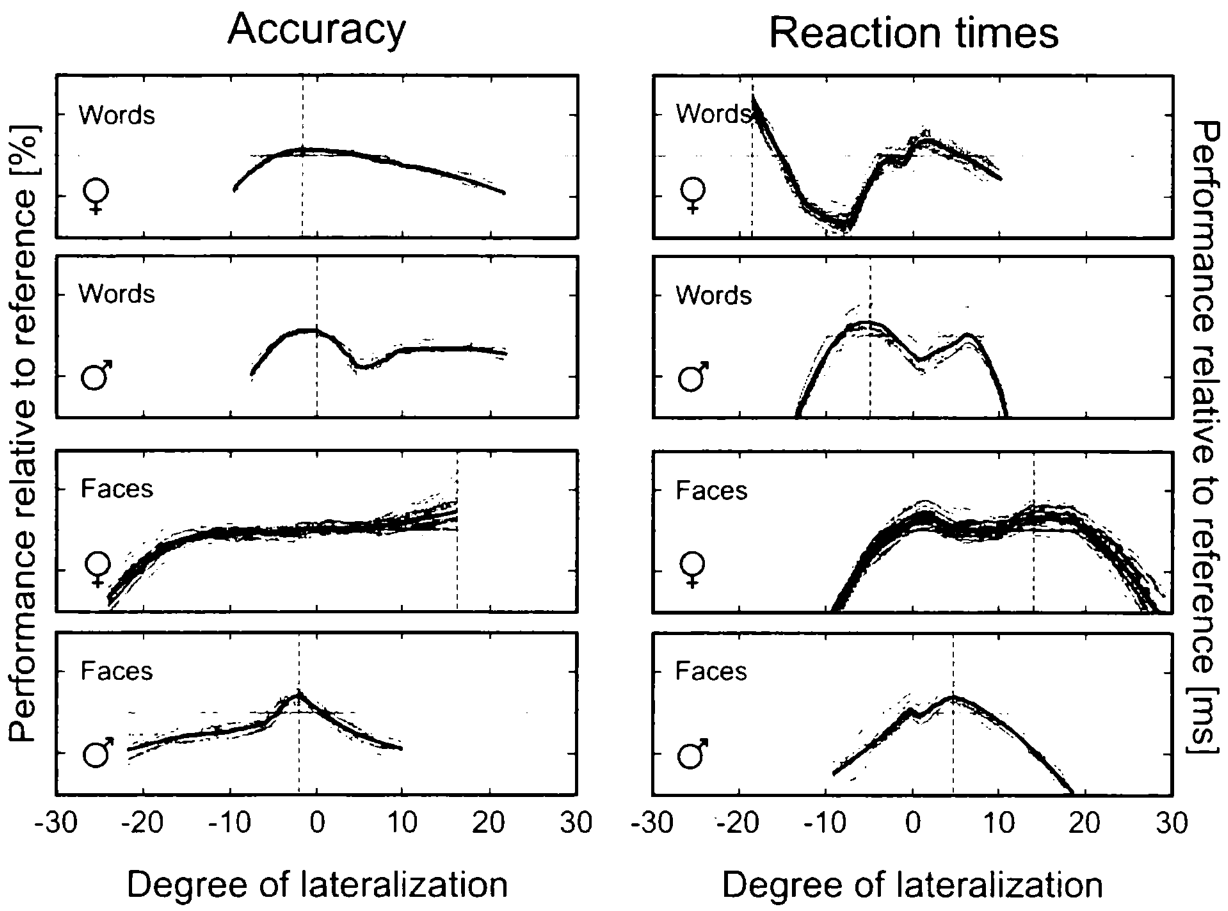
4. *The optimal degree of lateralization*

In most cases, plots revealed performance optima at specific degrees of lateralization (LIs are based on mean reference lines and give a rough estimate of the optimum LI) are difficult to estimate as a result of the noise in the data). If optimal degrees of lateralization emerged, these LIs were not necessarily related to the dominant hemisphere in a particular task. For instance, in the face-decision task, where participants showed a LVF/RH advantage, the optimal mean performance of males was found in the lower LVF/RH advantage range (negative LIs). Women however, who also showed a LVF/RH bias, were more accurate when showing a slight RVF/LH bias (positive LI), though optimal mean performances in reaction times was also achieved with LVF/RH biases. Performance optima of both women and men in the word-matching task were associated with a slight LVF/RH bias despite the fact that both sexes showed a left-hemispheric bias. That means the task-specific degree of lateralization that is characteristic for a particular (sub-) population is not necessarily identical with the degree of lateralization that is associated with optimal performance (compare with Table 1).

5. *Sex difference*

The relationship between degree of lateralization and mean performance seems to be sex-dependent. Men consistently demonstrated a single optimum and deteriorating mean performances with highly positive and negative degrees of lateralization. Women performed similarly to men in only two cases (reaction times in face-decision task and accuracy in word-matching task). In two other cases (accuracy in face-decision task and reaction times in word-matching task) such a single, U-shaped relationship did not emerge. In both diverging patterns, extremely high LVF/RH biases were associated with poor performances and extremely high RVF/LH biases with high performances.

Figure 1



Degree of lateralization across performance (relative to reference) in the word-matching (words) and face-decision (faces) task for men and women. The horizontal line represents a relative performance of zero, that is, no difference between real data and references. Values above zero indicate higher accuracy and shorter reaction times and values below zero indicate lower accuracy and longer reaction times (relative to reference). Grey lines were obtained by subtracting low-correlation references from the real data – their distribution serves as an estimate of uncertainty. Optimal LIs are indicated by dashed lines. In accuracy, positive LIs indicate a RVF/LH and negative LIs a LVF/RH advantage. In reaction times, positive LIs indicate a LVF/RH and negative LIs a RVF/LH advantage.

Discussion

Most theories about potential evolutionary advantages of hemispheric asymmetries imply that lateralization enhanced cognitive processing and that accordingly a higher degree of lateralization is associated with enhanced cognitive performance in specific cognitive functions. There is indeed empirical evidence coming from an animal study to support this notion. Güntürkün et al. (2000) found that the more pigeons were lateralized in discriminating grain from grit with either the left or right eye (i.e., the right or left hemisphere respectively due to complete decussation of the optic nerves), the more successful were they in a foveal condition (general performance). The literature on humans however is less supportive of this theory. While mathematical models (Kosslyn, Sokolov & Chen, 1989; Reggia, Goodall & Shkuro, 1998) and a recent study (Chiarello et al., in press) are in accordance with this notion, other studies reveal either ambiguous (Birkett, 1977; Boles et al., 2008; Bryden & Sprott, 1981; Springer & Searleman, 1978) or contrary results (Hirnstein et al., 2008; Ladavas & Umilta, 1983; Leask & Crow, 2006; O'Boyle et al., 2005). A further problem is that some of these studies (e.g. Birkett, 1977; Boles et al., 2008) used the traditional approach of simply calculating correlations, which is vulnerable to misinterpretations as pointed out by Leask and Crow (2006). The alternative approach (Leask & Crow, 2006) overcomes this problem and has also got the advantage that it does not require any prior assumptions about the relationship between lateralization and cognitive performance and can therefore look for any relationship. On the other hand, however, the alternative approach is essentially descriptive while the traditional approach provides statistical significances. The present study therefore sought to combine both methods to investigate the relationship between lateralization and cognitive performance. Although both methods are quite different, they often led to similar results.

No positive relationship between lateralization and performance

First of all, both approaches revealed that a relationship between lateralization and cognitive performance does exist. Our findings are thus in accordance with a number of studies (Birkett, 1977; Boles et al., 2008; Bryden & Sprott, 1981; Leask & Crow, 1997, 2006; Springer & Searleman, 1978; Chiarello et al., in press) and corroborate the view that cognitive performance might have indeed played a part in why hemispheric asymmetries have developed and why they still persist.

However, taken together both approaches also correspondingly suggest that this relationship does not follow the rule 'the more lateralized, the better the cognitive performance'. On the contrary, high degrees of lateralization led to poor mean performance according to the traditional approach and – perhaps with the exception of women with a strong left-hemispheric bias (see below) – also according to the alternative approach. Our results are thus in clear contrast to computational models (Reggia et al., 1998), animal data (Güntürkün et al., 2000) and a recent study, which found a positive, albeit weak correlation between visual field asymmetries and reading performance (Chiarello et al., in press). Although two reliable LH- (word-matching) and RH-superior (face discrimination) tasks have been investigated, our findings of a rather negative relationship obviously cannot be generalized and hence it cannot be argued that hemispheric asymmetries and cognitive performance in humans are always negatively related to each other. For example, Boles et al. (2008) have found that in a single dataset of a large number of lateralized tasks, sometimes positive and sometimes negative correlations emerge. Although these results have to be interpreted with caution given the criticism of the traditional approach that was used, this study suggests that the relationship between lateralization and cognitive performance might be task-dependent. Our data are in accordance with this view. In the traditional approach, for example, all but one significant relationship between degree of lateralization and mean performance were found in the word-matching task and not in the face-decision task. Still, the notion that higher degrees of lateralization inevitably lead to better cognitive performance was disconfirmed.

Inverted U-shaped curve

As far as directional asymmetries are concerned, both approaches correspondingly suggest that the relationship between lateralization and cognitive performance can be best described by an inverted U-shaped curve. This finding is in accordance with Leask and Crow (2006), who also revealed that performance was optimal at a certain degree of lateralization and deteriorated towards extremely high and low degrees. In contrast to our data, however, where different optimal degrees of lateralization were found across both tasks and both sexes, Leask and Crow (2006) found a single optimal lateralization degree (at about LI = 10) across various tasks. However, the degrees of lateralization of the present study and the study of Leask and Crow (2006) are difficult to compare, although the same formula to calculate the LIs was used. First, Leask and Crow investigated other cognitive functions and the degree of lateralization was determined via hand performance with box-marking and match-picking tasks. Second the degree of lateralization was based on a dependent variable other than accuracy and reaction time as in the present study. Finally, multiple optimal degrees in lateralization as observed in the present study might be the result of a rather heterogeneous sample (men and women of different ages) compared to the homogeneous sample (10 to 11 year old boys) used by Leask and Crow (2006). An inverted U-shaped relationship between hemispheric asymmetries and cognitive performance with a performance peak slightly shifted to either LH or RH would also be in accordance with a recent notion of Corballis (2006; see also his comment in Vallortigara & Rogers, 2005). His notion is based on the Right-Shift Theory, according to which handedness is mediated via a balanced polymorphism for cerebral dominance and cognitive processing (Annett, 1995), which predicts poorer performance at extremes of lateralization, the so-called 'heterozygote advantage'. Corballis has suggested that an extremely symmetrical brain might be disadvantageous, because it is detrimental for complex processes such as language, whereas an extremely asymmetrical brain might be disadvantageous, because it would result in poor sensor analysis or motor control on the sub-dominant side of the body/brain. Therefore, symmetry and asymmetry should be held in balance, to prevent those disadvantages. Our findings, and those of Leask and Crow (2006), fit the notion of Corballis in so far as extreme lateralization seems to be detrimental for cognitive performance. Despite sensorimotor deficits, a rather less lateralized functional brain organization however may contain the advantage of an enhanced cognitive performance.

It also becomes apparent from both the traditional and the alternative approach that the slight advantage of a quadratic over a linear relationship would disappear if analyses were based on absolute and not directional degrees of lateralization. This is in accordance with Boles et al. (2008) who also found consistently higher linear relationships for absolute rather than directional degrees of lateralization. Unfortunately, (Boles et al., 2008) did not provide correlation coefficients of quadratic regressions to test whether they were also higher than directional linear coefficients. Boles et al.'s explanation for higher and more frequent linear correlations in absolute rather than directional degrees of lateralization also holds true for our data, that is, the relationships in the LH (LI < 0) and RH scale (LI > 0) are almost mirrored with an optimum close to virtual symmetry (LI = 0).

If, as in the present study or the study of Leask and Crow (2006), a specific degree of lateralization (i.e., a specific left- or right hemispheric bias) is associated with optimal performance, it seems reasonable to use directional rather than absolute degrees of lateralization to investigate the relationship between hemispheric asymmetries and cognitive performance. Otherwise information about the side/hemisphere ideally dominating a given function would be lost. However, if the optimal degree in lateralization is close to zero (virtual symmetry), as in the present study, it appears that the directional bias in the localization of the optimum is less relevant.

Other factors than cognitive processing contribute to hemispheric asymmetries

Finally, both approaches reveal that the average degree of lateralization in a population is not necessarily the same that is required to achieve an optimal performance. The traditional approach revealed that although men and women had a significant bias towards the left hemisphere in the word-matching task, optimal mean performances were even associated with a slight right-hemispheric bias (which might be still in the range of a bilateral functional brain organization, though). The alternative approach revealed a similar pattern for the word-matching task in accuracy for men. If cognitive performance were the only factor that decides about the adaptiveness of the degree in lateralization, one would expect that the vast majority of a population would gather around these optimal degrees of lateralization. However, this does not seem to be the case: Many individuals reveal a degree of lateralization which is suboptimal or even detrimental for cognitive performance. One might thus speculate that factors other than cognitive performance also contribute to the adaptiveness of the degree of lateralization.

Vallortigara and Rogers (2005), for example, put the idea forward that the direction of lateralization in animals is determined by social constraints, that is, the direction of lateralization of an individual depends on the direction of lateralization of the other individuals in the group. Similarly, social constraints, besides cognitive performance, might also be important for the adaptiveness of the degree of lateralization in humans. An additional adaptive value of hemispheric asymmetries might be the cerebral susceptibility to harmful events. For example, it has been shown that functionally a less lateralized neural network supporting language can be beneficial for compensation after unilateral lesions (Knecht et al., 2002).

Discrepancies between traditional and alternative approach

So far, findings were discussed in which there were large overlaps between the traditional and the alternative approach. However, both approaches also revealed discrepancies. For example, the existence of a relationship between degree of lateralization and mean performance was revealed by the traditional approach only in *some*, but by the alternative approach in *every* condition. This is obviously related to the fact that the alternative approach can reveal any relationship and is purely descriptive, while the traditional approach can reveal only one particular relationship and has an alpha-error level. In the traditional approach, all significant relationships in the word-matching task were found for accuracy, presumably because a hemispheric asymmetry only emerged in accuracy but not reaction times. In the face-decision task, however, a hemispheric asymmetry emerged for both accuracy and reaction times, yet only one significant relationship was found for reaction times. Also, this significant relationship was only found in men not in women. This further suggests that the relationship between lateralization and cognitive performance might be task- and possibly sex-dependent.

Sex differences

Both approaches also reveal different results regarding a potential sex difference in the relationship between lateralization and cognitive performance. In the traditional approach (except for a stronger relationship in men than women in reaction times of the face-decision task), relationships overlapped to a large extent, suggesting rather no sex difference. This would be in accordance with a previous study (Leask & Crow, 2001), in which a sex difference in the relationship between manual asymmetry and verbal abilities were investigated. The authors found that while schoolgirls were consistently better than boys with regard to performance in the verbal task, the relationship between manual asymmetry and verbal abilities was similar for both sexes: Increasing dominant hand skill was associated with increasing verbal ability. However according to the alternative approach, men consistently showed an inverted U-shaped curve, whereas on two occasions (accuracy in the face decision task and reaction times in the word-matching task) women with extremely high left-hemispheric biases demonstrated high mean performances. Possibly, there is a trade-off between reaction times and accuracy in women. For example, in the word-matching task women with extremely high left-hemispheric biases responded faster but also less accurately than expected. Moreover, they responded more accurately, but also more slowly in the face-decision task. However, such a (potential) trade-off was not found in men. Moreover, if extreme degrees of lateralization were associated with high mean performances in women, a left-hemispheric bias was found in all tasks used here. The traditional and the alternative approach come to different results in this case and it is rather difficult to decide which approach is better. Whether women are more flexible in the relationship between lateralization and performance, particularly when they have a strong left-hemispheric bias, remains an open question.

Dynamic changes in the relationship between lateralization and performance

Many researchers in this field seem to implicitly assume that the relationship between degree of lateralization and cognitive performance is robust and stable over time. Boles (Boles et al., 2008) is among the few who stated that this relationship can differ according to neuronal development. He specifically suggests that cerebral functions which lateralize early and late in ontogenesis have a positive relationship and functions which lateralize at intermediate ages have a negative relationship between hemispheric asymmetries and cognitive performance. The authors of the present study believe that changes in the relationship might be not only restricted to specific developmental stages but that an optimal degree in lateralization changes even more dynamically. A large number of studies suggest that the degree in lateralization underlies dynamic changes. These dynamic changes have been observed, for example, for different age ranges (Beste, Hamm, & Hausmann, 2006; Cherry & Hellige, 1999), as a result of hormonal fluctuation (Bayer & Erdmann, 2008; Bayer & Hausmann, 2009; Hausmann et al., 2002; Wisniewski, 1998), emotional and motivational state (Davidson, 1995; Kuhl & Kazen, 2008; Wacker, Heldmann & Stemmler, 2003), task requirements within a particular task (Czeh et al., 2008; Hausmann, Kirk & Corballis, 2004) etc. Why would hemispheric asymmetries be subjected to those dynamic changes if there is only one particular optimum in the degree of lateralization? A possible explanation would be that different degrees of lateralization are associated with different mental states and factors other than optimal cognitive performance are also relevant.

Conclusions

In sum, the present study suggests in alignment with previous studies (Boles et al., 2008; Leask & Crow, 2006) that lateralization is related to cognitive performance and that hence, cognitive performance – alongside with other factors like perhaps social constraints – might have played an important role in the development of hemispheric asymmetries. In contrast to the widely believed notion of a positive, linear relationship between hemispheric asymmetries and cognitive performance however, high degrees of lateralization are detrimental to cognitive performance and the relationship can be best described by an inverted U-shaped curve (with a performance optimum slightly shifted from a zero lateralization degree). Also, there are hints that the relationship is function and sex-dependent. In terms of evolution of hemispheric asymmetry, this might imply that initially a small dose of hemispheric asymmetry might have indeed enhanced cognitive performance, but then had to be kept in balance with bilateral symmetry before an overdose became detrimental.

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Chapter III

While the previous study dealt with the general relationship of lateralization and performance, the next study ought to investigate the specific notion that lateralization enhances parallel processing. Despite the results of the previous study, which suggested that low rather than high degrees of lateralization are associated with enhanced cognitive performance, it was hypothesized, in accordance with the animal literature, that participants with high degrees of lateralization would outperform participants with low degrees of lateralization.

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The evolutionary origins of functional cerebral asymmetries in humans: Does lateralization enhance parallel processing?

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Abstract

Functional cerebral asymmetries (FCAs) are a fundamental principle of brain organization in many species. However, little is known about *why* they have evolved. Since FCAs are such a widespread phenomenon they seem to constitute an evolutionary selective advantage. According to a prominent hypothesis, an asymmetric brain should be associated with advantages in parallel processing, i.e. doing two tasks simultaneously. The strong version of this hypothesis implies that lateralized, instantaneous and complementary tasks are performed more efficiently with a highly lateralized brain. Using a visual half-field procedure, we wanted to test this strong version of the parallel processing hypothesis in humans. Thirty-two participants (17 women, 15 men) were investigated. First, we assessed the degree of lateralization in a face/nonface and a word/nonword discrimination task favoring the right and left hemisphere, respectively. Based on a median split, subjects were divided into a rather symmetric and a rather asymmetric group. Then, all participants completed both tasks simultaneously. The results revealed that the rather symmetrically organized participants outperformed asymmetric participants in accuracy *and* response times. Hence, the strong version of the parallel processing hypothesis has to be revised.

Introduction

Hemispheric asymmetries are a widespread phenomenon among various species: They are present in most vertebrates, including fish, amphibians, reptiles (Bisazza, Rogers & Vallortigara, 1998; Vallortigara, Rogers & Bisazza, 1999), birds (Güntürkün, 1997) and mammals (Hopkins, 2006; for review Hellige, 1993; Rogers & Andrew, 2002; Vallortigara & Rogers, 2005), and they can be found on various levels, such as neuroanatomy, neurochemistry, and behavior. Recently, lateralization has also been shown in invertebrates, e.g., fruit flies (Pascual et al., 2004), honeybees (Letzkus et al., 2006) or octopuses (Byrne et al., 2006). Although a very large number of studies have described various asymmetries in dozens of species, there is still little known about why lateralization has evolved. Hemispheric asymmetries are not a static phenomenon, underlie dynamic changes and are rather relative than absolute (Pratt et al., 2002; Sinai & Pratt, 2003). However, given they are so ubiquitous, an evolutionary advantage for lateralization should exist.

It has been suggested that functional cerebral asymmetries (FCAs) might have arisen to avoid processing delays deriving from slow interhemispheric transfer (Ringo et al., 1994), or to prevent interhemispheric conflicts (Annett, 1995; Corballis, 1991; Vallortigara, 2000) or functional incompatibility (Vallortigara & Andrew, 1994; Vallortigara, 1992; Vallortigara & Andrew, 1991). Another long standing hypothesis to explain FCAs is by saving neural capacity due to a reduction of redundant processes. While a specific neural circuit in one hemisphere is processing a specific task, the homologous area in the opposite hemisphere can perform different or complementary processes, allowing a more efficient use of cortical capacity (Levy, 1969). Concomitantly, an asymmetric brain enhances parallel processing (Deacon, 1997; Dunaif-Hattis, 1984). Although the parallel processing hypothesis was originally adopted to account for human lateralization, most of the empirical support comes from animal studies. This hypothesis has a weak and a strong version. The weak version posits that participants freely allocate lateralized resources over time to use them sometimes in parallel, sometimes in succession. The strong version implies that task performance is optimized by always simultaneously using asymmetrical neural mechanisms. Up to now, all animal studies used a design that is similar to the weak version of the parallel processing hypothesis.

Rogers, Zucca, and Vallortigara (2004; see also Dadda & Bisazza, 2006; Dharmaretnam & Rogers, 2005; Rogers, 2006; Rogers, 2000) tested chicks in a parallel task paradigm. They had to discriminate grain from small pebbles, and simultaneously, detect a predator overhead (silhouette of a hawk that was moved over the cage). Previous studies with chicks or pigeons revealed a left hemispheric superiority for the grain-pebble discrimination task (Güntürkün & Kesch, 1987; Rogers, 1990) and a right hemispheric superiority for the detection of predators (Evans, Evans & Marler, 1993; Rogers, 2000). To test the parallel-processing hypothesis Rogers et al. (2004) compared the performance of lateralized and non-lateralized chicks. The results revealed that in contrast to non-lateralized chicks, lateralized ones showed better grain-pebble discrimination and additionally were less disturbed by the predator (Dharmaretnam & Rogers, 2005). However, the lower performance of the non-lateralized chicks was not simply due to an overall reduced performance, since both groups did not differ when only a single task (the grain-pebble discrimination without a predator) was accomplished. In support of the hypothesis, the results suggest that FCAs are adaptive for parallel processing. However, an asymmetrical cerebral organization does not seem to reveal any advantage, if parallel processing is kept to a minimum (as in the single task condition).

In humans, processing two concurrent events has been extensively investigated, e.g. by using tachistoscopic paradigms as we did here. However, nobody so far to our knowledge has addressed how the degree of asymmetry affects performance on parallel processing. The seminal experiments by Marie Banich and colleagues (Banich & Weissman, 2000; Banich & Belger, 1990; Belger & Banich, 1998; Belger & Banich, 1992), for instance, revealed that when different stimuli are presented to both visual fields, the performance was enhanced in demanding tasks, when processing is distributed among both hemispheres, whereas in simple tasks the performance is enhanced when processing is restricted to a single hemisphere. Similarly to the experiments we conducted here, Nettleton and Bradshaw (1983) presented faces and names to both visual fields simultaneously. They found that both hemispheres are capable of processing either stimuli but with varying levels of efficiency. However, none of these studies reported whether high degrees of lateralization were associated with better performance.

On the other hand in *single* task conditions the relationship between FCAs and performance has been investigated. Surprisingly, a negative correlation has been reported between an asymmetry index derived from both visual fields and the reaction time of a centrally presented stimulus (Ladavas & Umilta, 1983), indicating that slower responses correspond to larger differences between visual fields. According to the authors, this finding is due to a better cooperation between both hemispheres in a less lateralized brain, presumably mediated by interhemispheric crosstalk. In support of this notion there is evidence for a link between the size of the corpus callosum, which is likely to mediate the interhemispheric crosstalk, and cognitive performance. For example, a larger corpus callosum (and hence an enhanced cooperation between the hemispheres) is associated with higher intellectual abilities (Cherkassky et al., 2006; Fine et al., 2007; Hulshoff Pol et al., 2007; Nosarti et al., 2006; Tramo et al., 1998) and shorter interhemispheric transfer time (Jäncke & Steinmetz, 1994).

Taken together, the existing animal studies support the parallel-processing hypothesis. Our aim was to seek for similar evidence in humans. Based on the animal literature, we expected more lateralized participants to outperform less lateralized ones in parallel processing. According to the weak and the strong version of the parallel processing hypothesis, there are two different ways to approach the question. One is to test differently lateralized subjects in a dual task that avoids the need for instantaneous parallel processing. This is the design employed up to now in animal research using, e.g., birds with their laterally placed eyes. Here, chicks are faced with two separate task demands that require asymmetrical and complementary resources but are rather free to allocate their visual attention over time. The other alternative is to require participants to instantaneously respond to two different tasks given to the left or the right hemisphere. Here, the participants have no degrees of freedom but have to simultaneously respond to both tasks at a time point determined by the experimenter. This is the approach taken by the present experiment.

Methods

Participants

Thirty-two neurologically healthy subjects (17 women, 15 men) participated in this study. The mean age for women was 25.12 years (SD = 5.77, range: 19 – 39 years) and 24.87 years (SD = 7.00, range: 18 – 47 years) for men. All participants were right-handed, as determined by the Edinburgh Handedness Inventory (Oldfield, 1971). The laterality-index (LQ), provided by this test is calculated by LQ = [(R-L)/(R+L)] × 100, resulting in values between -100 and +100. Positive values indicate a preference for the right hand, while negative values indicate left handedness. Women had a mean LQ of 89.74 (18.87, range: 43 – 100), while the mean LQ for men was 86.24 (15.86, range: 50 – 100).

Lateralization measures

To test the hypothesis that stronger FCAs are associated with better parallel processing of the two hemispheres, we used a face- and a lexical-discrimination task which are known to reveal robust right- and left-hemispheric superiorities, respectively (Hausmann et al., 2002; Hausmann & Güntürkün, 1999). In the first step of our experiment, both visual half-field (VHF) tasks were applied separately, i.e. participants had to discriminate either faces from non-faces or words from non-words. This procedure allowed us to quantify the advantage of the left (LVF) and right visual half-field (RVF) for both tasks.

Participants were asked to place their head on a chin rest, at a distance of approximately 57 cm from a monitor, so that 1 cm represents 1° visual angle. To ensure that lateralized stimuli were presented more than 2° visual angle to the left or right of a central fixation cross, we instructed our participants to keep their head and body still and to fixate that cross during the whole experiment. All stimuli were presented in a frame of 3.9 cm width and 5.1 cm height. As in (our) previous studies, all stimuli were presented tachistoscopically for 185 ms.

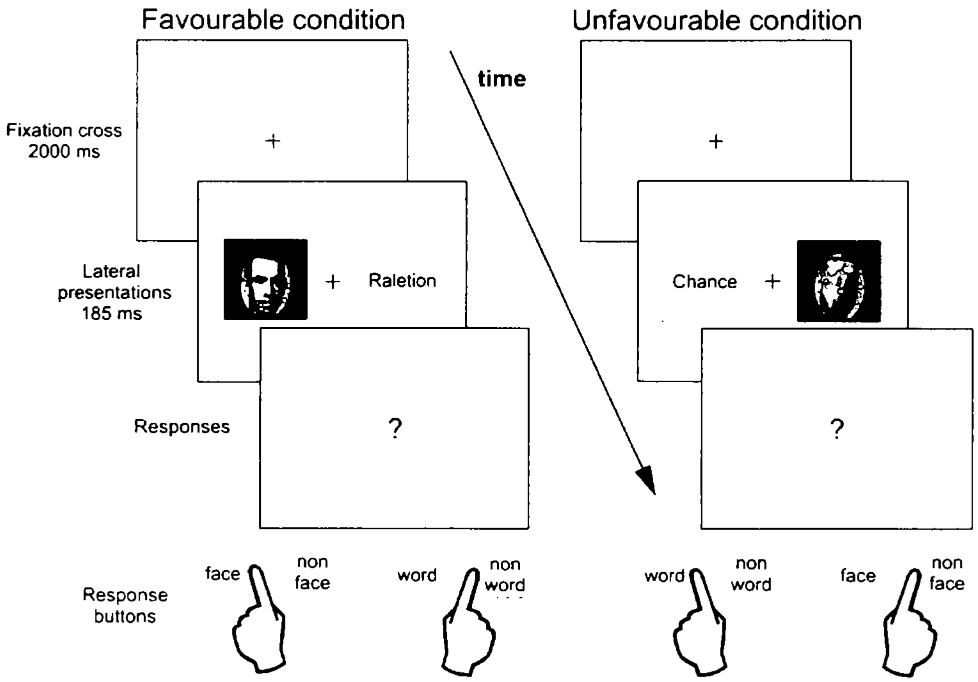
In the face-discrimination task, participants had to indicate as quickly and correctly as possible whether the presented stimuli was a "normal" face or an altered "non-face". The faces were taken from a US college album from the 1950s, showing male, clean shaven, short haired students without glasses in their early 20s (Hausmann & Güntürkün, 1999). All face stimuli were framed with an ovoid overlay to cover distractors like clothes or background. In some photographs typical facial characteristics have been altered resulting in a non-face, e.g., the position of an eye and a mouth was swapped or everything was deleted except for the nose etc. All faces had the same orientation and an unemotional, neutral expression. A trial started with a 2s presentation of a central fixation cross. Then the stimulus was displayed in the LVF or RVF (in a pseudo-randomized order), while an empty frame appeared simultaneously in the contralateral VHF. Subsequently, a question mark instructed our participants to indicate by pressing a "Yes" or "No" button, whether the stimulus was a normal face. Seventy trials were employed by this procedure, the first ten practice trials were excluded from the analysis. After forty trials the responding hand was changed in a balanced order.

In the lexical-discrimination task, participants had to indicate as quickly and correctly as possible whether a true German word or a non-word was presented. Only abstract nouns of at least four up to a maximum of eight letters were used to maximize the left hemispheric advantage (Baschek et al., 1977). The experimental procedure was identical to the face-discrimination task. In previous studies (e.g. Hausmann, Güntürkün & Corballis, 2003; Hausmann et al., 2002; Hausmann & Güntürkün, 2000; Hausmann & Güntürkün, 1999) both tasks revealed the expected functional asymmetries, i.e. a LVF advantage for face discrimination and a RVF advantage for lexical decision. Although the purely behavioral tasks used in the present study are indirect measures of hemispheric activation, a recent functional imaging study has shown that lateralization patterns are highly related to the underlying neuronal activation patterns if the half-field technique fulfils the appropriate standards (Hunter & Brysbaert, 2008). For both tasks, frequency and median reaction time for correct responses were measured for each VHF. To determine the absolute individual degree of asymmetry, we calculated an asymmetry index (AI) for the frequency of correct responses and the reaction times as AI = | [right - left visual field performance] / [right + left visual field performance] |.

The Parallel task

For the parallel task, we used the same stimuli as in the face and word discrimination task. A trial started with presentation of the fixation cross (duration 2s). Then, a face/non-face was tachistoscopically presented within LVF or RVF while in the contralateral VHF a word/non-word was presented simultaneously. The exposure time for all stimuli was again 185ms. Thus, by using the VHF paradigm two different conditions are possible: a "favorable" condition in which the face/non-face appeared in the superior LVF and a word/non-word in the superior RVF and an "unfavorable" condition, where the face/non-face was presented in the inferior RVF and the word/non-word in the inferior LVF (Figure 1). This procedure allowed investigating whether a potential advantage of an asymmetric brain also persists, if the stimuli are presented to the subdominant hemispheres. The frequency of words and faces vs. non-words and non-faces was counterbalanced and our participants completed 48 trials in the favorable and 48 trials in the unfavorable condition. Prior to every condition, ten practice trials were completed. After presentation of the stimuli, participants had to make *two* responses as quickly and correctly as possible. Participants responded with the *left* hand to stimuli in the LVF *and* with the *right* hand to stimuli in the RVF, respectively. That is, in the favorable condition, they responded with the *right* hand to words/non-words in the RVF and with the *left* hand to faces/non-faces in the LVF. Likewise in the unfavorable condition, they responded with the *right* hand to faces/non-faces in the RVF and with the *left* hand to words/non-words in the LVF. A trial was considered only as correct, if *both* responses were correct. For both conditions, we measured the frequency of correct responses, and the median reaction time of the second button press.

Figure 1



Experimental setup of the parallel task. In the "favorable" condition a face or a non-face was always presented in the superior LVF and a word or a non-word in the superior RVF, whereas in the "unfavorable" condition a face or a non-face was presented in the inferior RVF and a word or a non-word in the inferior LVF.

Results

Single tasks

The effect size is given as the proportion of variance accounted for (partial eta^2) throughout. To investigate whether the face and lexical discrimination task revealed a LVF and RVF advantage, respectively, a mixed 2 × 2 × 2 ANOVA with VHF (LVF, RVF) and hand (left, right) as repeated measures and sex as between-participants factor for the frequency of correct responses and median reaction times was computed. In the *face-discrimination task*, a significant main effect VHF for both frequency of correct responses ($F(1,30) = 7.6$, $p = .01$, $\eta^2 = 20.3$) and reaction time ($F(1,30) = 8.2$, $p = .008$,

$\eta^2 = 21.4$) was found. As expected, participants responded more accurately to the LVF (76.6% ± SE = 1.9) than to the RVF (71.4% ± SE = 1.7) and faster in the left (951ms ± 30.2) than in the RVF (985 ms ± 30.9), indicating a robust LVF advantage, corresponding to a right hemispheric superiority. All other main effects and interactions were not significant (all $F \leq 1.3$, $p \geq .26$, $\eta^2 \leq 4.1$). The *lexical-discrimination task* also yielded a significant VHF advantage for the frequency of correct responses ($F(1,30) = 20.7$, $p < .001$, $\eta^2 = 40.9$) and the reaction times ($F(1,30) = 8.6$, $p = .006$, $\eta^2 = 22.2$). Participants were more accurate in the RVF (82.8 % ± 2.2) than in the LVF (71.2 % ± 3.4) and made faster responses in the RVF (1160 ms ± 49.2) right than in the LVF (1280 ms ± 67.1), indicating the predicted robust left hemispheric advantage. Again, no further main effects or interactions were found (all $F \leq 2.6$, $p \geq .12$, $\eta^2 \leq 7.9$).

The results revealed that the lexical- and the face-discrimination task were strongly lateralized to the left or right cerebral hemisphere, respectively. Furthermore, no significant sex differences were found (all $F \leq 2.6$, $p \geq .12$, $\eta^2 \leq 7.9$).

Parallel task

It is important to bear in mind that participants were asked for two responses – each with a hit rate of 50%. Thus, overall chance level was at 25%. All groups in subsequent analyses differed highly significantly from chance level (all $t(15) \geq 7.9$, $p < .001$), indicating that participants were capable of the task.

To obtain an overall degree of lateralization, we calculated a mean asymmetry index (AI_M), derived from the asymmetry indices of the face and the lexical decision task. Since both reaction time and accuracy consistently revealed FCAs, one AI_M was computed for accuracy and one AI_M was computed for reaction times.

We started our analysis with the AI_M based on accuracy. Participants with high AI_M scores had strong asymmetries in both tasks, while participants with low AI_M scores were rather symmetrically organized. We then performed a median split, resulting in a more lateralized and a less lateralized group (for results see Table 1 below). The frequency of correct responses and the reaction times in the parallel task were compared using a mixed 2 × 2 × 2 ANOVA with condition (favorable vs. unfavorable) as within- and group (more vs. less lateralized) and sex as between-participants factors. Participants responded faster ($F(1,30) = 6.6$, $p = .016$, $\eta^2 = 19.1$) and more accurate ($F(1,30) = 22.8$, $p < .001$, $\eta^2 = 44.9$) in the favorable than unfavorable condition as indicated by significant main effects of condition. Unexpectedly, a main effect group emerged, revealing that less lateralized participants responded significantly faster (1713 ms ± 90.3) than more lateralized ones (2004 ms ± 90.3, $F(1,30) = 4.9$, $p = .035$, $\eta^2 = 14.9$). There was no significant difference ($F(1,30) = .3$, $p = .56$, $\eta^2 = 1.2$) between less lateralized (42.7% ± 2.0) and more lateralized participants (40.8% ± 2.0) in accuracy.

We then repeated the whole procedure with AI_M based on reaction times, i.e. a median split was performed for AI_M based on reaction times, resulting in a less and a more lateralized group and a mixed 2 × 2 ANOVA with condition (favorable vs. unfavorable) and group (more vs. less lateralized) for the frequency of correct responses and reaction times in the parallel task was computed. Similarly, participants responded faster ($F(1,30) = 6.6$, $p = .016$, $\eta^2 = 19.1$) and more accurate ($F(1,30) = 21.9$, $p < .001$, $\eta^2 = 43.4$) in the favorable than in the unfavorable condition. Surprisingly, less lateralized participants (44.9% ± 1.8) responded more accurately than more lateralized ones (38.7% ± 1.8) as indicated by a main effect group ($F(1,30) = 7$, $p = .013$, $\eta^2 = 20.1$), but they did not respond significantly faster ($F(1,30) = 1.6$, $p = .217$, $\eta^2 = 5.4$). In neither analysis did significant interactions between group and condition emerge (all $F \leq 1.9$, all $p \geq .183$, $\eta^2 \leq 6.3$). Also no sex effects were found (all $F \leq 2.3$, all $p \geq .144$, $\eta^2 \leq 7.5$). Thus, when the groups were split according to accuracy, the difference between less and more lateralized participants emerged for reaction times, whereas, when the median split was based on reaction times, a difference was observed in accuracy. Although we do not see a plausible explanation on a methodological level, it should be noted that no trade-off between accuracy and reaction times exists (neither analysis revealed better performance of more lateralized participants), and thus cannot explain the main finding of the present study, namely a superiority in parallel processing for less-lateralized individuals.

Table 1

Lateralization (AI_M)		**Mediansplit (accuracy)**		**Mediansplit (reaction times)**	
		Reaction time (ms)	Correct responses (%)	Reaction time (ms)	Correct responses (%)
Strong	Favorable condition	**1945.4** (95.4)	**45.1** (2.1)	**1847.1** (102.6)	**41.1** (1.8)
	Unfavorable condition	**2063.6** (99.7)	**36.6** (2.3)	**2011.9** (103.3)	**36.2** (2.3)
	Overall	**2004.5** (90.2)	**40.8** (2.0)	**1929.5** (96.1)	**38.7** (1.8)
Weak	Favorable condition	**1629.8** (95.4)	**45.7** (2.1)	**1728.1** (102.6)	**49.6** (1.8)
	Unfavorable condition	**1795.7** (99.7)	**39.6** (2.3)	**1847.4** (103.3)	**40.1** (2.3)
	Overall	**1712.8** (90.2)	**42.7** (2.0)	**1787.7** (96.1)	**44.9** (1.8)

Mean frequencies of correct responses and reaction times (SE in brackets) across strongly and weakly lateralized participants for favorable and unfavorable conditions. Results for AI_M based on accuracy are on the left hand, results for AI_M based on reaction time on the right hand. Note that chance level is at 25%.

Correlation between degree of asymmetry and parallel task performance

Bivariate correlations with AI_M (based on accuracy and reaction times) and the frequency of correct responses and reaction times in the parallel task were calculated (see Table 2 below). We found a significant positive correlation between AI_M based on accuracy and the reaction times in the favorable condition ($r = .37$, $p = .037$), indicating slower responses in these participants who were more lateralized. No further correlations between AI_M and performance in the parallel task were significant (all $r \leq .28$, all $p \geq .128$).

Table 2

Performance parallel task		**AI_M (based on accuracy)**	**AI_M (based on reaction time)**
Correct responses	Favorable condition	-.275	-.202
	Unfavorable condition	-.027	-.012
Reaction time	Favorable condition	**.370***	.220
	Unfavorable condition	.267	.237

Pearson product moment correlation coefficients and associated probability (two-tail) between mean asymmetry index (AI_M) based on either accuracy (left hand) or reaction times in the single tasks (right hand) and frequency of correct responses and reaction times in the parallel task. Bold values indicate $^*p < .05$.

Is the advantage of a less lateralized brain in parallel processing a result of single processing?

The previous analyses cannot clearly answer the question whether the superior performance of the less lateralized participants is only restricted to the parallel task, or whether less lateralized participants were also better in the single tasks and just maintain their superiority in the parallel task. However, the classification in less or more lateralized participants is based on a mean asymmetry index (AI_M) which itself has been obtained from the performances in the LVF or RVF in the single tasks. Thus, FCAs and performance are interrelated, making it difficult to disentangle both measures. We try to address this issue by restricting any further analysis to reaction times in single tasks, when AI_M was based on accuracy and by restricting our analyses to accuracy in single tasks, when AI_M was based on reaction times. Nevertheless, reaction time and accuracy in the single tasks were not independent of each other, so any result should be interpreted carefully.

We repeated the 2 × 2 ANOVA we computed for the *single tasks* (with hand and VHF as between-participants factors), but now with group (less vs. more lateralized) as between-participants factor, resulting in a 2 × 2 × 2 mixed ANOVA. When the median split was based on accuracy, less lateralized participants responded faster in the face and lexical decision task, as expressed by main effects of group for faces ($F(1,30) = 8.5$, $p = .007$, $\eta^2 = 22.1$) and words ($F(1,30) = 11.8$, $p = .002$, $\eta^2 = 28.2$). Accordingly, when the analysis was based on reaction times, less lateralized participants responded more accurate in the face ($F(1,30) = .4$, $p = .523$, $\eta^2 = 1.4$) but significantly more accurately in the lexical decision task ($F(1,30) = 10.2$, $p = .003$, $\eta^2 = 25.4$).

Discussion

According to the hypothesis of parallel processing it has been claimed that one reason why FCAs have evolved is because they allow two different or complementary processes simultaneously. This has been supported by studies on chicks, fish, and marmosets (Dadda & Bisazza, 2006; Dharmaretnam & Rogers, 2005; Rogers, 2006;

Rogers et al., 2004; Rogers, 2000). In the present study, we aimed to test this hypothesis in humans. In accordance with animal studies, we hypothesized that participants with strong FCAs would outperform less lateralized participants in a parallel-task paradigm. However, we found the exact opposite: Less lateralized participants responded faster and more accurate than more lateralized participants. We also found evidence for a better performance of less lateralized participants in the single tasks, making it difficult to disentangle whether the superiority of the less lateralized participants is attributable to a better parallel or "single"-processing. But wherever the advantage of the less lateralized participants stem from, our data – at first glance – are not in alignment with the strong version of the parallel-processing theory.

This raises a number of questions: First, why did our results differ fundamentally from previous animal studies? Second, which neural mechanisms might account for the superiority in parallel (and possibly single) processing of the less lateralized participants? Third, what implications can be derived from our data for the evolution of FCAs?

Animal Studies

At a first glance, our results seem to be fundamentally different to previous animal studies. While the species tested up to now were more efficient in dual tasks when being highly lateralized (Dadda & Bisazza, 2006; Dharmaretnam & Rogers, 2005; Rogers, 2006; Rogers et al., 2004; Rogers, 2000)., we obtained the reverse data pattern. However, as outlined in the introduction, our differing results were obtained with a different experimental design. In contrast to chicks, for example, who were allowed to "choose" which eye or which hemisphere to use at a certain time, the stimulus presentation to each hemisphere of the participants in the present study was experimentally constrained in terms of side and time point. Thus, our data pattern probably does not reflect a species but, at least more likely, a design difference. A second point of divergence are the less lateralized individuals. While they represent the lower half of the normal fluctuation in case of our human participants, they are, for the avian studies, constituted by dark-incubated chicks (Rogers et al., 2004). These animals lack an asymmetrical prehatch light input and substantially differ in terms of asymmetrical behavior and anatomy from light-reared chicks (Rogers, 2006). Thus, the difference between lateralized and non-lateralized individuals is probably smaller in our participants.

It is important to note at this point that we obtained highly significant differences between the more and the less lateralized participants. So, we did not find the expected pattern. But we discovered an equally fascinating effect into the reverse direction. We therefore have to discuss why participants with lower asymmetry scores obtain superior results in our parallel processing paradigm. This is what we will discuss in the next section.

The role of the corpus callosum

In the following we will argue that that interhemispheric transfer via the corpus callosum plays a key role in understanding why an increase of asymmetry reduces performance in our dual task paradigm. First of all, several neuropsychological models suggest that interhemispheric cross-talk is an essential mechanism in establishing FCAs. The most widespread view in explaining FCAs by callosal mechanisms is reciprocal inhibition in which a stimulus-specific activation of one hemisphere inhibits the other one during task processing (Chiarello & Maxfield, 1996; Cook, 1984). Second, transecting the corpus callosum affects parallel processing. Split brain patients and neurologically healthy participants had to search for a target item in stimulus arrays that were presented unilaterally either in the LVF or RVF or in both VHF (bilaterally). In the control group, the search rate between the bilateral and unilateral condition did not differ, whereas split-brain patients responded about twice as fast for the bilateral condition than for the unilateral arrays (Arguin et al., 2000; Luck et al., 1989). The authors conclude that after resection of the corpus callosum, split-brain patients are capable of directing attention to both VHF simultaneously. Similarly, it has been shown that callosotomized monkeys show less interference between the two hemispheres than neurologically intact monkeys when two concurrent stimuli are presented to each visual field (Ringo, Doty & Demeter, 1991). Given that interhemispheric transfer is essential for FCAs and parallel processing, why should this lead to a better performance of less lateralized participants?

The re-analysis of the data suggests that the superiority of the less lateralized participants in the parallel condition might have resulted from a superiority in the single condition. One should bear in mind, however, that even in the single condition both hemispheres are involved. Hemispheric asymmetries always represent only relative differences between hemispheres. Therefore, the single condition might also involve parallel processing albeit reduced to a minimum. In either case a model has to explain both the superiority of the less lateralized participants in the parallel and in the single task condition.

We propose that less lateralized participants benefit from a better cooperation between hemispheres. Although the right hemisphere is superior in processing faces and the left hemisphere in processing words, the contralateral, non-specialized hemisphere contains at least some capabilities for processing faces or words. This can be seen, for instance, from our data in the single condition or from neuroimaging studies which typically reveal bilateral activations, though with stronger activations in the specialized hemisphere (Carreiras et al., 2007; Ishai, Schmidt & Boesiger, 2005; Nettleton & Bradshaw, 1983). Via interhemispheric transfer the non-specialized hemisphere might assist the superior one proportional to its own capabilities. However, the more capabilities the non-specialized hemisphere has, the less is the function lateralized, resulting in an enhanced performance of the less lateralized group. But an enhanced cooperation between the hemispheres would not only be beneficial for the parallel condition, which might account for the superiority of the less lateralized participants in the single condition. This nicely fits the data of Ladavas and Umilta (1983), who also found that less lateralized participants responded faster than more lateralized ones in a single task paradigm. Although we can only speculate about the underlying neural mechanisms of our results, interhemispheric transfer might play a crucial role.

Conclusions

What implications can we derive from our data about the evolution of FCAs and the parallel-processing hypothesis? Prima facie our data suggest that parallel (and single) processing in humans is enhanced with a rather symmetric brain. This is true at least for the strong version of the parallel-processing hypothesis as used here as a starting point.

This strong version posits that lateralized, instantaneous and complementary tasks are performed more efficiently with a highly lateralized brain. Our data show that this conception is certainly wrong and that even the reverse applies.

This, however, does not necessarily mean that the parallel processing hypothesis of the evolution of asymmetries has to be abandoned. It has, however, to be more precisely specified. It is possible that tasks that allow participants to more freely allocate resources over tasks, hemispheres and time might reveal an advantage of being asymmetric. If this would be the case, the evolutionary advantage of FCAs might come into play when individuals are allowed to sequence their complementary tasks according to their own mental strategy. They might then switch to the highly specialized and asymmetrically organized system when focusing on a certain problem.

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Chapter IV

In the previous chapter a specific cognitive process was investigated that is supposed to be *enhanced by* hemispheric asymmetries, namely parallel processing. This chapter deals with a specific cognitive function that is supposed to be enhanced by, and *rely on,* hemispheric asymmetries, namely the ability to discriminate left from right. The idea that only an asymmetric organism is able to tell the difference between left and right, was introduced by Ernst Mach, an Austrian philosopher. On a purely theoretical basis he argued that asymmetry is a prerequisite for discriminating left from right (1897). Chris McManus (2002) nicely illustrated the rationale behind this idea with the example of a perfectly symmetrical machine: This perfectly symmetrical machine, say a robot, has learned to make an asymmetric response to a certain stimulus, for example, lift the right arm when the letter 'p' is presented. If a mirror-image of the letter 'p' is presented, a 'q', a perfectly symmetrical robot would inevitably produce a mirror-image response, that is, lifting its left arm. Conversely, only an asymmetric machine would be able to raise its right arm as a response to 'p' and its left arm to a non-mirror-imaged stimulus like 'u'. This however, is exactly what human beings do when they are asked to lift their left or right arm, since 'left' and 'right' are arbitrary phonemes. Corballis and Beale (1976, 1971, 1970) picked up this idea and suggested that the lateralized brain in particular is the prerequisite for left-right discrimination. They further argued that a more asymmetric brain would be associated with enhanced left-right discrimination. The next study tested this assumption with a special focus on sex differences. Women are supposed to be less lateralized and to have more difficulty with left-right confusion. Moreover, the first study raised the possibility that the relationship between lateralization and cognitive performance might be sex-dependent.

Cortex, in press

Sex differences in left-right confusion depend on hemispheric asymmetry

Marco Hirnstein, Sebastian Ocklenburg, Daniel Schneider, Markus Hausmann

Abstract

Numerous studies have reported that women believe they are more susceptible to left-right confusion than men. Indeed, some studies have also found sex differences in behavioral tasks. It has been suggested that women have more difficulties with left-right discrimination, because they are less lateralized than men and a lower degree of lateralization might lead to more left-right confusion (LRC). However, those studies reporting more left-right confusion for women have been criticized because the tasks that have been used involved mental rotation, a spatial ability in which men typically excel. In the present study, 34 right handed women and 31 right-handed men completed two behavioral left-right discrimination tasks, in which mental rotation was either experimentally controlled for or was not needed. To measure the degree of hemispheric asymmetry participants also completed a dichotic listening test. Although women were not less lateralized than men, both tasks consistently revealed that women were more susceptible to left-right confusion than men. However, only women with a significant right ear advantage in the dichotic listening test had more difficulties in LRC tasks than men. There was no sex difference in less lateralized participants. This finding suggests that the impact of functional verbal asymmetries on LRC is mediated by sex.

Introduction

Discriminating left from right is a useful and sometimes crucial (e.g. driving) ability in human everyday life, which is acquired through different stages in childhood. For instance, children at seven years of age are able to correctly discriminate their own left and right body parts but even at 11 years of age only about 50% of the children are able to apply the word left and right to other persons correctly (Dellatolas et al., 1998; Rigal, 1994). According to Benton (1968) an adult level of left-right orientation is normally attained at 12 years of age. However, there are still inter-individual differences in the performance of left-right discrimination in adults, particularly between males and females.

Previous research unequivocally suggests that women believe their performance is inferior to that of men when discriminating left from right. In an early study by Wolf (1973), physicians and their spouses were asked whether they have difficulties in quickly identifying left versus right. Only 8.8% of the males but 17.5% of the females answered they get confused “frequently” or “all the time”. Since then, many other self-evaluation studies have revealed that women rate themselves more susceptible to left-right confusion (LRC) than men (Hannay et al., 1990; Harris & Gitterman, 1978; Jaspers-Fayer & Peters, 2005; Jordan et al., 2006; Snyder, 1991; Teng & Lee, 1982; Williams et al., 1993). Williams et al. (1993) found a relationship between self-ratings in LRC and social desirability for women but not for men, suggesting that sex differences in self-ratings might simply reflect a gender stereotype. Accordingly, this study failed to show any sex differences in a behavioral LRC task (see also Hannay et al., 1990; Hannay et al., 1983).

Whether sex differences in self-rating actually reflect sex differences in performance remain controversial. One of the first experimental studies that investigated behavioral performance was carried out by Bakan and Putnam (1974). Their participants, 400 undergraduate students, accomplished the Laterality Discrimination Test (Culver, 1969), in which they were asked to label pictures of human body parts as left or right. In fact, females had higher error rates than males (for more recent studies see Ofte, 2002; Ofte & Hugdahl, 2002). Similarly, Snyder (1991) found that men responded faster in the Right-Left Orientation Test (Benton, 1983) in which participants had to manually localize lateral body parts in response to the examiner's commands (e.g. "Touch your right ear with your right hand."). Moreover, reaction times in these tasks were moderately correlated with self-evaluated left-right confusability, indicating that self-evaluation possesses at least some behavioral validity.

However, as Jordan et al. (2006) pointed out, those behavioral studies that found sex differences in LRC might be confounded by sex differences in mental rotation. Mental rotation refers to the ability to rotate mental representations of two- and three-dimensional objects and is known to be one of the most sex-sensitive cognitive abilities, with men outperforming women by about one standard deviation (Linn & Petersen, 1985; Masters & Sanders, 1993; Peters et al., 1995; Voyer et al., 1995). Indeed, mental rotation has often been involved in LRC tasks. For example, Ofte and Hugdahl (Ofte, 2002; Ofte & Hugdahl, 2002) presented their participants human stick figures which were either viewed from the front or back with arms outstretched or crossed. Participants were then asked to mark with a pen either the right or left hand. In other studies (Snyder, 1991; Bukan & Putnam, 1974), participants were asked to label photographs of body parts depicted from different viewing positions or label body parts of people sitting opposite to them as left or right (Culver, 1969; Benton, 1959). In all those tasks participants have to abandon an egocentric point of view and take another person's perspective – a cognitive manipulation which involves a certain degree of mental rotation. Hence, the observed sex differences in LRC might be superimposed on mental rotation and it is crucial, therefore, to control mental rotation in left-right discrimination when evaluating sex differences.

The first attempt to take mental rotation into account during LRC was made by Jordan et al. (2006). In this study, participants had to indicate via a button press whether a bunch of pencils presented on photographs was to the left or right of an iced-tea can. No sex difference in accuracy or reaction time emerged. Due to the simplicity of this task, the authors carried out a second experiment, in which women and men had to navigate through a virtual reality maze, while making several left-right decisions. Here, a significant sex difference was found, with men navigating faster through the maze than women. Since the latter task was significantly related to mental rotation performance, the authors concluded that sex differences in LRC do not emerge in simple tasks, but in difficult tasks when mental rotation is involved.

However, we hypothesize that hemispheric asymmetries are another factor of crucial importance for potential sex differences in LRC. First of all, there is evidence showing that LRC depends particularly on the left hemisphere. For example, Sholl and Egeth (1981) have demonstrated that LRC is based on verbal labeling, i.e. participants do not mix up left and right, but have difficulties with labeling the directions correctly as 'left' or 'right'. Since labeling is a verbal process, it probably involves the language dominant left hemisphere. Moreover, patients suffering from Gerstmann's syndrome, a neurological disorder characterized by four major symptoms, agraphia, acalculia, finger agnosia and LRC, (Gold et al., 1995; Gerstmann, 1940) have lesions in the angular gyrus or supramarginal gyrus of the *left* hemisphere. Further empirical evidence for a specific involvement of the left hemisphere comes from a study of Hannay et al. (1983) who measured regional cerebral blood flow during the Laterality Discrimination Test for men and women separately. Activations in bilateral occipital and left parietal areas were found for both sexes. In men, however, better performance in left-right discrimination was associated with less activation in the left occipital lobe. These findings suggest that if LRC and hemispheric asymmetries are linked, sex differences in hemispheric asymmetries might also underlie sex differences in LRC. In fact, women are generally considered as being less lateralized than men (e.g. Hausmann & Güntürkün, 1999; McGlone, 1980).

Corballis and Beale (1976, 1970) argued that a perfectly bilaterally symmetrical organism could not respond differentially to a stimulus and its mirror-image. Conversely, a lateralized brain serves as a prerequisite for left-right discrimination. This could imply that stronger lateralization might be associated with less LRC. Following this rationale, women should be more susceptible to LRC, because they are less lateralized than men. However, the empirical evidence for this notion is rather sparse possibly because those studies that found more LRC in women are confounded by mental rotation as indicated above. Other researchers have tried to test Corballis and Beale's notion by comparing right- with left-handers (the latter are also supposed to be less lateralized). The results have been contradictory. While Silverman et al. (1966) found that left- and mixed-handers performed more poorly on left-right discrimination tasks (see also Hannay et al., 1990; Harris and Gitterman, 1978), other studies failed to find significant effects of handedness (Bakan & Putnam, 1974; Maki et al., 1979; Snyder, 1991).

One explanation for this inconsistency might be inappropriate measurement of hemispheric asymmetry, or that measurement was lacking altogether. Instead of measuring the degree of hemispheric asymmetry directly, it was simply assumed that women/left-handers are less lateralized than men/right-handers (e.g. Bakan & Putnam, 1974). Also, as pointed out above, LRC might depend on verbal labeling. It is thus reasonable to assume that hemispheric asymmetries in language are particularly relevant for LRC. Although handedness is related to language lateralization, it is more appropriate to measure the degree of language lateralization more directly, for example by using a dichotic listening task.

The purpose of present study is twofold: Firstly, this study investigates whether sex differences in LRC do exist, if mental rotation is controlled for. Secondly, we want to examine whether reduced lateralization (in language) is associated with an increase in LRC (Corballis & Beale, 1976; 1970) and whether potential sex differences in LRC are based on reduced lateralization in women. In contrast to previous studies and due to the importance of language lateralization, a dichotic listening test was used to determine the degree of lateralization. In addition, the present study addresses whether self-ratings in LRC are related to performance in those LRC tasks used here.

Methods and Results

Participants

Overall, 65 neurologically healthy women (N = 34) and men (N=31) participated in the present study. Students from different faculties of the Ruhr-University Bochum were tested, with the vast majority being psychology undergraduates. The mean age for women was 24.12 years (SD = 6.57) and 25.65 years (SD = 4.30) for men. All participants were right-handed, as determined by the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). The laterality-index, provided by this test is calculated by $LQ = [(R-L)/(R+L)] \times 100$, resulting in values between –100 and +100. Positive values indicate a preference for the right hand, while negative values indicate left handedness. Women had a mean LQ of 89.14 ($SD = 15.47$, range: 50-100), while the mean LQ for men was 90.11 ($SD = 12.54$, range: 62.5-100). There was no sex difference in LQ ($t(63) = .28$, $p = .78$).

Procedure

Participants started the experiment with two behavioral experiments, the 'Left-right commands task' and the 'Pointing-hands task', in a counterbalanced order. Subsequently, they completed a dichotic listening test, the EHI and a left-right self-rating questionnaire. Performing the behavioral tasks first prevented possible stereotype activation effects of the self-rating questionnaire.

Dichotic listening

The degree of language lateralization was assessed by the Fused Rhymed Words Test (FRWT) by Hättig and Beier (2000), a German adaptation of a dichotic listening test by Wexler and Halwes (1983). In previous studies, the FRWT achieved a concordance rate of 86% with the WADA-tests and a test-retest reliability of .65 to .87 (Hättig & Beier, 2000). The test consists of ten pairs of rhyming words which differ only in the initial letter. When presented dichotically, paired words fuse into a single percept. After each trial, participants were asked to indicate the word they had heard. The test starts with 40 unilateral practice trials, followed by four blocks of 40 trials, resulting in a total of 160 trials. In line with Hättig and Beier (2000), the number of items correctly reported from left (LOP) and right ear points (ROP) were used to calculate the degree of asymmetry (λ) as $\lambda = \ln(ROP/LOP)$, with values ranging from –4.38 to +4.38. Negative values indicate a left ear advantage (LEA), that is, a presumed right-hemispheric advantage for language, while positive values indicate a right ear advantage (REA), a left-hemispheric advantage for language. A value of 0 indicates no ear/hemisphere advantage. As expected, 57 out of 65 participants had a right ear/left-hemispheric language advantage. To investigate the relationship between verbal hemispheric asymmetry and LRC, we checked for each individual via Chi-square tests (see Wexler, Halwes & Heninger, 1981) whether the LEA or REA (i.e. the relative difference between LOP and ROP) was actually significant. Of 65 participants, 37 (19 women, 18 men) showed a significant REA, four a significant LEA (two women, two men) and 24 (13 women, 11 men) no significant ear advantage. Due to the small number of LEA participants, these participants were excluded from subsequent analyses. Of those remaining 61 participants, women had a mean λ of 1.64 (SD = 1.19, range –1.1 - 3.99) and men a mean λ of 1.49 (SD = 1.23, range –.81 - 3.99). There was no sex difference in λ ($t(59) = .49$, $p = .63$).

Behavioral LRC tests

Left-right commands task

Method

While in many previous behavioral LRC experiments, participants typically responded to visually presented stimuli, in everyday situations people often respond to verbal instructions, such as “Turn left” or “Please, give me the book to your right”, etc. In the Right-Left Orientation Test (Benton, 1959), participants followed verbal commands, but as pointed out above, the results of this test might be confounded by mental rotation. The ‘Left-right commands’ task thus involved following verbal instructions, but did not require mental rotation.

Participants were sitting upright on a chair with their hands on their knees (starting position). All participants were recorded with a video camera. The verbal instructions consisted of sixty verbal commands, 20 simple, 20 complex and 20 neutral commands in a pseudorandomized order. Verbal commands were presented via loudspeakers (approximately 2m away from the participants). In the simple condition, participants were asked to move one part of their body, e.g. “Lift your right foot” or “Lift your left arm”. To increase the probability of LRC, participants were confronted with more complex verbal commands which included two left/right commands at the same time, such as “Touch your right ear with your left hand” or “Lift your right hand and your left foot”. In the control condition, participants were asked to e.g. “Raise both arms” or “Fold your hands”. To increase the probability of LRC, a time limit of two seconds was set for each command. Thus after two seconds the next command started. Participants were asked to follow the commands and, after the appropriate response, to return to their starting position. Only if participants followed the command correctly, e.g. “Lift your right foot”, but mixed up left and right, i.e. they lifted the left instead of the correct right foot, was this considered as LRC. LRC error percentage scores were calculated for both simple and complex commands.

Results

Table 1

Error rate in %		**Simple Condition**	**Complex condition**
Women	REA	**1.58** (.56)	**7.90** (1.16)
	No ear advantage	**2.31** (.67)	**3.85** (1.40)
Men	REA	**0**	**1.94** (1.19)
	No ear advantage	**0**	**3.18** (1.52)

Mean error rate in % (SE in brackets) for women and men of different ear advantages across the simple and complex condition in the 'Left-right commands task'.

A mixed 2 × 2 × 2 ANOVA with difficulty (simple, complex) as a repeated measures factor and sex (males, females) and lateralization group (significant REA, no ear advantage) as between-participant factors was computed (Table 1). Throughout, effect sizes are given as the proportion of variance accounted for (partial η^2) and p-levels for post hoc t-tests were adjusted using Bonferroni correction. Overall, women made more errors than men (main effect sex: $F(1,57) = 11.26$, $p = .001$, $\eta^2 = .17$) and since there was no sex by difficulty interaction ($F(1,57) = 1.00$, $p = .32$, $\eta^2 = .02$), this was true for the simple ($t(31) = 3.22$, $p = .003$) and the complex condition ($t(59) = 2.89$, $p = .005$). However, lateralization group interacted with sex and difficulty ($F(1,57) = 4.88$, $p = .031$, $\eta^2 = .08$). As can be seen in Table 1, men and women with no ear advantage performed about equally well in the complex condition ($t(22) = .40$, $p = .70$), whereas the performance of women with significant REA was significantly worse than that of men with significant REA ($t(31.13) = 3.31$, $p = .002$). In the simple condition, no sex differences emerged (all $t < 2.51$, ns). Finally, participants showed, as expected, more LRC in the complex than in the simple condition, as indicated by a main effect of difficulty ($F(1,57) = 22.71$, $p < .001$, $\eta^2 = .29$).

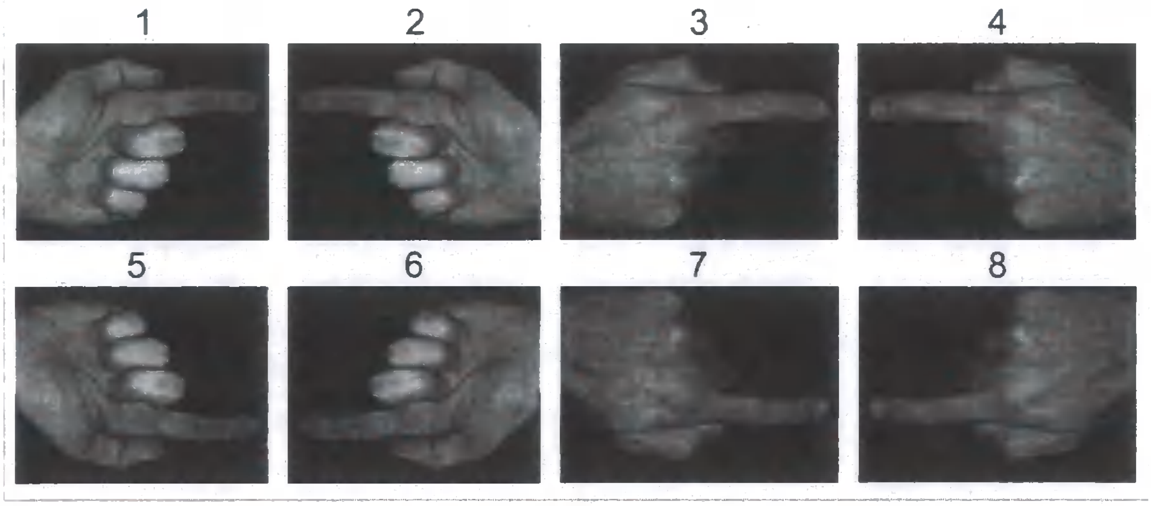
Pointing-hands task

Method

For the ‘Pointing-hands task’, stimuli were adopted from Brandt and Mackavey (1981). The stimulus set consists of photographs of left and right hands taken in eight different orientations (Figure 1). In the first condition, all hands pointed either upwards- or downwards and participants were instructed to label them as “up” or “down”. This condition (“up/down-pointing”) served as a control condition. In the second condition, all hands pointed towards the left or right. Accordingly, the participants had to label them as pointing towards the “left” or “right” (“left/right-pointing”). The left-right-pointing condition requires no mental rotation. In the third condition, hand stimuli were presented in the same orientation as in condition two, but now participants had to identify whether they saw a *left* or *right hand*, regardless of its pointing direction (“left/right-hand”). As can be seen from Figure 1, hand stimuli 3) to 8) need to be mentally rotated because they are presented in unusual orientations (rotated hands). In contrast, hand stimuli 1) and 2) are shown in more familiar orientations, and thus mental rotation was assumed to be less essential (not-rotated hands). If sex differences in LRC result from mental rotation, they should only emerge in condition three and particularly for the rotated hands. However, sex differences should be minimal for not-rotated hands.

The participants completed all three conditions in a randomized order. The stimuli were presented separately for two seconds on a PC screen. Each stimulus was presented ten times in a pseudorandomized order, resulting in 80 trials for each condition. During each trial, participants were asked to indicate verbally the pointing direction, i.e., "up/down" (up/down-pointing condition), "left/right" (left/right-pointing condition) or whether a left or right hand was presented (left/right-hand condition). To increase the probability of LRC, a response was only considered to be correct if it was made within two seconds. Error rates (in percent) were used as the dependent variable.

Figure 1



Stimuli of the 'Pointing-hands task'. Note that hands 1) and 2) are in rather familiar (not-rotated) orientations whereas hands 3) – 8) are in rather unfamiliar (rotated) orientations.

Table 2

Error rate in %		**up/down-pointing**	**left/right-pointing**	**left/right-hand**		
				Total	**Rotated hands**	**Not-rotated hands**
Women	REA	**.22**	**.44**	**30.37**	**35.39**	**15.29**
		(.13)	(.18)	(3.28)	(3.99)	(2.57)
	No ear advantage	**.29**	**.58**	**18.56**	**21.54**	**9.62**
		(.14)	(.20)	(3.76)	(4.56)	(3.72)
Men	REA	**.14**	**.28**	**8.61**	**10.28**	**3.61**
		(.12)	(.17)	(3.19)	(3.88)	(2.50)
	No ear advantage	**.11**	**.11**	**18.30**	**22.27**	**6.36**
		(.16)	(.22)	(4.08)	(4.96)	(3.20)

Mean error rate in % (SE in brackets) for women and men of different ear advantages across all conditions in the 'Pointing-hands-task'.

Two participants had to be excluded because their responses have not been recorded due to technical problems. The data from the remaining 30 women and 29 men were analyzed with a mixed 3 × 2 × 2 ANOVA with condition (up/down-pointing, left/right-pointing, left/right-hand) as repeated measures and sex and lateralization group (significant REA, no ear advantage) as between-participants factors (Table 2). As in the 'Left-right commands task', women committed more errors than men (main effect sex: $F(1,55) = 9.86$, $p = .003$, $\eta^2 = .15$). Also, all participants made more errors in the left/right-hand than in the up/down-pointing or left/right-pointing condition (main effect condition: $F(2,110) = 108.74$, $p < .001$, $\eta^2 = .66$). A significant interaction between sex and condition ($F(2,110) = 9.07$, $p < .001$, $\eta^2 = .14$) further revealed that women showed LRC particularly in the difficult left/right-hand condition ($t(57) = 3.47$, $p = .001$, whereas no sex differences emerged for up/down-pointing ($t(59) = .81$, $p = .42$) or left/right-pointing ($t(59) = 1.62$, $p = .11$). Moreover, sex interacted significantly with lateralization group ($F(1,55) = 8.37$, $p = .005$, $\eta^2 = .13$). Whereas men and women with no ear advantage did not differ in LRC ($t(22) = .14$, $p = .89$), women with significant REA were clearly outperformed by men with significant REA ($t(26.69) = 4.27$, $p < .001$). Finally, the three-way interaction between sex, lateralization group and condition was significant ($F(2,110) = 9.17$, $p < .001$, $\eta^2 = .14$). The interaction was mainly driven by the sex difference for participants with significant REA in the left/right hand condition. Here, mean error rates in women with significant REA were about four times the size of those in men with significant REA.

To further investigate whether women only made more LRC errors in the left/right-hand condition because of mental rotation, a separate 2 × 2 × 2 ANOVA with stimulus set (rotated, not-rotated hands) as a repeated measures factor and sex and lateralization group as between-participants factors was computed (Table 2). As expected, the analysis revealed strong main effects of stimulus set ($F(1,55) = 41.32$, $p < .0001$, $\eta^2 = .43$) and sex ($F(1,55) = 10.72$, $p = .002$, $\eta^2 = .16$), indicating higher error rates for the rotated-hands stimuli and women, respectively. However, stimulus set did not interact with sex ($F(1,55) = 1.24$, $p = .27$, $\eta^2 = .02$), i.e. women showed more LRC for both rotated hands (women: Mean = 29.39% ± SE = 3.43; men: 14.83% ± 2.94; $t(57) = 3.21$, $p = .002$) and not-rotated hands (women: 12.83% ± 2.36; men: 4.66% ± 1.42; $t(47.78) = 2.97$, $p = .005$). Again, there was no sex difference in LRC in participants with no ear advantage ($t(22) = .23$, $p = .81$), but men with significant REA clearly outperformed women with significant REA ($t(24.78) = 5.44$, $p < .001$), as indicated by a sex by lateralization group interaction ($F(1,55) = 8.15$, $p = .006$, $\eta^2 = .13$). Finally, there was a three-way interaction between sex, lateralization group and stimulus set ($F(1,55) = 4.21$, $p = .045$, $\eta^2 = .07$). Men with significant REA revealed lower error rates than men with no ear advantage, particularly when LR judgments were based on rotated hand stimuli. In contrast, women with significant REA showed higher mean error rates than women with no ear advantage on rotated hand stimuli.

Left-right self-rating questionnaire

Method

We adopted the LRC self-rating questionnaire from Jordan et al. (2006). The questionnaire consists of eight items. The first four items were derived from Hannay et al. (1990) and the last four items from Jaspers-Fayer and Peters (2005; see also Jordan et al., 2006). For each item participants had to indicate on a five-point scale whether they have got "*no problems at all*" ("1") or "*severe*" problems ("5"). According to Jordan et al. (2006) the first four items specifically deal with left-right judgments (LRC-items, e.g. "Do you know left from right?"), whereas the other four items are more generalized directional questions (DIR-items, e.g. "Do you consider yourself to have a good sense of direction?"). Means of LRC- and DIR-Items were calculated for 59 participants (30 women, 29 men). Two participants had to be discarded from analyses because they did not answer all questions.

Results

A mixed 2 × 2 × 2 ANOVA with between-participants factors sex and lateralization group (significant REA, no ear advantage) and question type (LRC, DIR) as repeated measures was calculated (Table 3). Participants rated themselves more prone to LRC with situations described in DIR-questions than those described in LRC-questions (main effect question type: $F(1,55) = 20.97$; $p < .001$, $\eta^2 = .28$). Although self-ratings were rather low for both sexes (see table 3), women judged themselves less capable in differentiating left from right than men, indicated by a significant main effect of sex ($F(1,55) = 11.17$; $p = .001$, $\eta^2 = .17$). No further effect approached significance (all $F(1,55) \leq 1.98$; $p \geq .17$, $\eta^2 \leq .04$).

Table 3

Mean		**LRC Questions**	**DIR Questions**
Women	**REA**	**1.79**	**2.51**
		(.15)	(.17)
	No ear advantage	**1.961**	**2.48**
		(.19)	(.20)
Men	**REA**	**1.42**	**1.78**
		(.15)	(.17)
	No ear advantage	**1.64**	**1.93**
		(.19)	(.21)

Mean LRC and DIR self-ratings (SE in brackets) on a five-point scale (1 = "no problems at all", 5 = "severe problems") for women and men of different ear advantages.

Relationship of LRC, asymmetry and LRC self-rating

The previous analyses have suggested that verbal hemispheric asymmetries affect left-right performances of men and women. We thus wanted to investigate the relationship between LRC and lateralization more thoroughly; specifically whether there is a linear relationship as implied by Corballis and Beale (1976; 1970). Also, we were interested in whether LRC self-ratings can predict LRC performance for both sexes. Therefore, multiple linear regressions were carried out, separately for men and women, with LRC performance in the 'Left-right commands' (separately for simple and complex condition) and the 'Pointing-hands task' (separately for rotated and not-rotated hands stimuli of the left/right-hand condition) as the dependent variable and asymmetry (λ for dichotic listening, LQ for hand preference) and self-rating (LRC and DIR questions) as predictors. For males, no multiple regression was calculated for the simple 'Left-right commands task', since none of the men made any mistakes. For all other LRC performances, no significant model was found (all $F(4,28) \leq 2.60$, $p \geq .06$). For women, multiple regressions revealed a significant model for the complex 'Left-right commands task' (*F*(4,29) = 4.66, *p* = .006) accounting for 43% of variance. Only LRC-questions contributed significantly to the regression (β = .58, *p* = .003), i.e. the more females rated themselves being prone to LRC, the higher was their error rate. Also, a significant model for not-rotated hands in the 'Pointing-hands task' emerged (*F*(4,27) = 4.45, *p* = .008), which accounted for 44% of variance. The model was mainly based on DIR-questions (β = .37, *p* = .038) and LRC-questions (β = .44, *p* = .029). Again, women who rated themselves more prone to LRC indeed revealed higher error rates.

Discussion

The aim of the present study was to investigate the influence of hemispheric asymmetry on sex differences in LRC. Males and females completed two behavioral LRC tasks and a dichotic listening test. Specifically, we intended to answer the following two main questions: (a) Do sex differences appear in LRC tasks which do not require mental rotation? (b) Is LRC performance related to language lateralization? In addition, we were interested in whether (c) sex differences in LRC self-rating reflect sex difference in LRC performance.

Do sex differences appear in tasks which do not require mental rotation?

Both the 'Left-right commands' and the 'Pointing-hands task' revealed robust sex differences accounting for up to 17% of variance (note that effect sizes higher than 14% are considered as large effects (Cohen, 1988). Women clearly made more errors than men, a finding which is in alignment with previous studies (Bakan & Putnam, 1974; Ofte, 2002; Ofte & Hugdahl, 2002; Snyder, 1991). However, those previous studies have been criticized by Jordan et al. (2006), because the reported sex differences in LRC might have been confounded by sex differences in mental rotation. In the present study, however, a profound sex difference was found in the 'Left-right commands task', in which no mental rotation was required. None of the 29 men committed any left-right errors in the simple condition. Also, although in the 'Pointing-hands task' the degree of mental rotation varied (rotated versus not-rotated hands), sex differences in LRC remained stable. These findings clearly suggest, for the first time, that sex differences in LRC exist independently of sex differences in mental rotation.

Is LRC performance related to language lateralization?

It has been suggested that a lower degree of lateralization is associated with more LRC (Corballis & Beale, 1976; 1970). As a result, women, who are assumed to be less lateralized than men, should also be more susceptible to LRC. Indirect support for a link between LRC and hemispheric asymmetry comes from Manga and Ballesteros (1987) who applied a lateralized reaction time task to participants who reported themselves to be highly or less susceptible to LRC. The participants had to decide whether a 'T' presented to the left or right visual field was tilted 45° to the left or right. Participants who rated themselves less susceptible to LRC responded faster when the stimuli were presented in the right than in the left visual field. Participants who rated themselves highly susceptible to LRC did not show any reaction time difference between visual fields. Based on these findings, the authors concluded that participants who are more susceptible to LRC are also less lateralized. However, the present study has demonstrated (see below) that LRC self-ratings are not necessarily a good predictor for actual performance in laboratory-based LRC tasks (see also Jordan et al., 2006).

The present study also challenges the assumption that a reduced lateralization is associated with more LRC (Corballis & Beale, 1976; 1970) and that women are more susceptible to LRC than men because they are less lateralized. Although the present study revealed no sex differences in dichotic listening (and handedness), men and women differed in their susceptibility to LRC. Nevertheless, the presence of a REA in dichotic listening was linked to a sex difference in LRC, supporting the notion that language lateralization is relevant for LRC. Although the relationship between language lateralization and LRC is not linear, women with a significant REA were more highly susceptible to LRC than men with a significant REA, whereas no sex differences in LRC emerged for less lateralized participants (no ear advantage).

Voyer and Ingram (2005) have shown that the right ear/left hemisphere advantage in fused dichotic listening as used in the present study can be a result of a consistent attentional bias. This attentional bias, however, has been suggested to be partly a result of a larger activation of the language dominant left hemisphere, leading to a greater attentional bias towards the right ear (Voyer & Ingram, 2005; Voyer, 2003). Thus, we cannot rule out that hemispheric asymmetries in attention might have additionally affected LRC.

The lack of sex difference in dichotic listening might be explained by the hormonal status in women during testing which has not been controlled for and which was not the focus of the present study. Previous studies have shown that the degree of lateralization can fluctuate during the menstrual cycle (e.g. Hausmann, 2005; Hausmann et al., 2002; Hausmann & Güntürkün, 2000; Holländer et al., 2004; Sanders & Wenmoth, 1998). Future studies might address the question of whether LRC is affected by natural fluctuations in sex hormone levels.

Although women who are strongly lateralized in dichotic listening revealed LRC in the 'Pointing-hands task' particularly when stimuli were rotated and less LRC if they were not-rotated, this does not explain why they are also more prone to LRC in the complex 'Left-right commands task' where no mental rotation was needed. This suggests that deficits in mental rotation are not exclusively responsible for LRC in strongly lateralized women.

The question why the influence of verbal (and maybe attentional) lateralization on LRC differs according to sex remains unanswered. However, the present data indicate that men and women with a similar degree of language lateralization do not necessarily perform equally well in LRC. Possibly, men and women apply different cognitive strategies to solve left-right discrimination problems. Which specific cognitive strategy they employ or whether a specific strategy is superior or not might be partly influenced by the way cognitive skills are organized (and lateralized) in the brain.

Time restrictions in LRC tasks in the present study might have increased the likelihood of LRC in women. Studies that have employed similar tasks but had no time restriction have failed to find sex differences (Teng & Lee, 1982; Snyder, 1991). Time restrictions may increase the probability of LRC since it impedes use of cognitive strategies such as “I know I’m right-handed, so the hand I use for writing indicates right” (McMonnies, 1996). Therefore, sex differences in LRC in the present study might have emerged because women lack the time to apply those strategies adequately. However, the reason why time restrictions should especially affect women with significant REA (and not men with significant REA) remains unclear.

Do sex differences in LRC self-rating reflect sex difference in LRC performance?

In accordance with previous studies women rated themselves as being more prone to LRC than did men (Jordan et al., 2006; Williams et al., 1993; Hannay et al., 1990; Teng & Lee, 1982; Harris & Gitterman, 1978; Wolf, 1973). This effect thus seems to have remained stable for the last 35 years (from 1973 until now). Moreover, a sex difference emerged in the *relationship* between self-rating and actual performance: while in women self-rating questions were significantly related to performance, this was not the case for men, that is, only women rated their left-right discrimination abilities with any degree of accuracy. Interestingly, this result is in alignment with Jordan et al. (2006), who reported a weak correlation between self-ratings and a behavioral LRC task for women, but not for men. Although self-ratings were already relatively low for all participants, they were even lower for men, indicating that men hardly reported having any problems with LRC at all. Possibly, men are just less likely to admit that they have problems with LRC, maybe because this is not in accordance with the stereotype of men being superior in spatial abilities.

One should bear in mind, however, that even though self-ratings had some predictive value, at least in women, they only marginally translate into behavioral sex differences in LRC. Sex differences in LRC should therefore be investigated directly via behavioral tasks instead of self-reports.

Limitation to egocentric bodily stimuli

Apart from the fact that previous studies investigating sex differences in LRC might have been confounded by mental rotation, some of these studies used bodily stimuli while others used non-corporeal objects or navigation. This could have further contributed to inconsistencies between studies focusing on sex differences in LRC, because mental rotation of bodily stimuli activates different brain networks than mental rotation of objects (Blanke et al., 2005; Zacks et al., 1999). In the present study, only egocentric bodily stimuli were used in the 'Pointing-hands task' (mental rotation needed) and in the 'Left-right commands task' (mental rotation not needed). According to Seurinck et al. (2004) there is no sex difference in brain activation when hands need to be rotated. So, it is unlikely that sex differences in LRC in the 'Pointing-hands task' results from sex-specific brain activations. However, it might be interesting to investigate whether similar results can be obtained for non-corporeal objects or extrapersonal/allocentric space.

Handedness and LRC

To investigate potential relationships between lateralization and LRC the present study compared men with women, because women are thought to be less lateralized (e.g. Hausmann & Güntürkün, 1999; McGlone, 1980). Conversely, other researchers have compared right- with left- and mixed-handers, because left- and mixed-handers are thought to be less lateralized (Hellige, 1993). The decision to compare men with women was partly driven by the very inconsistent findings regarding handedness and LRC. Silverman et al. (1966) and Hannay et al. (1990) found left-handers to be more affected by LRC than right-handers, while Jordan et al. (2006) and Bakan and Putnam (1974) found no differences. Snyder (1991) even found no difference in accuracy but reported that left-handers responded faster to left-right decisions than right-handers. These contradictory results might have emerged because LRC was based only on self-reports instead of experimental studies (Jordan et al., 2006, Hannay et al., 1990). The present study has demonstrated that in addition to simply comparing supposedly more and less lateralized participants (such as left- or right-handers), it is important directly to measure the degree of (language) lateralization. However, it would be interesting to compare left- with right-handers, if behavioral LRC tasks are used and hemispheric asymmetries are assessed experimentally.

Conclusion

In sum, the present study suggests that behavioral sex differences in LRC do exist. Women are more susceptible to LRC than men, even if mental rotation is experimentally controlled for. This sex difference in LRC may be mediated by hemispheric asymmetries for verbal material. Women with significant REA had more difficulties with left-right discrimination than men, whereas women without an ear advantage made roughly the same number of left-right errors as men. Hence, in contrast to the literature, our data suggest that whether a high degree of lateralization relates to reduced LRC depends on the participant's sex.

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Chapter V

General Discussion

Hemispheric asymmetries are a basic principle of brain organization and a widespread phenomenon among both animals and humans, suggesting hemispheric asymmetries are evolutionary advantageous. Yet, research on potential evolutionary advantages of hemispheric asymmetries is in its early stages of development. There are a few notions and theories about potential evolutionary advantages of hemispheric asymmetries available, all of them sharing the basic idea that hemispheric asymmetries somehow enhance cognitive processing. However, there is only little direct empirical evidence for either of them, and if there is evidence available, it usually rests on animal studies. The aim of the present thesis was therefore to directly investigate theories about evolutionary advantages of lateralization in humans. The first study examined the general relationship between the degree of lateralization and cognitive performance. The final two studies tested two specific notions about potential advantages of hemispheric asymmetries, according to which a higher degree of lateralization leads to enhanced parallel processing (study two) and enhanced left-right discrimination (study three).

General relationship between degree of lateralization and cognitive performance

To investigate the general relationship between the degree of lateralization and cognitive performance, data from more than 200 participants, who completed two visual half-field tasks (a verbal left-hemispheric and a facial right-hemispheric task), were analyzed (Hirnstein et al., submitted). Two different statistical approaches revealed a similar result. High degrees of lateralization were detrimental for cognitive performance. More specifically, the relationship between the degree of lateralization and the mean cognitive performance was best approximated by an inverted U-shaped curve, that is, optimal cognitive performance was achieved with a single, rather low degree of lateralization and extremely high positive and extremely high negative degrees of lateralization (corresponding to left- and right-hemispheric biases, respectively) were associated with poor cognitive performance. Another interesting finding was that optimal degrees of lateralization were quite distant from populational average degrees of lateralization. For example, the optimal degree of lateralization for the verbal task was a mild right-hemispheric bias, although the vast majority of participants showed a left-hemispheric bias in this task.

Parallel Processing

Study two (Hirnstein, Hausmann & Güntürkün, 2008) investigated the currently prevailing theory about evolutionary advantages of lateralization according to which a lateralized brain enhances parallel processing. It was hypothesized that participants with high degrees of lateralization would outperform participants with low degrees of lateralization when the verbal left-hemispheric and facial right-hemispheric tasks from the previous study had to be performed at the same time. Surprisingly however, less lateralized participants outperformed highly lateralized participants. Also, participants with low degrees of lateralization outperformed participants with high degrees of lateralization when only one of those tasks was performed.

Left-right discrimination

Left-right discrimination is a special case, because it is supposed to not only be enhanced by, but also to rely on, hemispheric asymmetries (Mach, 1897; Corballis & Beale, 1970; 1971; 1976). The last study (Hirnstein et al., in press) therefore tested the hypothesis that participants with high degrees of lateralization are less prone to left-right confusion than participants with low degrees of lateralization. The degree of lateralization was assessed via a dichotic listening test and the ability to discriminate between left and right by two behavioral tasks. Females, who are supposed to be less lateralized than males, indeed made more left-right errors than males. However, they were not less lateralized according to the results of the dichotic listening test. Moreover, contrary to our predictions, highly lateralized female participants had more difficulty with discriminating left from right than less lateralized female participants. In men, less lateralized participants were about as accurate as highly lateralized participants.

Interim summary

Although quite distinct aspects of potential advantages of hemispheric asymmetries in humans were investigated with different methods in the present thesis, one can discern a common pattern: High degrees of lateralization were always detrimental for cognitive functions. A highly lateralized brain was associated with poor cognitive performance in processing of facial and verbal stimuli (studies one and two), parallel processing of facial and verbal stimuli (study two), and left-right discrimination (study three). In turn, enhanced cognitive performance was consistently associated with relatively low degrees of lateralization (studies one, two and three). Hence, all three studies do not just fail to support current theories and notions about evolutionary advantages of lateralization, their results show the exact opposite. The present thesis therefore challenges some long and widely held views about why hemispheric asymmetries are advantageous for humans. First, it challenges the notion of a positive relationship between the degree of lateralization and cognitive performance, that is, that high degrees of lateralization are associated with enhanced cognitive processing and low degrees of lateralization with reduced cognitive processing. Second, it challenges the notion that hemispheric asymmetries are advantageous for parallel processing and left-right discrimination. This finally challenges the inherent assumption of all major theories about potential evolutionary advantages of lateralization, namely that hemispheric asymmetries are advantageous for cognitive processing *per se*. In the next two paragraphs, findings from other studies are taken into account to discuss, whether we may need to reconsider some of the current views as a result of the present findings.

Is the relationship between the degree of lateralization and cognitive performance positive?

The present thesis, alongside other studies, clearly demonstrates that the relationship is not generally positive. In fact, high degrees of lateralization are actually associated with reduced cognitive performance under certain circumstances (e.g. parallel processing) or in certain functions (left-right discrimination, face-discrimination, word-nonword discrimination and word-matching). More specifically, study one implies that an inverted U-shaped relationship between the degree of lateralization and cognitive performance exists. These results are in accordance with a study of Leask and Crow (2006), who reported an inverted U-shaped relationship between the strength of handedness and a couple of manual and cognitive tasks in 10 to 11-year old school children. On the other hand, there are studies available, which show the opposite results. Pure mathematical models (Kosslyn, Sokolov & Chen, 1989; Reggia, Goodall & Shkuro, 1998), an animal study (Güntürkün et al., 2000) and a recent study in humans (Chiarello et al., in press) suggest a positive relationship between hemispheric asymmetries and performance. In addition, Nettle (2003) reported that a higher degree of hand laterality (i.e. stronger left- or right handedness irrespective of whether it is the left or right hand) is associated with higher cognitive abilities. Similarly, Crow et al. (1998), for example, determined lateralization in terms of relative hand skills and reported that participants with no clear left- or right-hand advantage achieved lower scores in tasks said to assess academic skills. Yet these results were obtained from the same dataset that revealed an inverted U-shaped relationship between lateralization and cognitive performance in a later study from the same authors (Leask & Crow, 2006). The latter however, seems to be more reliable. First, in the study by Leask and Crow (2006) participants, who had a hand skill score of zero, were removed from the sample, because it was impossible to tell whether they actually performed poorly or did not complete the test. Second, the earlier study by Crow et al. (1998) used a methodological approach which could have been confounded by interdependencies between lateralization and cognitive performance. In another study participants completed a number of cognitive neuropsychological tests and the activation of their left and right hemisphere during verbal and spatial tasks was measured via functional magnetic resonance imaging. A laterality index derived from the brain activation was positively correlated with performance in a verbal task and a spatial task of the neuropsychological test battery. Participants with a strong left-hemispheric bias in a verbal task showed higher verbal IQs and participants with a strong right-hemispheric bias in a spatial task showed higher scores in visuospatial abilities (Everts et al., 2009). Finally, Boles, Barth and Merrill (2008) found positive and negative relationships between lateralization and performance depending on the task used. However, this study, too, might be confounded by interdependencies between left and right visual half-field performances. Given the contradictory data, it might be questionable, whether an inverted U-shaped relationship between hemispheric asymmetries and cognitive performance as reported in the first study reported here and by Leask and Crow (2006) is the general principle. However, it demonstrates that the relationship between degree of lateralization and cognitive performance is clearly not always positive. Moreover, it suggests that the notion of a *linear* relationship – be it positive or negative – might be an oversimplification.

Do hemispheric asymmetries enhance parallel processing and left-right discrimination?

Study two and three suggest that high degrees of lateralization are detrimental for parallel processing and left-right discrimination, respectively. A lack of previous studies makes it difficult to evaluate these findings. With respect to parallel processing, there are at least two animal studies, one with chicks (Rogers, Zucca & Vallortigara, 2004) and one with fish (Dadda & Bisazza, 2006), which support the notion that lateralization facilitates parallel processing. However, to our knowledge there are no studies, except for our own, that investigated whether lateralization enhances parallel processing *in humans*. While carrying out two tasks simultaneously has been extensively investigated in humans, to our knowledge no study so far investigated the relationship between the degree of asymmetry and parallel processing. The contradictory results of our study and those animal studies can obviously be explained in two ways: either by differences in the experiments or by differences across the species. In study two we discussed how differences in the experiments could have led to the different outcome (e.g. stimulus presentation and time was experimentally constrained in our visual half-field study, but not in the animal studies). Alternatively however, it cannot be ruled out that lateralization does not facilitate parallel processing in every species. Chicks and fish, for example, lack a corpus callosum and humans do not have laterally placed eyes. Especially the corpus callosum might make a difference since it allows exchanging information between hemispheres. This might also explain why the empirical evidence in animals *with* a corpus callosum is extremely sparse. Only one study in marmosets reports a small negative correlation between handedness and the latency to react to a predator after they had found food, that is, the stronger the hand preference, the faster they reacted to the predator (Rogers, 2006). Yet, it is questionable whether this experiment actually tested parallel processing, because the predator was introduced *after* food was presented. In sum, further studies, particularly with humans, are necessary to reveal whether our *results* are an exception to the finding that lateralization enhances parallel processing or whether *humans* are an exception to the notion that lateralization enhances parallel processing.

When it comes to left-right discrimination, there are a few studies available which investigated hemispheric asymmetries and left-right discrimination. However, the hypothesis that high degrees of lateralization are associated with better left-right discrimination was assessed rather indirectly in these studies. Instead of actually determining the degree of lateralization as we did in study three, it was simply assumed that left-handers are less lateralized that right-handers and women less lateralized than men. This lack of control for the degree of lateralization might explain the contradictory findings of these previous studies. Hence, apart from our study there are hardly any direct, empirical studies on the notion that lateralization enhances left-right discrimination. As in the case of parallel processing, it thus remains to be seen whether our finding of high degrees of lateralization being associated with poor left-right discrimination can be replicated and generalized. Nevertheless, study two and three clearly shed some doubt on whether the notions of lateralization enhancing parallel processing and left-right discrimination might be universally true.

Thus finally, the present thesis also provides evidence against the general notion that lateralization is advantageous for cognitive processing *per se*, an inherent assumption in all theories about evolutionary advantages of hemispheric asymmetries. On the other hand however, one cannot conclude that hemispheric asymmetries are detrimental for cognitive processing per se either, because whether cognitive processing, parallel processing, and left-right discrimination was enhanced (or not) depended on the *degree* of lateralization (high versus low). Hence, the degree of asymmetry seems to play a crucial role for the evolutionary advantages of hemispheric asymmetries. But what could be potential advantages (and disadvantages) of different degrees of lateralization and how and where are they encoded?

The importance of the degree of lateralization: Encoded by genes?

There is considerable evidence that the degree of lateralization is at least partly under genetic control. For instance, the strength of handedness – often regarded as an indicator of the degree of lateralization appears to be heritable. Parents with a strong hand preference usually have offspring, which also has a strong hand preference irrespective of which hand is dominant (Porac & Coren, 1981). This is in accordance with studies in great apes and other nonhuman primate species (Hopkins, 2006) and the classical experiments on mice (Collins, 1985), which demonstrated that the strength of handedness but not the direction of handedness/pawedness can be bred for. Based on these and other studies, Hopkins (2008) argued that the degree of lateralization is of particular importance for the evolution of hemispheric asymmetries and that the degree of lateralization is largely mediated via genes. But if genes encode high and low (and perhaps intermediate) degrees of lateralization by what mechanisms is this genetic variation preserved in the population and what does this imply for the evolution of hemispheric asymmetries?

According to Penke, Denissen and Miller (2007), there are three mechanisms through which genetic variation can be maintained in a population. The first mechanism is selective neutrality. That is, variation in the degree of lateralization is preserved, because the degree of lateralization is not related to the fitness of an organism at all and therefore not subject to selection pressures. In other words, in terms of fitness or adaptiveness it does not matter whether an individual is strongly or weakly lateralized and, as a consequence, both phenotypes remain in the population. The data of the present thesis along with other studies however, suggests that the degree of lateralization is associated with enhanced or reduced cognitive processing, depending on what function is examined. Since cognitive processing is likely to be related to fitness, it seems rather unlikely that hemispheric asymmetries are not related to fitness at all. Also, the fact that hemispheric asymmetries are so widespread among various species suggests they have an adaptive value, although, of course, a wide distribution does not imply per se that a trait is adaptive. Hence, though it cannot be entirely ruled out that the degree of lateralization has no impact on the fitness of an organism, selective neutrality does not seem to be responsible for the variation in the degree of lateralization. The second mechanism Penke et al. (2007) describe is mutation-selection balance. Here, genetic variation is the result of "an accumulation of many old and new, mildly harmful mutations that selection has not yet wiped out of the population" (p. 555). Penke et al. (2007) list general health and intelligence as examples for mutation-selection balance, that is, traits that reflect the overall functional integrity of an organism. This mechanism also seems unlikely to be responsible for the variation in the degree of lateralization: For example, two important features of mutation-selection balance are strong mate preferences and assortative mating. Strong mate preference refers to the phenomenon whereby individuals, who signal they carry a lot of (mildly) harmful mutations, will be disadvantaged when it comes to finding a partner, whereas individuals, who signal they carry only few of them, will be advantaged. For example, individuals, who signal they have bad health, will find it relatively difficult to find a partner compared to individuals, who signal they have good health. However, to my knowledge there is no evidence showing that individuals who signal a high or low degree of hemispheric asymmetries are advantaged or disadvantaged in mating. Assortative mating refers to the effect that individuals tend to mate with individuals who are similar in sexually attractive traits. For example, highly intelligent individuals prefer having sexual relationships with also highly intelligent individuals (Miller, 2000). However, I do not know of any evidence showing that individuals with a high degree of lateralization prefer having sexual relationships with other highly lateralized individuals (or individuals with a low degree of lateralization with other individuals with low degrees of lateralization). Thus, mutation-selection balance is also unlikely to be responsible for the variation in degree of lateralization. The last mechanism is balancing selection. Here, genetic variation is maintained, because different phenotypes are favored under different conditions, that is, the fitness of an organism varies across different environments. As for the degree of lateralization this would mean that depending on the environment sometimes individuals with high and sometimes individuals with low degrees of lateralization have a greater fitness. Indeed, this is what the literature to date suggests. The present thesis showed that (parallel) processing of words and faces and left-right discrimination might be enhanced by low degrees of lateralization, while other studies showed that cognitive processing in certain tasks may be enhanced by high degrees of lateralization (e.g. Chiarello et al., 2009; Boles et al., 2008). If one agrees that cognitive processing is related to the fitness of an individual, it follows that in certain tasks or in certain environments sometimes a high and sometimes a low degree of lateralization is advantageous, which would be in accordance with balancing selection.

There are different forms of balancing selection, for example, evolutionary stable strategies or a heterozygous advantage. Both forms have been associated with hemispheric asymmetries. In the Introduction it was outlined how Vallortigara & Rogers (2005) seek to explain hemispheric asymmetries on a population level (i.e. the majority is lateralized towards a specific side while the minority is lateralized to the other) by means of evolutionary stable strategies and predator/prey relationships. While this may account for the different frequencies of left versus right lateralized individuals in a given population, it does not explain individual differences in the degree of lateralization. Here, the Corballis model (2009, 2006, 2005), which is based on a heterozygous advantage and which was also briefly introduced in the Introduction, seems more appropriate, because it a) takes individual differences in the degree of lateralization into account and b) attempts to incorporate different advantages and disadvantages of high and low degrees of lateralization. This model is largely based on the right-shift theory, according to which a heterozygote advantage for handedness exists (Annett, 1995). The basic idea is that extremely low and extremely high degrees of lateralization are disadvantageous. Therefore symmetry and asymmetry should be held in balance to guarantee optimal processing. More specifically, following genetic theories about handedness (Annett, 2002; McManus, 1999), it is assumed that two alleles exist on a single gene: one allele encodes a hemispheric bias (B) and the other one encodes a lack of hemispheric bias (L). Hence, a double dose of the hemispheric bias allele (BB) would result in extreme lateralization, whereas a double dose of the lack of bias allele (LL) would result in a rather symmetric brain. People with a heterozygotic allele combination (BL) on the other hand would possess a more balanced brain. Now, if heterozygotic (BL) individuals are superior to both (BB) and (LL) individuals in terms of better fitness, both alleles would be maintained in stable equilibrium and remain in the population (balanced polymorphism). It has been argued that potential disadvantages of homozygotes with a hemispheric bias (BB) may be deficient spatial abilities, whereas homozygotes with a lack of bias (LL) may run the risk of verbal impairments (Annett, 2002) or lower academic abilities (Crow et al., 1998). In contrast, heterozygotes would be less prone to either of these impairments, and hence would have a greater fitness.

Although this model might explain why individual differences and genetic variation in the degree of *lateralization* are kept, there are also a number of problems. For example, the notion that hemispheric asymmetries are under genetic control is disputable. First, even handedness, for which the evidence for heritability is strongest, is not entirely under genetic control. Schaafsma (2008) recently argued that certain handedness patterns in twins and other phenomena cannot be readily explained with genetic models of handedness – at least not the models we have to date. Second, the evidence for a genetic basis in other hemispheric asymmetries like language lateralization in humans, for example, is sparse at best. Twin studies using dichotic listening found no or only little support for the hypothesis that either the degree or the direction of language lateralization is a heritable trait (Springer & Searleman, 1978; Jäncke & Steinmetz, 1994). Third, epigenetic factors that affect the direction and degree of lateralization are well described both in humans and animals. In humans, for example, sex hormones (Pfannkuche, Bouma & Groothuis, 2008) or the *intrauterine* position of the fetus has an impact on handedness (Schaafsma et al., 2008) and in birds, light stimulation during the last days before hatching determines the degree of lateralization (Rogers, 1990).

Taken together, the degree of lateralization does not seem to be solely under genetic control. However, the basic idea of the heterozygous advantage model, that is, that different degrees of lateralization are associated with different advantages (and disadvantages) and therefore variation in lateralization may be maintained in the population, is still in accordance with the empirical data so far. The next paragraph therefore briefly summarizes potential advantages and disadvantages of low, intermediate and high degrees of lateralization.

Advantages and Disadvantages of high and low degrees of lateralization: An overview

The heterozygous advantage model implies that the advantage of intermediate degrees of asymmetry is to prevent detrimental effects of either too much or too less lateralization, i.e. they suffer less from spatial deficits and verbal impediments (Corballis, 2009, 2006, 2005; Annett, 2002). On the other hand, while individuals with intermediate degrees of lateralization may be relatively safe from detrimental effects of too much or too less lateralization, they also might not take full advantage of the potential advantages of a more symmetric or extremely asymmetric brain. Obviously, an advantage of a less lateralized brain also reflects a disadvantage of a highly lateralized brain and conversely, an advantage of a highly asymmetric brain also represents a disadvantage of a more symmetric brain. For instance, Corballis (2006) suggested that creativity and lateral thinking are more pronounced in individuals with low degrees of lateralization and speculated people like Leonardo da Vinci and Albert Einstein could have been (LL) homozygotes. Thus conversely, highly lateralized individuals may, on average, be disadvantaged in terms of creativity. Moreover, the present thesis implies that further advantages of people within the low range of lateralization might be enhanced (parallel) processing of words and face and left-right discrimination.

Originally, however, the present thesis was expected to reveal advantages of participants with *high* degrees of lateralization. So far it is widely believed that the advantage of a highly lateralized brain is enhanced parallel processing, but study two shed some doubt on this theory. Corballis (2009) argued that the avoidance of hemispheric indecision, which is essentially the same as the aforementioned elimination of interhemispheric conflict, might be an advantage in highly lateralized participants. Another advantage might be avoiding interhemispheric transfer time loss. As described earlier in the Introduction, a smaller corpus callosum is associated with stronger (structural) hemispheric asymmetries (Dorion et al., 2000; Aboitiz et al., 1992), which has been interpreted to indicate that a more asymmetric brain relies less on interhemispheric transfer and consequently loses less time to interhemispheric transfer (Ringo et al., 1994). The study of Chiarello et al. (2009) further suggests that reading might be enhanced by high degrees of lateralization, and Boles et al. (2008) argue that auditory linguistic processes may be facilitated by a highly asymmetric brain. Taken together, while the present thesis demonstrated very clearly the advantages of a less lateralized brain (and therefore the disadvantages of a highly lateralized brain), the advantages of an extremely asymmetric brain (and therefore the disadvantages of an almost symmetric brain) remain relatively obscure, at least in humans.

Alternative advantages of hemispheric asymmetries

All those theories about potential evolutionary advantages of hemispheric asymmetries listed so far share the idea that hemispheric asymmetries have arisen because they have facilitated cognitive processing. And indeed the fact that several studies (e.g. Chiarello et al., in press; Ladavas & Umilta, 1983; O'Boyle et al. 2005; Leask & Crow, 2006; 2001; 1997; Crow et al., 1998; Birkett, 1977; Bryden & Sprott, 1981; Springer & Searleman, 1978; Everts et al., 2009), including all studies in the present thesis, demonstrate that hemispheric asymmetries and cognitive performance are related to each other (though not all of them show that higher lateralization is related to enhanced cognitive performance), suggests that cognitive processing does play a role for the adaptiveness of hemispheric asymmetries. However, it seems unlikely that enhanced cognitive processing is the *only* advantage of hemispheric asymmetries. First, if cognitive processing were the only advantage of hemispheric asymmetries, one would expect that all individuals would group around that specific degree of lateralization which is optimal for cognitive performance. But according to study one there is a discrepancy between the optimal degree of lateralization and the populational average bias. In study two, participants with a right hemispheric bias achieved the best performance in a word-matching task, although most of the participants had a left hemispheric bias. Second, if significant correlations between hemispheric asymmetries and cognitive performances emerge, they are usually no higher than $r = .50$ (e.g. Boles et al. 2008; Everts et al., 2009; Hirnstein et al., 2008, submitted), suggesting other factors might contribute to lateralization as well. Finally, a plethora of different species show lateralized behavior and some of them possess rather simple brains like low vertebrates or invertebrates. Doubtless, these species carry out basic cognitive processes, but it is difficult to see how particularly in these 'lower' species enhanced cognitive processing might have become the driving evolutionary force for such a fundamental, organizational principle as hemispheric asymmetries. Rather it seems reasonable to assume that there is another, more basic reason for adopting an asymmetric brain.

Such an explanation for the rise of hemispheric asymmetry has been recently provided by Claude Braun (2007). Braun argued that the advantages of hemispheric asymmetries do not lie in enhanced cognitive processing, but that hemispheric asymmetries emerged as primitive, “antagonistic systems of management of the body’s energy resources” (Braun, 2007, p. 397). Central to Braun’s theory is the assumption that an organism would need as much facilitation of mental and behavioral action as it would need its inhibition. In other words, an organism has to show exploratory behavior, must imagine and generate different ideas to solve everyday life situations and needs to act these ideas out, but at the same time it also has to impede too much exploration, too much imagination and has to inhibit uncontrolled behavior before it can do any harm. Braun (2007) therefore proposed a dichotomy of the two cerebral hemispheres according to which the left hemispheres facilitates and the right hemisphere inhibits behavior. Purely based on lesion and brain stimulation studies in rodents and humans, he concludes that lesions to the left hemisphere would “render us parasympatheticotonic, immunosuppressed, lethargic, avoidant, hypognosic, hyposexual, hypolalic, unimaginative” (p. 413, Braun, 2007). In contrast, lesions of the right hemisphere would “render us sympatheticotonic, immunostimulated, agitated, active, dysfunctionally hypermnesic, hypergnosic, hypersexual, hyperlalic, overimaginative” (p. 413, Braun, 2007). Though hemispheric dichotomies typically have the inherent problem that they are oversimplifying (and certainly Braun is no exception to that rule), the theory makes a valuable point: Given how widespread lateralization in the animal kingdom is, the advantage of hemispheric asymmetries may not solely lie in cognitive processing. However, since several studies demonstrate that cognitive processing is related to hemispheric asymmetries, it seems likely that both cognitive processing and other more basic factors (like perhaps the antagonistic energy systems proposed by Braun, 2007), constitute the evolutionary advantages of lateralization.

Possible neural mechanisms of enhanced cognitive performance in a less asymmetric brain

The present thesis along with other studies (e.g. O’Boyle et al., 2005) suggests that participants with low degrees of lateralization perform relatively well in certain cognitive functions. The question thus arises, what the underlying neural mechanisms of the low performance in highly and the relatively high performance in less lateralized participants might be? We hinted in study two that a more efficient cooperation between the two hemispheres might provide an explanation for the higher cognitive performance in less lateralized participants. The early works of Dimond and colleagues (Dimond, 1972; Dimond & Beaumont, 1971; Davis & Schmit; 1971, 1973; Guiard & Requin, 1977; Beaton, 1979; for review see Beaton, 1985) as well as the more recent studies of Marie Banich and colleagues (Banich & Belger, 1990; Belger & Banich, 1992; Belger & Banich, 1998; Banich & Weissman, 2000) have shown that if information is shared between the left and right hemisphere, performance is higher than if a single hemisphere processes a task, particularly when task difficulty is high. Sharing information between the two hemispheres however, most likely involves interhemispheric communication mediated via the corpus callosum. If a less lateralized brain were associated with better interhemispheric communication, one would also expect that less lateralized participants also share information between the two hemispheres more easily than highly lateralized participants. This enhanced sharing of interhemispheric information would then lead to a higher cognitive performance than in highly lateralized participants given the results of Marie Banich and her colleagues described above. Indeed, hemispheric asymmetries and interhemispheric transfer seem to be related inversely, at least neuroanatomically (Jäncke & Steinmetz, 2003). For example, the density of callosal terminations and volumetric asymmetries of the motor cortex are negatively correlated, that is, as density of callosal terminations increases, volumetric asymmetry decreases (Rosen, Sherman & Galaburda, 1989; Rosen et al., 1990). Also, a negative correlation was found between the size of the corpus callosum and the right-ear advantage in dichotic listening (Clarke, Lufkin & Zaidel, 1993; Yazgan et al., 1995). Finally, a larger corpus callosum was related to shorter reaction times and hence to better overall performance in a dichotic consonant-vowel task (Jäncke & Steimetz, 1994). Although one has to be cautious in drawing conclusions from the anatomy of a structure (here the corpus callosum) to its function, the data so far suggest that low degrees of lateralization are associated with increased interhemispheric communication. Accordingly, Christman and colleagues argue that mixed-handers, who are said to be less lateralized than left- or right-handers also show increased interhemispheric interaction compared with participants with strong hand preferences (e.g. Propper, Christman & Phaneuf, 2005; Christman et al., 2008). An increased interhemispheric interaction would be a better basis for a cooperation between the two hemispheres and might explain the cognitive performance advantage of less lateralized participants in certain tasks of the present thesis and previous studies (e.g. O'Boyle et al., 2005).

Evolutionary advantages of hemispheric asymmetries in the dynamic brain

So far the impact of *inter*individual differences in hemispheric asymmetries on evolutionary advantages was discussed and it was argued that both high and low degrees of lateralization might contain certain advantages and disadvantages, depending on the context. It appears that this more complex picture (as opposed to the more simple view "the more lateralization, the better") is yet even more complicated. Some scientists in the field of evolutionary advantages of hemispheric asymmetries seem to think of functional hemispheric asymmetries as invariant traits. That means somebody who has a high degree of lateralization in a certain function is also expected to be highly lateralized in other functions and to maintain this high degree more or less unaltered throughout his whole life. But this view is wrong, at least for *functional* hemispheric asymmetries. Apart from interindividual differences, there are also *intra*individual differences across different functions and across time. For instance, it has been demonstrated that different lateralized functions are basically independent of each other (Boles 1998a, b, 2002). Knowing that somebody has a very asymmetric representation of language does not tell us whether face perception in this individual is also highly lateralized. Furthermore, functional hemispheric asymmetries are subjected to a variety of factors. Fluctuations in sex hormones, for example, lead to dynamic changes of hemispheric asymmetries over daytime, seasons and the menstrual cycle. Besides hormonal effects, there are various other factors such as task requirements (Czéh et al., 2008; Hausmann, Kirk & Corballis, 2004) or emotional states (Davidson, 1995), to mention only a few. So how do these dynamic changes in hemispheric asymmetries fit the idea that different degrees of lateralization are associated with different advantages? It is possible that depending on the specific needs of a certain situation, different advantages of hemispheric asymmetries might be required. For example, a number of studies demonstrated that during menses, when sex hormone levels are low, women usually display a more 'male-like' asymmetric pattern, while during the luteal phase, when sex hormone levels are high, hemispheric asymmetries are reduced (Hausmann & Güntürkün, 2000; Hausmann et al., 2002; Hausmann, 2005).

Many studies also demonstrated that women's face preferences change across the menstrual cycle (e.g. Peters, Simmons & Rhodes, 2009; Little et al., 2007). Studies one and two suggest that face processing is enhanced in participants with low degrees of lateralization. Perhaps, hemispheric asymmetries are reduced during the luteal phase, because it is related to altered face preferences or maybe even enhanced face processing, which might, for instance, lead to a more optimal (mating) partner choice. However, it is unlikely that every little shift in the degree of lateralization is related to a better fitness. There are simply too many factors that can alter the degree of lateralization and many of those changes will be meaningless biological noise. But why would our brain not take advantage of those dynamic changes in the degree of lateralization when these changes are accompanied with different strengths and advantages, particularly when these changes are related to such important aspects as reproduction as in the case of dynamic changes of hemispheric asymmetries across the menstrual cycle?

General conclusion

The present thesis sought to investigate evolutionary advantages of hemispheric asymmetries in humans. In line with previous studies, it was hypothesized that participants with high degrees of lateralization would outperform less lateralized participants in certain cognitive functions. However, participants with high degrees of lateralization were consistently outperformed by less lateralized participants, suggesting that some long and widely held views about evolutionary advantages of hemispheric asymmetries may need to be revised. First, the present thesis gives evidence against the notion that high degrees of lateralization are associated with enhanced cognitive processing. Second, low rather than high degrees of lateralization seem to be associated with enhanced parallel processing and enhanced left-right discrimination. Possibly, this advantage of participants with low degrees of lateralization is the result of a more efficient cooperation between the two hemispheres. Third, taken together with previous studies the present thesis also argues against the notion that hemispheric asymmetries are advantageous for cognitive processing *per se*. Instead, whether cognitive processing is enhanced or reduced depends on the *degree* of lateralization.

Different degrees of lateralization may be associated with different advantages (and disadvantages) and whether a highly or less lateralized brain is advantageous (or disadvantageous) depends on specific requirements in a given situation. Hence, the question "what is the evolutionary advantage of a lateralized brain?" appears to be oversimplified and should rather be replaced with "under which circumstances/conditions is which degree of lateralization advantageous?". Initially the degree of lateralization is probably encoded by genes (Corballis, 2006), but is subsequently subject to various dynamic changes, which further highlights the suggestion that evolutionary advantages of hemispheric asymmetries might be more complex than previously thought. Finally, the evolutionary advantages of hemispheric asymmetries may not solely lie in enhanced cognitive processing, as it is widely believed. Most likely, an ancient, more basic mechanism, like facilitating behavior versus inhibiting behavior (Braun, 2007) for example, was and still is at least partly responsible for the emergence and persistence of hemispheric asymmetries.

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