Hemispheric interaction: when and why is yours better than mine?

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Declaration

I, Nicolas Cherbuin, hereby declare that, except where acknowledged, that this work is my own and has not been submitted for a higher degree at any other university or institution.

Nicolas Cherbuin

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Publications arising from the thesis

Experiments 3, 5, 6, and 7 have been published in the following articles:

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Cherbuin, N., & Brinkman, C. (2005). Practice makes two hemispheres almost perfect. *Cognitive Brain Research*, 24, 413-422.

Cherbuin, N., & Brinkman, C. (2005). Hemispheric activation and interaction: past activity affects future performance. *Laterality,* 10, 563-579.

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Abstract

The performance of most tasks requires some interaction between the cerebral hemispheres. Despite this fact, research has focused on demonstrating that each hemisphere is specialised for certain processes and has largely neglected this interaction.

Recent research has recognised the need for a better understanding of how resources are shared between the cerebral hemispheres. While these studies have shed light on factors external to the participants being tested, such as the type of task and stimuli used, presentation times, and different measurement methods, they have neglected variables that differ between individuals. The studies reported here focused on factors internal to the participants. They include sex, age, handedness, functional lateralisation, practice, attention, and hemispheric activation, which vary between individuals or within individuals across time, and have been shown to influence the structure and morphology of the corpus callosum which is the main pathway for hemispheric interactions.

This thesis examines the relationship of these variables to the efficiency of hemispheric interactions.

A literature review of the factors affecting hemispheric interactions and interhemispheric transfer is presented in Chapter 1, and methodological issues relating to the measurement of these variables in Chapter 2. Based upon this research, two tasks, the Poffenberger paradigm and a letter-matching task, were selected to assess interhemispheric transfer time and hemispheric interactions, respectively, and to investigate the relationship between these two variables.

Chapters 3 and 4 present the findings of the principal study, using a large sample of participants and regression analysis, which demonstrate that both faster interhemispheric transfer and more extreme left-handedness are associated with greater efficiency of hemispheric interaction. Surprisingly, other factors which were expected to influence hemispheric interactions (age, sex, functional lateralisation, and attention) did not have a significant effect on this variable.

A strong practice effect found in the task used in Chapters 3 and 4 is analysed in Chapter 5. Contrary to previous findings, this practice effect seems not to be due to a shift from sequential, rule-based processing to memory-retrieval, but rather, is a more general practice effect consistent with progressively more efficient use of neural resources.

Chapter 6 shows that individuals with dyslexia not only demonstrate an abnormally fast interhemispheric transfer, but also attentional deficits, due probably to decreased efficiency in hemispheric interactions. Because some clinical populations, such as individuals with dyslexia, have been shown to have hemispheric interaction deficits, the study of such clinical samples can provide valuable information about the relationship between hemispheric interactions and other individual variables.

In Chapter 7 it is demonstrated that both latent and induced patterns of lateralised hemispheric activation affect hemispheric interactions. This suggests that

assessment of hemispheric activation is important not only in this field, but probably also more generally in neuropsychological research. These findings highlight the need for a simple, inexpensive measure of hemispheric activation that can be applied routinely in cognitive experiments.

Chapter 8 presents a new technique to measure lateralised brain activation in typical psychological experiments using functional tympanic membrane thermometry (fTMT). This measure relies on the measurement of ear membrane temperature as an index of hemispheric activation. The technique is simple and inexpensive, and is shown to be suitable for the assessment of hemispheric activation patterns during typical experiments.

In conclusion, individual characteristics such as the efficiency of interhemispheric transfer, handedness, functional lateralisation, attention, and hemispheric activation are important factors to consider when researching hemispheric interactions in both normal and clinical populations. Furthermore, future research will benefit from this newly developed measure, fTMT, by allowing the systematic study of the effects of hemispheric activation in brain processes.

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CHAPTER 1

1.1 General Introduction

The cerebral hemispheres do not function independently; although even in the scientific literature, the popular notion of left- and right-brainedness seems to dominate, since a large amount of research has focused on demonstrating differences between the brain's hemispheres. This research has produced fascinating results but it has also created stereotypes which have contributed in shaping research questions stressing differences, dichotomies, and oversimplified descriptions of the respective roles of the two cerebral hemispheres.

More recently, researchers have become more interested in explaining how the two cerebral hemispheres share their cognitive resources, contribute to decision making, and learn new tasks.

This is important because, under normal circumstances, the performance of most tasks involves some interaction between the hemispheres. For instance, although speech perception and production is, in most people, performed by the left hemisphere, the right hemisphere is instrumental in interpreting voice intonation conveying emotion or deceit and in using complex syntactic rules. Thus the properties of an isolated hemisphere are often not good predictors of behaviour.

The aim of this thesis is to elucidate how hemispheric interactions are affected and shaped by factors which have received little attention to date: individual variables such as sex, age, handedness, and functional lateralisation, cognitive states such as practice effects and attention, and hemispheric activation and arousal.

This chapter will present evidence suggesting that individual variables such as these should modulate hemispheric interactions. Chapter 2 will discuss methodological issues relating to the measurement of hemispheric interactions and specific individual variables. Chapters 3, 4, and 5 will present results which show that the efficiency of hemispheric transfer significantly affects the quality of hemispheric interactions and how both interhemispheric transfer and hemispheric interactions interact with variables such as practice, functional lateralisation, handedness, age, and sex. An example of the implications of these results in neurological populations will be demonstrated in Chapter 6 where hemispheric interactions are investigated in individuals with dyslexia. In chapter 7, it will be demonstrated that activation of one or the other hemisphere significantly affects hemispheric interactions. Finally, chapter 8 will present a novel method to assess such hemispheric activation which can be used in typical psychological experiments and particularly those researching hemispheric interactions. A concluding chapter will summarise and discuss the implications of these findings.

1.1.1 Historical Perspective

The concept that each hemisphere is specialised for specific tasks can be traced back to the discovery of the lateralisation of language centres in humans. Broca (1824-1880) has usually been credited as being the first to demonstrate that the left hemisphere is essential in the production of speech. However, there is strong evidence suggesting that Dax (1771-1837), a GP in southern France, was the first (27 years before Broca) to suggest that left hemisphere damage was associated with right hemiplegia and in some cases loss of speech (cited in Finger, 2004; Finger & Roe, 1999). His son, Gustave Dax (1815-1893), who was also a GP, built on his father's research, and appears to have been the first to locate language centres in the temporal lobe (Dax, 1865 reported in Finger & Roe, 1999) while Wernicke (1848-1904) is usually credited with this finding in his 1874 paper. These discoveries have led to a large body of research investigating functional differences between the two hemispheres, and as more such differences were uncovered, the concept of functional lateralisation was developed.

Early neurosurgical studies played a particularly important role in laying the foundations which would allow a more systematic enquiry into the brain and led to a better understanding of the functions of the two cerebral hemispheres and of the localisation of lateralised processes (see Sabbatini, 1997, for a detailed historical overview). Rolando (1773-1831) was the first electrophysiologist to stimulate the brain with electricity, which was made possible by the discovery of the battery by Volta (1745-1827), to study brain functions (Figure 1-1). This line of research was pursued and perfected by a number of physiologists and neurosurgeons, and made possible by advances in the control and production of electricity, the development of new experimental tools, and the improvement of surgical techniques.

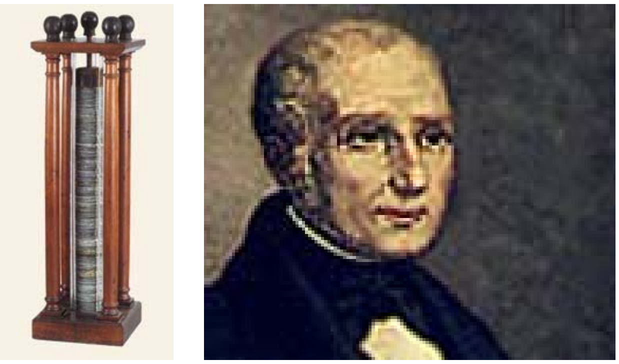

Figure 1-1. Electrical pile (battery) discovered by Volta in 1802 (Left, Chemical Heritage News Magazine, 2005). Luigi Rolando (1773-1831), pioneer in electrical brain stimulation (right, Universita di Torino, 2005).

Flourens (1794-1867) demonstrated, by mechanically stimulating and producing lesions in pigeons' and rabbits' brains, that motor control was exercised by the hemisphere contralateral to the moving muscles. Other researchers, such as Fritsch (1838-1927), Hitzig (1838-1907), Jackson (1835-1911), and Ferrier (1843-1924) conducted further research in animals which demonstrated the presence of motor maps and the hierarchical organization of the brain (Sabbatini, 1997).

It is only in the early 1900s that substantial systematic physiological research of the human brain started taking place. Penfield (1891-1976), a Canadian neurosurgeon, was particularly influential in developing our understanding of the organization of the human brain (Penfield, 1958; Penfield & Rasmussen, 1950; Penfield & Roberts, 1959). He developed neurosurgical techniques involving operating on patients who were under regional anaesthesia. This permitted the stimulation of different brain areas during surgery and the reporting, by patients, of memories, emotions, and sensations that these stimuli elicited. Penfield is particularly famous for his study of the sensory and motor centres which he precisely mapped and presented in his human homunculi (Figure 1-2).

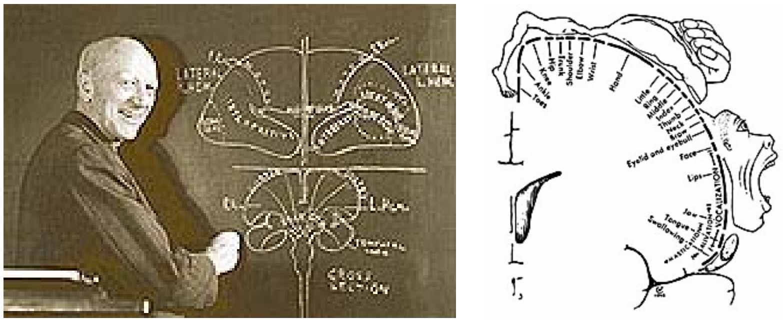

Figure 1-2. Wilder Penfield (1891-1976), neurosurgeon renowned for his study of the cortical organization of the human brain (Left, People and Discoveries, 2005). Penfield's human motor homunculus (Right, The Miller Laboratory, 2005).

Better understanding of the structural organization of the brain progressively led to new surgical treatments of neurological disorders. In the first half of the 20th century a new treatment for intractable epilepsy was trialed and produced positive results (see Harris, 1995 for a historical overview). This treatment consisted in sectioning the main fibre tract, the corpus callosum, linking the two cerebral hemispheres together and thus stopping the spread of chaotic electrical activity from one hemisphere to the other.

Surprisingly, the initial assessment of split-brain patients showed almost no adverse effects (Akelaitis, 1944-45), which prompted some researchers to jokingly suggest that the corpus callosum was a structure whose only role was to prevent the hemispheres from sagging or permit the spread of epileptic seizures (see Harris, 1995; Hoptman & Davidson, 1994).

However, more careful study revealed that callosal section has unintended side effects. The divided cerebral hemispheres were suddenly limited in the way information and resources could be shared between them. The study of "split-brain" patients, which Sperry (1913-1994) pioneered (Figure 1-3), was probably the single most important step in our understanding of functional differences between the two cerebral hemispheres. These studies confirmed that in most individuals, certain language functions essential to produce speech were only present in the left hemisphere (Sperry, 1981). They also showed that the right hemisphere tended to be specialised for visuo-spatial tasks (Franco & Sperry, 1977; Levy, Trevarthen, & Sperry, 1972; Levy-Agresti & Sperry, 1968). Split-brain studies have, however, been biased towards emphasising differences between the cerebral hemispheres.

In the last twenty years, hemispheric interaction, and the role of the CC in it, has attracted more attention. Two types of findings, in particular, have contributed to this. Firstly, those showing that one hemisphere could, depending on its specialisation and processing style (Levy et al., 1972), assume control and influence how a task would be performed. Secondly, the findings that interactions between the two hemispheres could have a beneficial effect on performance of tasks with high processing demands (Banich & Belger, 1990; Belger & Banich, 1998; Liederman, Merola, & Martinez, 1985; Norman, Jeeves, Milne, & Ludwig, 1992; Pollman, Zaidel, & Cramon, 2003; Reuter-Lorenz & Stanczak, 2000; Weissman & Banich, 2000) either by recruiting and synchronising the resources of the two hemispheres, or, where two conflicting tasks needed to be performed at the same time, by isolating the cerebral hemispheres from each other (Liederman & Meehan, 1986; Weissman & Banich, 1999). It has also been shown that hemispheric interaction can have a negative effect, when irrelevant information presented to one hemisphere interferes with task processes in the other hemisphere (e.g., Grimshaw, 1998; Kavcic & Clarke, 2000; Ratinckx & Brysbaert, 2002).

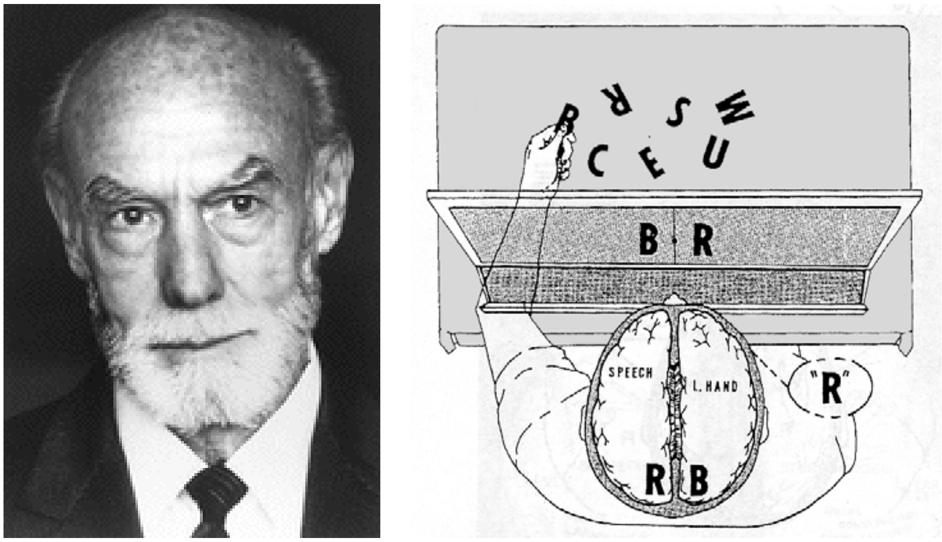

Figure 1-3. Roger Sperry (1913-1994, University of Chicago, 2005) whose research in split-brain patients was recognised by a Nobel prize in 1981. Right, a split-brain patient is able to perceive letters in both the left and right hemispheres but is unable to voice the letter perceived by the right hemisphere (e.g., Sperry, 1970).

The capacity of one hemisphere to assume control and determine the strategy with which a task is processed is often referred to as meta-control. It has been shown in split-brain individuals that for a given task, the hemisphere that is better equipped for that task takes control (Levy & Trevarthen, 1976). However, if the least efficient hemisphere is activated, for instance by manipulating instructions, it will assume control despite its lower ability to perform the task. Similar findings have also been produced in macaques (Kavcic, Fei, Hu, & Doty, 2000) and in intact humans (Hellige, Jonsson, & Michimata, 1988; Urgesi, Bricolo, & Aglioti, 2005).

A high degree of interaction has been demonstrated in tasks for which neither cerebral hemisphere is specialised. Diamond and Beaumont (1971) were probably the first to show that under certain circumstances performance of a task was improved when each hemisphere perceived part of the stimuli compared to when a single hemisphere perceived all the stimuli to be reported. However, it was not until the 1980s that a number of studies started clarifying the origin of this “bilateral advantage”. Banich and colleagues (e.g. Banich & Belger, 1990; Belger & Banich, 1998; Weissman & Banich, 2000) found that hemispheric interactions were more beneficial in more complex or demanding tasks and that this applied to a variety of stimuli in the visual, tactile, and auditory modalities. They proposed that the advantage provided by hemispheric interactions increases for tasks requiring a greater number of processing steps. Other researchers (Merola & Liederman, 1990) confirmed these results and also showed that hemispheric interactions are beneficial when two conflicting tasks are processed concurrently, in that conflicting processes of two tasks (e.g. matching normal and up-side-down letters) could be better performed when the competing processes were isolated in different hemispheres.

Recently, interest in how the two cerebral hemispheres interact has increased. Findings in this field have been integrated to better define the role of hemispheric interactions in attentive processes, emotions, memory and unified consciousness. For instance, in relation to attention, it has been shown that hemispheric interaction might function as a gating system that allows the sharing of resources when one hemisphere is heavily taxed and the other can spare some processing capacity, whereas it might isolate processes taking place in each hemisphere when these processes might otherwise conflict (Banich, 1998; Hoptman & Davidson, 1994; Liederman, 1998; Mikels & Reuter-Lorenz, 2004). A great deal of attention has been paid to measurement issues, task characteristics, and methodological concerns. However, relatively little attention has been paid to individual differences, either relating to anatomical or physiological variations, and their impact on the way in which the brain's hemispheres interact, despite a large body of evidence suggesting that hemispheric interactions are likely to vary substantially between individuals in both normal and clinical populations (e.g. in relation to handedness, sex, age, and practice).

In this context, it is particularly surprising that the properties of the corpus callosum (CC), which is critical for the transfer of information necessary in the completion of tasks requiring interactions between the hemispheres, have not attracted more interest. This is especially so given the subtle interactions between CC structure, anatomy, sex, handedness, and functional lateralisation, and the evidence of abnormal hemispheric lateralisation and interactions in pathologies such as schizophrenia (Endrass, Mohr, & Rockstroh, 2002; Hulshoff Pol et al., 2004; Phillips, Woodruff, & David, 1996), dyslexia (Robichon, Levrier, Farnarier, & Habib, 2000), alcoholism (Bookstein, Streissguth, Sampson, Connor, & Barr, 2002; Schulte, Pfefferbaum, & Sullivan, 2004), bipolar disorder (Brambilla et al., 2003), multiple sclerosis (Moroni, Belin, Haguenau, & Salama, 2004), Alzheimer's disease (Dorion et al., 2002), and changes associated with the normal aging process (Cabeza, Anderson, Locantore, & McIntosh, 2002; Reuter-Lorenz, 2002; Reuter-Lorenz & Stanczak, 2000).

1.2 Hemispheric Interaction: What? Where? How?

Hemispheric interaction is a broad term. It encompasses any exchange of information between the cerebral hemispheres, from the most basic neural level to more complex, high order representations and their physiological, cognitive, and behavioural effects. It is therefore important to specify what is meant by hemispheric interaction in the present thesis. The focus of this thesis will be to further determine how the exchange of complex visual and cognitive information affects behaviour. Thus hemispheric interactions will be experimentally measured by systematically modulating which hemisphere first perceives certain visual stimuli while also varying which hemisphere controls the responding hand. Certain conditions will require a certain degree of hemispheric interaction in order to perform the tasks while others will not. Accuracy and reaction times will be contrasted across different conditions to assess the efficiency of hemispheric interaction in different individuals.

However, before these issues are discussed further, two points need to be clarified. First it is important to review past findings in the field of hemispheric interaction since they will be the foundation on which the present thesis is built. Secondly, since hemispheric interaction requires the exchange of information between the hemispheres it is critical to have a good understanding of how information transfer occurs in the human brain and what factors affect it.

1.3 Hemispheric Interaction and Behaviour

Despite having demonstrated some striking differences between the two "isolated" cerebral hemispheres in split-brain patients, Sperry was also well aware of the importance of hemispheric interaction. After two decades of work with split-brain individuals he noted: "in the normal state the two hemispheres appear to work closely together as a unit, rather than one being turned on while the other idles" and further asked "why is it that the right hemisphere is able to do things after commissurotomy, such as reading, that it fails to do in the presence of focal damage in the left hemisphere?" suggesting hemispheric interaction as the answer (Sperry, 1981, p. 3).

Sperry's work and that of others (e.g. Dimond & Beaumont, 1971) provided the impetus for new research on hemispheric interaction in the last two decades of the 20th century. This research can be broadly categorised in two parts. First, research investigating the influence that one hemisphere can exercise over the other in determining the strategy to be applied to a specific task, often referred to as meta-control. Second, research of how processing resources can be shared across the two hemispheres, often called the bilateral distribution advantage (BDA). In this thesis, the main focus will be on the latter type of hemispheric interaction. However, meta-control will be briefly reviewed.

1.3.1 Meta-Control

Meta-control refers to the neural mechanisms determining which hemisphere will attempt to control cognitive processes. It was first demonstrated by Levy and Trevarthen (1976) in split-brain patients. In a matching task, they presented participants with images in each visual field that could be matched either by appearance or function to target images laid in front of participants (e.g. a round cake on a plate could be matched with a fork– function – or with a hat – appearance). When different images were presented to different hemifields, left visual field images (LVF) would normally be matched based on appearance whereas right visual field stimuli (RVF) would be matched based on function. Since each visual field is perceived by the contralateral hemisphere, these findings suggested a specialisation of the right hemisphere for appearance matching and a left hemisphere specialisation for function matching. In a second experiment, in which instructions were manipulated, the participants would mostly conduct the match based on the RVF image when the instructions were biased towards a function match, indicating that the left hemisphere had acquired control. In contrast, when instructions were biased toward an appearance match, the right hemisphere assumed control and matches occurred mostly based on the LVF image.

To demonstrate the presence of meta-control in intact individuals Hellige, Jonsson, & Mishimata (1988) devised a face matching task in which facial features (hair, eyes, mouth, jaw) were manipulated. The task consisted in determining whether a centrally presented face matched a second face presented to the LVF, RVF, or bilaterally. The pattern of responses in the bilateral condition resembled closely that of the RVF/left hemisphere condition while differing significantly from the LVF/right hemisphere condition. This pattern held even when a LVF/right hemisphere strategy would have been more beneficial. These findings suggest that, when stimuli were presented bilaterally, the left hemisphere assumed control over the right hemisphere, and support the concept of meta-control in neurologically intact individuals.

In another experiment (Hellige, Taylor, & Eng, 1989), participants were required to report consonant-vowel-consonant syllables presented to the LVF, RVF, or bilaterally. The pattern of errors in the bilateral condition was similar to that in the LVF/right hemisphere condition but significantly different from that of the RVF/left hemisphere condition. This suggests that, despite the RVF/left hemisphere performance being more accurate, the mode of processing of the LVF/right hemisphere was nonetheless adopted in the bilateral condition. To explain these types of results, Hellige (1991, pp. 126-129) hypothesised that it might be advantageous to adopt a less efficient mode of processing in the bilateral condition but one that is available in each hemisphere, and therefore possibly more compatible, so that processing resources in each side can be recruited.

In summary, little is know about meta-control but it appears that it is a mechanism that determines which hemisphere controls a process, based not only on which hemisphere is more competent in a certain task, but also based on the cognitive resources available in each hemisphere, and how to best recruit and synchronise them.

1.3.2 Resource Sharing across Hemispheres: the Bilateral Distribution Advantage (BDA)

While the effects of interhemispheric interaction in bi-manual control and processing of visual information have been investigated in monkeys (Hamilton, Hillyard, & Sperry, 1968; Mark & Sperry, 1968) and split-brain patients (Sperry, 1970), Diamond and Beaumont (1971) were the first to specifically design a study interested in quantifying the effect of hemispheric interaction in intact humans. They tachistoscopically presented two digits to participants while they were performing a manual nut and bolt sorting task. The digits were presented either to a single hemifield or with one digit in each visual field. Digit report and sorting performance were higher when the digits were presented to separate visual fields and therefore required hemispheric interaction. Dimond and Beaumont (p. 271) concluded that “each hemisphere possesses its own perceptual analysing system” and that during a demanding task the distribution of the perceptual load between the cerebral hemispheres is beneficial.

Similar results were found in a study involving matching two complex figures (Dimond & Beaumont, 1972) but not in another, involving matching words (Dimond, Gibson, & Gazzaniga, 1972). However, these different results can be attributed to methodological differences, such as the types of stimuli and responses (verbal/manual) used, the difficulty of the task, and the position of the stimuli in the visual field.

These early findings inspired a string of studies aimed at clarifying the conditions in which hemispheric interactions are advantageous. Liederman, Merola, and Martinez (1985) showed, by manipulating the position of words in a matching task so that the across visual field match could occur horizontally or diagonally, that the advantage in the across hemisphere condition was not due purely to scanning habits (although an effect of scanning habit was found), and that it decreased with practice. Liederman and Meehan (1986) further demonstrated that just dividing the perceptual load between the two hemispheres was not sufficient to produce a bilateral advantage. They asked participants to report letters that were briefly presented either upright or upside down. In all conditions, two pairs of letters were presented, with each pair made up of letters of opposite orientation, or with both pairs made of one upright and one upside down letter. In the unilateral condition, the two pairs were presented to the left or right visual field whereas in the bilateral condition one pair was presented in the left visual field and the other pair in the right visual field. A bilateral advantage was found, but only when each pair was made up of letters of the same orientation. This suggests that a processing advantage can be gained when two interfering tasks (perceiving upright or upside down letters) can be isolated from each other by performing each task in a different hemisphere.

Merola and Liederman (1990) used the same task but varied its complexity by using either two pairs of letters, or two single letters, and by applying a mask. They found that the bilateral advantage disappeared when the number of letters was reduced from four to two when no mask was used. However, they were able to re-establish the bilateral advantage by applying a 40ms mask after presentation of the letters. They concluded that hemispheric interaction is favourable only under more difficult conditions either because more stimuli need to be detected or because the iconic trace is disturbed and thus postexposal scanning of the stimuli is decreased.

Tasks like the above that require the verbal report of stimuli are not without problems in explaining hemispheric interaction. First, because the stimuli need only be reported, they do not necessitate the integration of stimuli across the two hemispheres. Therefore, they tell us more about intra- or inter-hemispheric interference than about the beneficial effects of hemispheric interaction. Furthermore, because naming requires the language centres normally localised in the left hemisphere, it is difficult to assess the origin of the interference and whether functional lateralisation has a role to play. Finally, the studies discussed so far did not consider the fact that the perceptual loads were different in the unilateral and bilateral conditions and that the possibility that the advantage found in the bilateral condition could simply be due to a decrease in perceptual load in this condition.

Banich and colleagues (Banich & Belger, 1990; Banich & Karol, 1992; Belger & Banich, 1992, 1998; Weissman & Banich, 1999; Weissman, Banich, & Puente, 2000) conducted a number of studies to address such issues. They used a tachistoscopic letter-matching task where three letters were presented in a V format. The top two letters were presented in the left and right visual fields respectively whereas the bottom letter was presented closer to the midline but in either the left or the right visual field. A match always occurred between the bottom letter and one of the two top letters. Thus, in the unilateral condition, the matching letters were presented to a single visual field, did not require interhemispheric integration and performance was therefore thought to reflect processing in the contralateral hemisphere. In the bilateral condition, each letter was presented to a different visual field, therefore integration between the hemispheres was necessary, and performance in this condition was thought to reflect hemispheric interaction, and subtracting performance in the unilateral condition from that in the bilateral condition provided an index of that hemispheric interaction. Using two versions of this task, one where all letters were written in the same case and therefore required only their shapes to be compared (perceptual match) and one where the bottom letter was presented in lower case but the top two letters were presented in upper case, thus requiring the identity of the bottom letter to be compared to that of the upper letters (identity match), Banich and Belger (1990) demonstrated that a bilateral advantage was present for the second, more demanding, task but not for first, simple one. Accuracy rates were higher and response times faster in the identity-match condition when each of the matching letters were presented to a separate hemisphere than when the two letters were presented to the same hemisphere. In two follow-up experiments, Banich and Belger (1992) replicated these results using digits. They found that when matches between identical digits needed to be detected, unilateral performance was better than across field performance. However, when further processing steps were added to the task by asking participants to determine whether two digits added together totalled 10 or more, or to decide if one number's value was less than that of either of the two other ones, response accuracy was greater and response times were faster in the bilateral.

Similar results were found when other types of stimuli and tasks were used, for instance, when the task consisted of determining whether pictures were identical (banana-banana) or whether they belonged to the same category (banana-apple, Koivisto, 2000); whether Chinese characters were visually similar or whether they were homophones or synonyms (Zhang & Feng, 1999); whether dot patterns containing 2, 4, or 6 dots were identical (Norman et al., 1992); whether faces were identical or not, or whether facial expression (angry, happy) was the same in different faces (Compton, 2002); or when the sum of 2 digits written in the same script (Arabic or Kanji) or each written in a different script was reported (Hatta & Yoshizaki, 1997). Bilateral advantages have also been demonstrated in the auditory and tactile modalities (Passarotti, Banich, Sood, & Wang, 2002).

Studies demonstrating a bilateral advantage have similar characteristics. The bilateral advantage is usually found in conditions that either comprise more stimuli, include more diverse stimuli, involve greater manipulation of stimuli, or involve more familiar tasks or stimuli. This fact was recognised by Banich and colleagues who attempted to integrate the diverse findings into a general theory (Banich & Belger, 1990; Belger & Banich, 1992, 1998; Weissman & Banich, 2000). Banich noted that more complex and demanding tasks produced a bilateral advantage whereas simpler task did not. Consequently, she proposed that the bilateral advantage was dependent on the number of processing steps required to complete a task. When a task was simple and required fewer processing steps, one hemisphere could complete it without the assistance of the other hemisphere. However, with increased task complexity involving a greater number of processing steps, a single hemisphere would be overwhelmed by the processing load. In these types of tasks, a bilateral advantage would be found because distributing stimuli and perceptual processing load between the two visual fields would lead to a more efficient use of cognitive resources across the two hemispheres than could be achieved if all relevant stimuli were presented to a single hemisphere. This occurs despite the potential cost of interhemispheric transfer. Due to this distribution of processing between the hemispheres the bilateral advantage is usually referred to as the bilateral distribution advantage (BDA).

In support of this theory, Weissman and Banich (2000) showed that when the processing load is decreased by presenting the target and probe stimuli sequentially, or with partial overlap, the BDA disappears. They also compared two conditions in which the bottom letter was either presented closer to the midline but within the left or right visual field, or where the bottom letter was presented on the midline. Thus, in the latter condition, processing of the task could theoretically always occur within one hemisphere and therefore should resemble single hemisphere performance. Interestingly, Weissman and Banich found that in the easier conditions (overlapping, sequential) processing in the midline condition resembled within hemisphere processing whereas in the more demanding condition, when all stimuli were presented simultaneously, performance in the midline condition resembled that associated with between hemisphere processing, suggesting to the authors that the type of processing (within/between hemispheres) used to perform a task might be selected by top-down processes resembling meta-control as described by Levy and Trevarthen (1976).

Past research clearly shows that the BDA is a robust phenomenon that depends on numerous variables. However, the BDA does not continue to increase with ever increasing task complexity. Belger and Banich (1992) suggest that the BDA might plateau at 10% of within hemisphere performance (see also Compton, 2002). With increased task complexity each hemisphere uses up more of their spare resources, thus, progressively, fewer resources are available to be shared with the other hemisphere, therefore, the benefit provided by hemispheric interaction diminishes. For example, when participants were presented with an identity letter-matching task containing four letters in a V-display with two letters in each visual field, the size of the BDA was substantially decreased compared to that of a similar task with three letters (Weissman et al., 2000). These findings suggest that the division of a task between the hemispheres is particularly beneficial when one hemisphere's available resources are higher (e.g. when its perceptual load is less than that of the other hemisphere) than the other hemisphere.

A substantial amount of data supports Banich's theory that a BDA is produced when more complex tasks with more computing steps are performed. However, other findings suggest that other explanations might be more appropriate. Although generally, more difficult tasks, as assessed by longer response time (RT) and lower accuracy, tend to produce larger BDAs, at least one study contradicts this pattern of results. Weissman and Banich (2000) manipulated stimulus/background contrast in a five stimulus category-match task (letter, digit, and symbol). They found that contrast did not modulate the BDA but response time in the low contrast condition was nevertheless significantly increased. The authors took this to mean that the BDA took place later in the processing chain and after early perceptual processing, but another explanation cannot be discounted, that increased task difficulty does not always equate with larger BDA. Similarly, BDAs are usually associated with tasks that have more processing steps, however, in the task described above, the BDA disappeared once target and probe stimuli were presented sequentially or even partly overlapping despite the fact that the two conditions did not involve a different number of processing steps (but a different sequence).

Using functional magnetic resonance imaging (fMRI), Pollman, Zaidel, and von Cramon (2003a) shed light on this issue. They investigated the neural mechanisms underlying the BDA in a letter-matching task similar to Banich and colleagues, comparing patterns of activation in the shape-match and identity match conditions, and in the within visual field and between visual field conditions of a letter-matching task. The task consisted in deciding whether two of four letters presented in a V-display matched. As in previous studies, the match occurred either in the left visual field (LVF), the right visual field (RVF) or between visual fields (BVF). The main findings showed that in the simpler shape-matching condition, unilateral matches produced less activation in the hemisphere of input than did bilateral matches (i.e. activation was lower in the left hemisphere during RVF matches than activation in the left hemisphere during bilateral matches). In contrast, in the more difficult name-matching task, unilateral matches produced more activation in the hemisphere of input than did bilateral matches. This suggests that during the simpler shape-matching task, the processing load is lower and dealt with more efficiently when one hemisphere processes all relevant inputs. On the other hand, during the more difficult name-matching task, the distribution of relevant inputs to the two hemispheres decreases the processing load. Thus the improved performance in the bilateral condition of more complex tasks cannot be simply explained by increased activation of the same cortical areas across the two hemispheres since more activation was detected bilaterally when matches were presented to a single hemisphere rather than two. This supports the idea that neither increased difficulty, nor a larger number of processing steps *per se*, underlie the BDA, but that the overloading of a specific processing stage in a single hemisphere creates a bottleneck in the unilateral conditions of more demanding tasks. Additional resources are then recruited in the other hemisphere but apparently in a sub optimal manner. However, when inputs are initially presented to each hemisphere, limited resources in the two hemispheres are apparently used more efficiently, which leads to a BDA.

1.3.3 Hemispheric Interaction, Functional Lateralisation, and Handedness

Since the BDA emerges when processing resources in one hemisphere are overloaded, it would be expected that hemispheric interaction would be particularly beneficial when the task to be performed is minimally lateralised. In the case of a highly lateralised task, if the specialised hemisphere were to run out of processing resources, the less specialised hemisphere would be unable to assist in resolving the task. Moreover, if Pollman, Zaidel & von Cramon (2003) are correct and the BDA is in fact due to the overloading of specific processing stages (as opposed to undifferentiated resources), the BDA would not only be affected by the load of a specific processing stage but also by whether this processing stage is highly lateralised or not. As a result, the BDA may be minimally affected by lateralisation even in highly lateralised tasks, if the processes that become overloaded in one hemisphere are themselves not lateralised. Alternatively, the BDA may be more affected in mildly lateralised tasks where the overloaded processing stage is lateralised to a specific hemisphere.

Belger and Banich (1998) hypothesised that a left-lateralised rhyming task would not produce a bilateral advantage despite being apparently more demanding than identity-matching letter tasks. They presented participants with two letters, one in each visual field above the fixation point, and a 3-letter word below the fixation point in either the LVF or the RVF but closer to the midline than the letters and printed vertically. The task consisted in determining whether one of the letters rhymed with the word (e.g. G – SEA, J – DAY). They also tested the same participants with 3-letter and 5-letter shape and identity matching tasks. They found that although the 3-letter identity matching task and the 5-letter shape and identity matching task produced a BDA, the rhyming task did not. They argued, based on response times, that since the rhyming task (~1300 ms) appeared to be more difficult than the 5-letter identity matching task (~800 ms), the lack of BDA was not due to the rhyming task being overly simple and therefore not requiring the distribution of the processing load between the hemispheres. Instead, the authors suggested that since only the left hemisphere can process rhymes, distribution of processing load to the right hemisphere was not possible and therefore this task favoured unilateral visual field processing and more specifically RVF processing. Another possible explanation is that the rhyming task used was too difficult, the processing load too high, and that irrespective of visual field conditions, stimuli needed to be processed serially at some processing stage(s). Unfortunately, varying the processing load in lateralised tasks compatible with the paradigm used by Banich and colleagues is difficult, and Belger and Banich did not attempt it.

Compton (2002), although not specifically interested in the influence of hemispheric lateralisation on hemispheric interaction, designed a task similar to that used by Banich and colleagues (e.g. Banich & Belger, 1990) but the three letters were replaced with faces. In the first experiment, matches occurred between faces presenting the same facial expression (happy/angry) either between identical faces (physical match) or between faces of different individuals with the same facial expression (categorical match). In the second experiment, the task consisted in determining whether two faces represented the same person when their expression was the same (physical match) or when their expression was different (categorical match). Compton found a BDA in both the expression-matching and the identity matching task; however, no difference in BDA was detected between the easier physical-match condition and the more demanding categorical-match condition despite a clear difference in performance between the conditions (expression matching: 81% vs 61% correct; identity matching: 77% vs 52% correct). These results are interesting in the context of hemispheric lateralisation because face perception has been shown to be lateralised to the right hemisphere in individuals suffering from prosopagnosia (Benton, 1990), split-brain individuals (Levy et al., 1972), and in neurologically intact individuals (Kelley et al., 2002; Wirsen, Klinteberg, Levander, & Schalling, 1990) although certain aspects of face recognition have also been shown to be lateralised to the left hemisphere (Everhart, Shucard, Quatrin, & Shucard, 2001; Rossion et al., 2000). Therefore, hemispheric lateralisation is not in itself incompatible with a BDA. It may be that face perception is less lateralised than rhyme perception and consequently has less impact on the BDA but it is also quite possible that in the task used by Compton, the lateralised processes are not those that are overloaded in the within visual field condition. It should be noted that the perception of emotion also involves lateralised processes but that their status remains controversial (see Demaree, Everhart, Youngstrom, & Harrison, 2005; Springer & Deutsch, 1993 for a review). However, since the BDA was present for both angry and happy faces in Compton's study it does not appear that an interaction between face and emotion lateralisation is sufficient to explain the presence of a BDA in the face perception task but not in the rhyme detection task. An alternative explanation is that Compton's tasks were more demanding (as demonstrated by low accuracy rates, averaging around 70%) compared to Banich & Belger's (1998) rhyming task (~80% correct). Unfortunately, response times cannot be compared as they were not reported in Compton's study.

Liederman, Merola, & Martinez (1985) also used a lateralised task in a study investigating hemispheric interaction. The task consisted in determining whether two words, presented either in the same VF or across VF, belonged to the same category. Participants' performance demonstrated a strong RVF/left hemisphere advantage, which was expected given the verbal quality of this task. More surprising was the presence of a significant BDA. Unfortunately, since only two words were used per trial, the perceptual load was not balanced across the two visual field conditions (two words per VF in the within condition and one word in each VF in the across condition) and might have biased performance towards a BDA. Overall, the results of these three studies suggest that a bilateral advantage can be present even in tasks that are lateralised but that the effect of task lateralisation might affect hemispheric interaction differently, depending on whether the lateralised processes are the ones particularly taxed in within visual field processing or, alternatively, depending on the stage of processing (perceptual, decision making, pre-motor) at which the lateralised processes take place. This latter suggestion is speculative, and does not fit well with the results of the studies reviewed above since the rhyme and the categorisation task both seem to rely on lateralised processes taking place at the decision making stage.

Since handedness is related to functional lateralisation (e.g. Cowell & Hugdahl, 2000; Eviatar, Hellige, & Zaidel, 1997; Sequeira et al., in press), it is also expected to affect hemispheric interaction. However, because handedness will be treated extensively in the fourth chapter, it will not be discussed further here other than to say that a limited number of studies mostly reported conflicting results on the effect of handedness on hemispheric interaction (Banich, Goering, Stolar, & Belger, 1990; Belger & Banich, 1998; Eviatar et al., 1997; Hatta & Yoshizaki, 1996).

1.3.4 Hemispheric Interaction and Sex

Many studies of hemispheric interaction have not found any sex differences (e.g. Banich et al., 1990; Liederman & Meehan, 1986; Liederman et al., 1985; Norman et al., 1992) or did not report any (e.g. Banich & Belger, 1990; Banich & Karol, 1992; Belger & Banich, 1992; Compton, 2002; Marsolek, Nicholas, & Andresen, 2002; Merola & Liederman, 1990; Passarotti et al., 2002; Weissman & Banich, 2000; Weissman et al., 2000). However, neurophysiological studies reviewed later in this chapter suggest that some sexual differences in hemispheric interaction are likely. Cowel & Hugdahl (2000) tested 25 males and 32 females in a dichotic listening task consisting of reporting one of two consonant-vowel syllables (/ba/, /da/, /ga/, /pa/, /ta/, or /ka/) presented to each ear. There were three conditions, where participants were asked to report either the left or right ear syllable (non-forced), to report the left ear syllable (forced left), or to report the right ear syllable (forced right). The typical right ear/left hemisphere advantage was found for all conditions and for all handedness groups (right-handed or left-handed/ambidextrous). A main effect of sex was also present indicating that the right ear advantage was greater in men than in women. This is of particular interest here because stimuli presented to the left ear are initially perceived by the right hemisphere, and reporting the syllable requires the left hemisphere, and therefore involves hemispheric interaction. Consequently, different rates of reporting of left and right ear syllable presentations are likely to reflect to some degree the efficiency of interhemispheric integration found in men and women. Cowel and Hugdahl also found that the pattern of responses for the forced right, forced left and the non-forced conditions differed between men and women and interacted with age and handedness suggesting that, in a task that requires hemispheric interaction, men tend to perform differently from women in subtle ways. These results were also consistent with a lower degree of functional lateralisation and greater hemispheric connectivity in females and left-handed males as well as with some interaction between hemispheric lateralisation and connectivity, and age.

1.3.5 Hemispheric Interaction with Regard to Age

1.3.5.1 Childhood and Adolescence

Due to the late development and long maturation of the CC (discussed later), lasting well into the third decade, and callosal changes in old age, behavioural age-dependent changes in hemispheric interaction are to be expected. Banich, Passaroti, & Janes (2000) researched developmental changes in hemispheric interaction in children aged 6 to 14 years. They tested them on the typical 3-letter shape- and identity-matching task and found that for the simple shape-matching task older age was associated with a larger response time BDA whereas for the more complex identity-matching task younger age was associated with a larger response time BDA. A within hemisphere advantage was demonstrated in the shape-matching task whereas a bilateral advantage was present in the identity-matching task. Banich and colleagues interpreted these results mainly as showing that in younger children within hemisphere resources were much more limited than in older children and that therefore younger children benefited much more from the recruitment of resources in the other hemisphere. This was particularly true for the more complex task. Opposite trends in the simpler task, however, suggest that age related differences in within hemisphere resources might interact with callosal development with age. Thus, these results also suggest that when the processing load is not too high, across hemisphere processing in older children is more beneficial because with increased myelination of callosal axons, there may be an associated increase of interhemispheric transfer speed.

This hypothesis is supported by another developmental study (Hagelthorn, Brown, Amano, & Asarnow, 2000) in which forty-two children aged 7 to 17 years performed a 2-letter matching task and in whom evoked potential interhemispheric transfer time was also measured. They found that the accuracy and RT BDAs increased with age, but interhemispheric transfer time decreased with age although the latter trend did not reach significance.

A relationship between callosal development and hemispheric interaction was also demonstrated in a study investigating the effect of phenylketonuria in children (Banich, Passarotti, Nortz, & Steiner, 2000). Phenylketonuria affects myelination of axons, including those that make up the corpus callosum. Therefore investigating hemispheric interaction in this population can indicate whether callosal conduction differences can affect hemispheric interaction. Banich et al. found that children treated for phenylketonuria performed similarly to aged-matched controls in the within hemisphere condition of shape and identity letter-matching task. However, in the more difficult identity matching task, they did not benefit as much as controls from hemispheric interaction. It could be argued that since phenylketonuria does not affect specifically myelination of callosal axons, factors other than callosal efficiency may have caused these results; however, the similar performance in all but across hemisphere conditions in the complex task suggest that an explanation based on general deficits of neuronal conduction is unlikely. Therefore these results are consistent with the view that callosal development as well as changes in hemispheric resources are associated with the BDA as a function of age.

A fourth study (Chicoine, Proteau, & Lassonde, 2000) used a different paradigm to demonstrate age-related differences in hemispheric interaction in children. Chicoine, Proteau, & Lassonde administered a manual aiming task to twenty 6-7 year old children, twenty 11-12 year old children, twenty adults and four acallosal participants. They hypothesised that since practice of skilled motor tasks with one hand facilitates learning of the same task with the other hand, differences in efficiency of callosal transfer should affect the transfer of motor skills across the hemispheres. The task consisted in aiming at a target (a light) in the LVF, RVF, or in the midline, on a digital tablet; the measure was the deviation from the target. It was found that although skill transfer between hands occurred in older children and adults, this was not the case for younger children and acallosals.

As a whole, the evidence presented above strongly suggests a relationship between efficiency of hemispheric interaction and age in childhood, with increased efficiency of hemispheric interaction in older children.

1.3.5.2 Old Age

Reuter-Lorenz & Stanczak (2000) specifically investigated the effect of old age on bihemispheric integration. They tested twenty-three healthy older adults (65-75 year old) and twenty younger adults (18-25 years old) on the three and five-letter shape and identity matching tasks. Older adults responded slower and less accurately than younger adults but demonstrated, in the simple shape-matching task, a within hemisphere advantage of a magnitude similar to that of younger adults. However, in the more complex identity-matching task, older adults demonstrated a greater across hemisphere advantage compared to younger adults. Reuter-Lorenz (2002) suggested that greater hemispheric interaction in older adults might reflect a compensatory process that counteracts the decline in cognitive resources (in one hemisphere) associated with the ageing process by recruiting more resources in the other hemisphere. Alternatively, older brains might become less specialised and less functionally lateralised, a process called de-differentiation, which might lead to a greater spread of activation across the two hemispheres, decrease the efficiency of cognitive processes, and favour hemispheric interaction.

An fMRI study (Cabeza et al., 2002) in older adults suggest that a compensatory role of hemispheric interaction in ageing is a more likely explanation. In this study, low and high functioning older adults performed a paired-associates word recall task and a source recognition task where participants had to determine whether list words had initially been presented to them visually or auditorily. Low-performing older adults demonstrated unilateral activation in these tasks similar to the younger controls, while high-functioning older adults showed bilateral patterns of activation. Furthermore, task performance was similar between high-functioning older adults and the younger controls, while the low-functioning older adults performed significantly worse than these two groups. This pattern of results is inconsistent with the de-differentiation hypothesis since it would predict lower functioning in less lateralised individuals; instead the results of this study suggests that in older individuals greater hemispheric interaction is associated with better performance and is consistent with a compensatory role of hemispheric interaction in old age, possibly to make better use of decreased cognitive resources.

1.3.6 Hemispheric Interaction and Attention

The role of attention in hemispheric interaction and the role of hemispheric interaction in attention have produced challenging questions ever since split-brain research demonstrated that attention was not a process as unitary as was originally thought (see Corballis, 1995; M. Gazzaniga, 2000, for a review). Performance of split-brain individuals showed that each hemisphere could concurrently attend to separate stimuli in certain circumstances (see McMains & Somers, 2004, for related findings in intact individuals), while in others they could not. For instance, split-brain individuals can conduct a simple visual search task in parallel in the two visual fields whereas intact individuals cannot, thus suggesting a role of the CC in attention. However, it has also been demonstrated that split-brain individuals are affected by negative priming (Lambert, 1993). Thus, split-brain individuals who were asked to categorise digits presented to the RVF as odd or even responded significantly slower, than did the controls, when a to-be-ignored digit was presented to the LVF. This shows that some attentional effects are not mediated by the CC (see also Lambert & Naikar, 2000). Overall, however, split-brain individuals demonstrate clear deficits in attention which may partly be related to the underlying pathology (epilepsy) but which are more likely to be the product of the section of the CC (Afraz, Montaser-Kouhsari, Vaziri-Pashkam, & Moradi, 2003; Corballis, 1995; Ellenberg & Sperry, 1979).

Levy, Trevarthen, and Sperry (1972) demonstrated that lateralisation of attentional control could be manipulated. They tested split-brain participants in a chimeric face recognition task in which halves of two different faces were presented to separate visual fields. The task consisted in reporting which face had been seen either by pointing in free vision to an array of faces positioned in front of participants or by naming the previously memorised identity of a face. When pointing, split-brain individuals reported significantly more faces (82%) viewed in the LVF than in the RVF. Remarkably, this was also the case when they used their right hand. However, when they were asked to voice the identity of the face, the pattern was reversed. This happened even when the responding instructions were switched just before a response was given. This suggests that faces presented to each visual field were attended concurrently and recognised, but that the attentional focus was shifted depending on response instructions. These findings also speak against a unified model of attention. Since such behaviours are not seen in intact individuals it is probable that some modulation of attentional control in each hemisphere is mediated by the CC.

A study (Hines, Paul, & Brown, 2002) investigating individuals with agenesis of the CC also supports this proposition. Ten individuals with agenesis of the CC and nine controls were tested in a cued target detection task in which cues were valid 80% of the time. In invalid trials, attention needed to be redirected to the target location which occurred within visual field for half of the trials and across visual field for the other half. It was found that although individuals with agenesis of the CC did not differ from controls in the cost of shifting attention within visual fields, shifting attention between visual fields was significantly slower in these individuals.

In neurologically intact individuals, a role of the CC and hemispheric interaction in attention has also been demonstrated. Rueckert, Baboorian, Stavropoulos, & Yasutake (1999) assessed the influence of callosal efficiency on attention in forty-two healthy adults. They used two tasks to assess the efficiency of callosal transfer. A bi-manual coordination task specifically relying on the transfer of motor signals was conducted to assess the efficiency of the anterior CC (where pre-motor and motor fibres cross). A line comparison task, relying on the transfer of perceptual information was conducted to assess the efficiency of the posterior CC (where perceptual and associative fibres cross). Another two tasks measured sustained and focused attention. Sustained attention was measured with a simple vigilance task lasting 20 minutes, in which participants were asked to press a button when an “X” appeared on screen at inter-stimulus intervals (ISI) varying between 2 and 18 seconds. Focused attention was measured in a tachistocopic letter task in which participants had to determine whether the middle-letter of three horizontally presented letters matched any of the other two letters lateralised to a separate visual field. Results suggested that the efficiency of the anterior CC was related to the capacity to sustain attention over the entire 20 minute of the vigilance task, while the efficiency of the posterior CC was related to the ability of maintaining attentional focus for longer ISIs of the vigilance task. A general attention measure did not correlate with either of the tasks assessing callosal efficiency.

While the studies reported so far necessarily involved hemispheric interaction, they were more focused on the integrity and efficiency of callosal transfer than interaction of the two hemispheres per se. Studies reviewed previously and interested in assessing hemispheric interaction by comparing within and across hemisphere performance, such as the shape and identity letter-matching tasks, suggest that hemispheric interaction might have an attentional effect by reallocating resources based on task demands (low/high) and on available hemispheric resources. Another line of evidence also suggests that hemispheric interaction might modulate attentional processes by acting as a filter or a gate, thus avoiding interference from irrelevant information (see Banich, 1998 for a discussion of the role of hemispheric interaction in attentional processes based on different models of attention). Banich & Passarotti (unpublished but reported in Banich, 1998) tested the role of hemispheric interaction in attentional filtering. They presented participants with coloured geometrical shapes. Participants had to determine whether two of three shapes, in a display similar to that of the letter-matching task, matched on their form while colour was ignored. The match occurred either within VF or across VF and the degree of selective attention required to perform the task was varied by changing the colour of the matching and non-matching shapes. There were four conditions with increasing attentional demands: the probe had the same colour as the target while the non-matching shape did not, thus providing redundant information congruent with the task; the probe had the same colour as the target but so did the non-matching shape therefore providing irrelevant information; the probe had a colour different from the target and so did the non-matching shape, thus like the last condition, also providing irrelevant information; or the probe had a colour different from the target while the non-matching shape had the same colour as the target, therefore providing conflicting information. Across hemisphere performance was found to be significantly better in the last condition which required the highest degree of attentional filtering since in this condition colour was completely misinformative. These findings, and consistent results using a global-local paradigm (Weissman & Banich, 1999), conflicting letter-colour matches (Sohn, Liederman, & Reinitz, 1996), or dual tasks (Merola & Liederman, 1990; Mikels & Reuter-Lorenz, 2004) demonstrate that hemispheric interaction plays a role in attentional processes, not only by allocating resources based on task demands and resources available, but also by filtering conflicting information.

1.3.7 Hemispheric Interaction and Practice

Very little is known about the effect of practice in a given task and hemispheric interaction. However, Liederman, Merola, & Martinez (1985) were the first to observe that the BDA decreases with practice. They tested thirty individuals in a word categorisation task which consisted in determining whether two words, presented either in the same VF or across VF, belonged to the same category. Performance in across hemisphere trials was faster and more accurate than in the within hemisphere trials in the first half of the experiment demonstrating a bilateral advantage. However, with practice RVF performance in the second half of the experiment became faster and more accurate than bilateral performance. The interpretation of these results is difficult due to the use of a lateralised task. Can these findings be generalised and do they apply to hemispheric interaction in general? Or are they an effect of the lateralisation of certain processes?

Weissman & Compton (2003) reanalysed data from a typical non-lateralised shape and identity letter-matching task (see Eviatar & Zaidel, 1992 for a discussion of letter processing lateralisation) as well as a modified version of this task where each letter is made up of smaller local letters which are either congruent with the global letter or not, to assess the effect of practice on hemispheric interaction. Performance in each task demonstrated a significant BDA in the first half. However, in the second half the BDA had disappeared. This change was achieved mostly by within visual field processing improvements, and minimal improvements in across visual field performance were detected.

Based on limited data it appears that hemispheric interaction is influenced by practice. However, the specific mechanisms underlying this effect are little understood. Presently there is no explanation for the lack of a practice effect in the bilateral condition.

1.4 Interhemispheric Transfer and the Corpus Callosum

Hemispheric interaction can be mediated via three main routes: the corpus callosum, the anterior commissure, or sub-cortically. The question of which route can transfer what sort of information has been hotly debated and it is only recently that more definitive answers have been found.

Split-brain studies have clearly demonstrated that certain types of information cannot be transferred after section or partial section of the corpus callosum. For instance, after full section, complex visual information cannot be compared across the visual hemifields and words presented to the right hemisphere cannot be voiced by the language centres in the left hemisphere; however, the left hand controlled by the right hemisphere can correctly identify them by pointing to images with the same meaning (Corballis, 1995; Gazzaniga, Bogen, & Sperry, 1965; Sperry, 1981; Sperry, Gazzaniga, & Bogen, 1969). Also, while each hand can only be controlled by the contra-lateral hemisphere, in contrast, both arms can be controlled by each hemisphere and temporal synchronisation of the two hands is possible in complex bi-manual movements (see M. Gazzaniga, 2000, for a review).

It has been more difficult to define precisely the type of higher-order information that can be transferred by routes other than the corpus callosum. Results of a number of experiments in split-brain individuals suggested that some complex information could be transferred sub-cortically. For example, split-brain individuals appeared to be able to compare digits, convey face information across the hemispheres (Sergent, 1990), and name letters (Lambert & Naikar, 2000) or even pictures presented to the left visual field (Myers & Sperry, 1985). However, such results can be better explained by specific strategies used by split-brain patients such as probability guessing and cross-cueing between the hemispheres (see Corballis, 1994; Corballis, 1995, for a review) or by control of the responding hand by the two hemispheres (Kingstone & Gazzaniga, 1995).

An alternative explanation is that in many split-brain patients some callosal fibres are spared during surgery. An MRI investigation found that the patients tested in one of the studies (Kingstone & Gazzaniga, 1995) reporting sub-cortical transfer of complex information had some spared callosal fibres and that part of this study's results may be explained by callosal transfer of semantic information (Funnell, Corballis, & Gazzaniga, 2000a). Other studies have shown that, without sparing of callosal fibres, there is no or minimal subcortical transfer of visual information such as colour, size, luminance, form, or letter information (Banich, Passarotti, Nortz et al., 2000; Corballis & Corballis, 2001; Forster & Corballis, 2000; Intriligator, Hénaff, & Michel, 2000).

Based on these studies and others (see Corballis, 1995; M. Gazzaniga, 2000; Springer & Deutsch, 1993; Zaidel & Iacoboni, 2002b, for a review) it is broadly accepted that sub-cortical transfer of information is only possible for some location, orientation, movement, and location-based attention information as well as some emotional information. In contrast, most high-level cognitive information necessary to complete complex perceptual, semantic, and visuospatial tasks cannot be transferred in the absence of the corpus callosum. However, to interpret correctly findings of such transfer it is particularly important to have a good understanding of the structure, and morphology of the CC as well as its relationship with other brain structures, and particularly its cortical projections in order to understand how it might affect hemispheric interaction.

1.4.1 Corpus Callosum: Structure and Function

1.4.1.1 Callosal Structure

The corpus callosum is the main fibre tract connecting the two cerebral hemispheres. It is composed of more than 200,000,000 fibres connecting most cortical areas of one hemisphere to those of the other hemisphere. However, the distribution of callosal connections is not even, so that some areas of the cortex have many interhemispheric connections while others only have few.

Most cortical areas have callosal connections so that approximately 70-80% of cortex is callosally connected (Kaas, 1995). It is still largely unknown why certain cortical areas differ in density and distribution of interhemispheric connections.

Callosal connections can be grouped in three types: homotopic, heterotopic, and heterolateral. Homotopic connections are those connections that connect one area of the cortex with the corresponding area in the opposite hemisphere and neurons in these areas show similar response properties. Heterotopic connections link portions of one area of the cerebral cortex with a portion of the same area in the other hemisphere that does not share the same receptor field. Typically, such connections link mirror-image positions in the same modality. Finally, heterolateral connections are those found between different areas of the cerebral cortex such as between the sensory area and the contralateral motor area. These connections can be homotopic or heterotopic, however, most heterolateral connections seem to be heterotopic. They also tend to be reciprocal and, in general, areas that are callosally connected are also connected intrahemispherically. As a consequence, areas in opposite hemispheres may be able to communicate via different routes (Innocenti & Bressoud, 2002).

Based on Witelson's (1995) partition, the CC is usually divided in three main regions which are themselves subdivided in sub-sections. The anterior third is composed of the rostrum and the genu, the middle third is made up of the body of the CC, and the posterior third consists of the isthmus and the splenium (Figure 1-4).

Interhemispheric fibres originating in different areas of the cerebral cortex cross the midline in specific locations in the CC (Aboitiz, Ide, & Olivares, 2002; Pandya & Seltzer, 1986): fibres with their origin in the frontal lobe traverse the rostrum and the ventral part of the genu, while pre-motor fibres, including those of the supplementary motor region, cross the rostralmost portion of the body of the corpus callosum. Fibres originating in the primary sensorimotor areas traverse the middle of the body of the corpus callosum, and posterior parietal cortex and mid- and caudal superior temporal fibres (including those from the primary and secondary auditory cortices) cross in the caudal portion of the body of the CC and the isthmus. The isthmus is also believed to contain fibres connecting the parasylvian regions involved in language processing (Aboitiz et al., 2002). Finally, fibres interconnecting the occipital lobes, Brodmann's areas 18 and 19, are restricted to the splenium. As a general rule, fibres connecting areas that are more rostral tend to cross the corpus callosum more rostrally and those connecting caudal areas of the cerebral cortex tend to traverse the corpus callosum in its caudal sections.

Commissural fibres from a specific cortical area tend to occupy a distinct location. This is especially true of the interhemispheric fibres of the primary and somato-sensory cortices as well as of the occipital lobes. In the CC, these fibres do not mingle with those of other fibre systems. Fibres originating in other cortical regions, however, do tend to be intermingle with fibres coming from other areas. This is probably due to their similar architectonic features, developmental time course and also the connectional patterns of the cerebral cortex, as overlap of callosal fibre populations tends to occur between cortical areas that have contralateral heterotopic connections (Hoptman & Davidson, 1994).

The distribution, type and size of callosal fibres are important since thicker (myelinated) fibres are able to transfer signals faster than smaller ones. Callosal fibres tend to be thicker in the middle of the CC (primary and secondary somato-sensory connections) in monkeys (La Mantia & Rakic, 1990). However, Aboitiz et al. (Aboitiz, Scheibel, Fisher, & Zaidel, 1992a) found that in humans, thicker callosal fibres tend to be found more caudally, in the posterior part of the body of the CC. These large fibres seem to connect the primary and secondary auditory areas and may contribute to the production of an auditory map in space. Another region with a high proportion of large fibres is the posterior splenium which may help to fuse the two hemifields and possibly participate in stereoscopy (Aboitiz, López, & Montiel, 2003).

Thinner fibres are found in higher density in the genu, and in the mid splenium which connect prefrontal areas and the higher-order processing areas of the temporal and parietal lobes respectively (Aboitiz et al., 1992a).

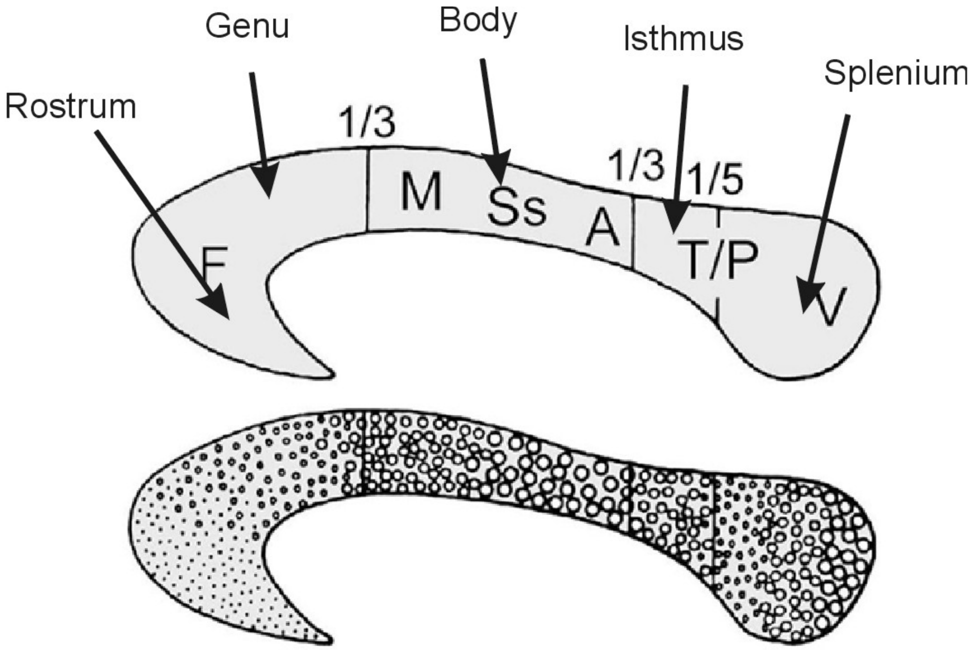

Figure 1-4. Cross-section of the human corpus callosum indicating the representation of different cortical regions (top). Regional differences in fibre composition along the corpus callosum (larger circles indicate larger fibre diameters) (bottom). A., auditory fibres; F, frontal fibres; M, motor fibres; Ss, somatosensory fibres; T/P, temporoparietal fibres; V, visual fibres. The corpus callosum is divided in thirds based on Witelson's partition (1995). The anterior third (left) consists of the rostrum and genu, the middle third forms the body, and the posterior third consists of the isthmus (one fifth of the total length of the CC) and the splenium. Adapted from (Aboitiz & Montiel, 2003).

In monkeys, the density of callosal connections increases from primary to association cortex for all sensory modalities, which suggests that information may be partially processed before being transferred (Hoptman & Davidson, 1994). It is unclear whether this is also the case in humans.

There is some uncertainty about the relationship between the size of the CC and fibre density. It was first thought, based on monkey studies, that CC size was not related to the number of callosal fibres (La Mantia & Rakic, 1990). However, two post mortem human studies seem to suggest otherwise: when fibres of all sizes (and not only large ones as in animal studies) are considered, CC size does correlate with number of fibres (Aboitiz et al., 1992a; Hoptman & Davidson, 1994). This is particularly important because, as we will see later, individual differences (sex, handedness, age), and some clinical differences (dyslexia, schizophrenia, bi-polar disorder) have been associated with significant CC size differences which may relate to different numbers of callosal fibres in specific regions of the CC.

1.4.1.2 Functions of the Corpus Callosum

The corpus callosum appears to have initially developed out of a need for fast interhemispheric transfer of visual and other sensory information in order to achieve midline fusion. It has been shown in cats that there are many more callosal fibres connecting receptor fields close to the midline in visual areas 17 and 18 and that the CC is necessary for the processing of depth information in stereoscopic vision (see Innocenti & Bressoud, 2002; Ptito, 2002 for a review) and for binocular integration (Saint-Amour, Lepore, Lassonde, & Guillemot, 2004). Aboitiz et al. (2002) argued that in evolutionary older mammals, such as monotremes (echidna, platypus) and marsupials (kangaroos) midline fusion was achieved by fibres crossing the anterior commissure and that it is probable that in modern mammals, with increased brain size and progressive migration of topographical sensory maps (originally located in the midbrain in reptiles and birds) to the cortex, the need for fibres crossing closer to the sensory centres became more pressing. Over time, the advantage of fast interhemispheric transfer via callosal fibres may have been extended to the midline fusion of sensory and motor information and used to synchronise processes in the two hemispheres, and share cognitive resources more efficiently.

Clinical and split-brain studies have shown that, in humans, visual information is transferred through the splenium, auditory information through the isthmus, somato-sensory information through the posterior midbody, and motor information through the anterior midbody. Furthermore a role of the isthmus in the transfer of linguistic information has been demonstrated (e.g. Funnell, Corballis, & Gazzaniga, 2000b). However, since most callosal fibres connect higher-order areas, this suggests that the CC is not involved only in the transfer of simple perceptual information but also transfers pre-processed information between the cerebral hemispheres. Callosal fibres also participate in the binding of stimulus features across the midline of the visual field (Engel, König, Kreiter, & Singer, 1991; Innocenti, Aggoun-Zouaoui, & Lehmann, 1995).

The participation of the CC in higher-order processes has been more difficult to demonstrate. However, in recent times more evidence has accumulated demonstrating a role of the CC in attentional processes. Dorion et al. (2002) showed that attention-shifting performance in Alzheimer patients was significantly related to the atrophy of the anterior CC although performance in attentionally more demanding tasks was also related to the posterior CC.

The CC has also been shown (in the cat) to be essential to the synchronisation of oscillatory neuronal responses in the visual cortex (Engel et al., 1991) which has been proposed to serve to bind stimulus features within and between the visual fields (see also Nowak, Munk, Nelson, James, & Bullier, 1995; Pulvermuller & Mohr, 1996). Engel et al. showed that when cells sensitive to movement in a specific orientation were stimulated close to the midline of the visual field, cells in the primary visual areas of the two hemispheres synchronised their oscillation so that no lag was detectable. To determine whether this synchronisation occurred through sub-cortical or callosal connections, the experiment was repeated in cats whose CC had been severed. The lack of synchronisation in these animals suggests that synchronisation of cells in the two hemispheres occurs via callosal fibres (see also Munk, Nowak, Nelson, & Bullier, 1995). Since cell oscillations synchronise at a frequency of around 40Hz, Aboitiz, Lopes, & Montiel (2003) have suggested that given the length and properties of callosal fibres, only very large (> 3 μm) callosal fibres would be able to convey these signals. They also hypothesise that this spread of activation is not limited to early perceptual information but might be involved in the synchronisation of higher-level cell ensembles.

A role of the CC in the formation of memory traces has also been demonstrated (Christman & Propper, 2001; Cronin-Golomb, Gabrieli, & Keane, 1996; Kavcic et al., 2000).

Clarke & Zaidel (1994) suggested that the CC might also be involved in the establishment and/or maintenance of an hemispheric arousal bias. This hypothesis is based on the relationship they found between CC size and functional lateralisation of certain visual and tactile discrimination tasks which at the group level are not performed better by the left or right hemisphere. They found that individuals with larger CCs tended to have better RVF and right hand performance whereas individuals with smaller CCs tended to have better LVF and left hand performance. This may reflect a greater capacity of the left hemisphere to inhibit the right hemisphere in individuals with larger CCs, and a decreased inhibition of the right hemisphere in individuals with smaller CCs. Although this hypothesis is speculative, supporting evidence has been found in a split-brain patient (Faure & Blancgarin, 1994).

Finally, the CC has also been shown to participate in attention processes and to act as a filter, thus diminishing the interference produced by irrelevant stimuli on the performance of certain processes (Sohn et al., 1996).

1.4.2 Corpus Callosum Development

In development, the CC originates from a section of the hippocampal commissure, from which it eventually separates and migrates to the dorsal part of the hippocampus. The development of the CC is not homogenous. It starts between 8 and 17 weeks gestation and follows an anterior to posterior progression with the genu developing first, followed by the body and the splenium; the rostrum being the exception and developing last at about 18 to 20 weeks (Thompson, Narr, Blanton, & Toga, 2002). Although the CC is formed at birth, it is the brain structure with the slowest maturation. CC fibres begin to myelinate around the fourth postnatal month (Hagelthorn et al., 2000) and continue to do so until the late teens or early 20s (Giedd et al., 1996; M. Keshavan et al., 2002; Rajapakse et al., 1996). Giedd et al. (1996) showed that midsagittal callosal size increases linearly between 4 and 18 years of age and that posterior and mid regions demonstrated more age-related changes than anterior regions. Keshavan et al. (2002) also found an increase in callosal size which was most pronounced in childhood and adolescence but which continued until the beginning of the third decade. Paradoxically, the increase in size of the CC is accompanied by a dramatic decrease in number of fibres (Innocenti et al., 1995). In cat and monkey, 70% of juvenile callosal axons are eliminated. Therefore the increase in CC size is mostly attributable to neural fibres' myelination and growth.

The process of callosal fibre pruning during maturation is particularly interesting because it has been suggested that it may be associated with the development of functional lateralisation and handedness in humans. In a histological study in rats, more symmetrical brains were associated with greater callosal connectivity (Rosen, Sherman, & Galaburda, 1989). In humans, similar findings have been found in post-mortem (Aboitiz, Scheibel, Fisher, & Zaidel, 1992; Aboitiz, Scheibel, & Zaidel, 1992), and MRI studies (Dorion et al., 2000). Thus in less symmetrical brains, fewer callosal connections are maintained which may lead to greater hemispheric isolation while within hemisphere connections are strengthened (Aboitiz, Scheibel, & Zaidel, 1992; Dorion et al., 2000).

These findings suggest that it is particularly important to take into account age, as well as measures of lateralisation (further discussed in the next section) when researching hemispheric interactions, since they may significantly affect the properties of interhemispheric transfer.

1.4.3 The Corpus Callosum, Lateralisation and Handedness

The size of the CC has been related to a number of other measures associated with anatomical and functional lateralisation, as well as handedness. Aboitiz and colleagues (Aboitiz et al., 2002; Aboitiz, Scheibel, Fisher et al., 1992; Aboitiz, Scheibel, & Zaidel, 1992) were amongst the first to clearly demonstrate a relationship between CC size and anatomical differences between the two cerebral hemispheres. More specifically, they found that in males the planum temporale's asymmetry and isthmus size were negatively correlated and that the size of the planum temporale and the size of the CC mid-body were also negatively correlated. Since the language centres are located in the planum temporale and the lateralisation of language has been shown to be also related to the size of the CC (O'Kusky et al., 1988), cerebral asymmetries (Chiarello, Kacinik, Manowitz, Otto, & Leonard, 2004), and to handedness (Moffat, Hampson, & Lee, 1998) these findings suggest an inter-relationship between corpus callosum size, and anatomic and functional lateralisation.

The relationship between CC size and lateralisation seems to be fairly consistent across studies (Aboitiz, Scheibel, Fisher et al., 1992; Aboitiz, Scheibel, & Zaidel, 1992; Dorion et al., 2000; Gootjes et al., 2005) suggesting that greater anatomical or functional lateralisation is associated with smaller callosal size (especially in the isthmus, see Thoma, Yeo, Gangestad, Lewine, & Davis, 2002) although some have argued that this is an oversimplification (Luders et al., 2003).

The relationship between handedness and corpus callosum size does not appear to be as clear (see Beaton, 1997, for a review). Some studies have shown a positive correlation between size of the CC and increased left handedness (Moffat et al., 1998) or mixed-handedness (Clarke & Zaidel, 1994; Habib et al., 1991) but other studies have failed to find any relationship between these measures (Luders et al., 2003; Preuss et al., 2002) or have found an inverse relationship (Hopper, Patel, Cann, Wilcox, & Schaeffer, 1994; Westerhausen et al., 2004). However, a meta-analysis of seven studies suggests that the difference in callosal size between left- and right-handed individuals, if small, is real, and might reflect a higher degree of connectivity in left-handed individuals (Driesen & Raz, 1995). This conclusion is also supported by a diffusion-tensor imaging study suggesting that the CC of left-handed individuals contains a higher density of fibres (Westerhausen et al., 2004). The mixed results of past studies may be partly explained by an inconsistent classification of handedness and/or different CC measurements methods (Clarke & Zaidel, 1994) but they are also likely to be related to complex interactions between functional lateralisation, handedness, and sexual differences (Habib et al., 1991; Moffat et al., 1998). As discussed above, the effect of handedness on hemispheric interactions has also been inconsistent, perhaps for the same reasons. It seems therefore that an effect of handedness is likely to be present but, in order to be detected, might require a continuous measure of handedness and/or the use of more than two handedness categories defining not only the direction (left/right) but also the strength of handedness (weak/strong).

1.4.4 Sexual Dimorphism of the Corpus Callosum

Some studies have demonstrated very clear differences in the CC size between sexes. However, while some studies suggested that the CC was larger in women (Allen, Damasio, Grabowski, Bruss, & Zhang, 2003; Clarke & Zaidel, 1994), others showed those of men to be larger (Aboitiz, Scheibel, & Zaidel, 1992; Sullivan, Rosenbloom, Desmond, & Pfefferbaum, 2001), or failed to show sexual differences (Habib et al., 1991; Luders et al., 2003; O'Kusky et al., 1988; Rajapakse et al., 1996). This inconsistent pattern of results has been partly explained by the use of different measurement methodologies (Cowel, 2002; Driesen & Raz, 1995; Jancke & Steinmetz, 2002; Sullivan et al., 2001).

Overall, differences in CC size are small (1-2%, see Westerhausen et al., 2004) and difficult to interpret. However, sex differences have also been found in callosal shape adding support to the notion that male and female CCs differ in subtle ways. Allen and colleagues (Allen, Richey, Chai, & Gorski, 1991) failed to show callosal area differences between sexes, but demonstrated that the width of the splenium was larger in females than males and reported that females tended to have a more bulbous splenium than men. These findings were confirmed in a study (Davatzikos et al., 1996) using a new mapping technique where MRI images were mapped on templates of typical brains to illustrate CC morphological differences from the norm. Davatzikos et al. (1996) found that the isthmus of female participants was thicker than that of male participants. Davatzikos & Resnick (1998) also found, in an MRI study, that females had a larger and more bulbous splenium.

At the histological level, Aboitiz and colleagues (Aboitiz, Scheibel, Fisher et al., 1992; Aboitiz, Scheibel, & Zaidel, 1992) found that brain asymmetries correlated with different populations of callosal fibres in the two sexes and that in males, but not in females, a population of fast, large (1-3 μm) fibres in the isthmus correlated with peri-sylvian asymmetries. They interpreted these results as showing that males are more likely to show a decrease in callosal connectivity which in turn may explain differences in the degree of functional lateralisation between the sexes. These results are complemented by the findings of other studies which showed that non-consistent right-handed males had a larger CC than consistent right-handed males; and a larger midbody and isthmus were found in consistent right-handed females (Habib et al., 1991), whereas a smaller isthmus was found in consistent right-handed males (Clarke & Zaidel, 1994). These findings also agree with studies showing that male brains are more anatomically (Kovalev, Kruggel, & Von Cramon, 2003; Luders et al., 2005) and functionally (Shaywitz et al., 1995) asymmetrical than female brains and that asymmetrical brains tend to have fewer callosal fibres (Aboitiz, Scheibel, Fisher et al., 1992; Aboitiz, Scheibel, & Zaidel, 1992) or to be associated with smaller callosal sizes (Dorion et al., 2000; Thoma et al., 2002). Put together, these results indicate a complex interaction between sex, handedness and CC size. It is therefore surprising that these differences in connectivity have seldom been shown to produce behaviourally measurable differences between the sexes in hemispheric interaction studies. It may be that subtle interactions between sex, handedness, lateralisation and callosal shape and size make the detection of such effects more difficult.

In addition, ageing also appears to affect the CC and to do so differently in women and men (Thompson et al., 2002).

1.4.5 Corpus Callosum and Ageing

Anatomical and behavioural studies suggests that significant callosal changes take place over the lifespan. Discussed above was the timeline of callosal development which continues into the third decade. However, callosal maturation appears to be detectable well into the six decade after which callosal degeneration seems to be more noticeable.

Aboitiz and colleagues (Aboitiz, Rodriguez, Olivares, & Zaidel, 1996) found an increase of large (> 3 μm) callosal fibres with age (at least until 68 years old). They interpreted this change as a possible consequence of increased automatisation of certain processes with age. Thus highly rehearsed processes such as movement control, might be associated with the thickening of callosal fibres linking the motor cortical areas. This increase was uniform throughout the CC in males, however, in females, it occurred in the anterior and posterior third of the CC indicating a faster communication between higher-order areas of the frontal and temporo-parietal lobes.

Ageing seems to be accompanied by a decrease in callosal size and degradation of callosal fibres (Driesen & Raz, 1995; Hopper et al., 1994; Shaywitz et al., 1995; Suganthy et al., 2003; Sullivan, Pfefferbaum, Adalsteinsson, Swan, & Carmelli, 2002a). However, not all parts of the CC are affected uniformly. Results showing no callosal size differences in older adults compared to younger controls suggest that these changes might occur or become apparent only in individuals over 65 or 70 years (Sullivan et al., 2001). Studies using diffusion tensor imaging (Moseley, 2002; Sullivan et al., 2002a) in men ranging from 23 to 76 year of age have demonstrated different rates of change in distinct sections of the CC. The genu was the region affected by the greatest decline, with the splenium showing only a modest deterioration. These changes are likely to be due to the demyelination of callosal fibres and loss of myelinated axons. Consistent with these results, a longitudinal MRI study of 215 men (Sullivan et al., 2002a) also showed a decrease in callosal size, defined by thinning (.9% per year over 4 years) and elongation of the CC. In this study, the rate of callosal decline was also shown to be associated with decline of cognitive performance as measured by a trail-making test and a Stroop task. In contrast, another MRI study (Salat, Ward, Kaye, & Janowsky, 1997) found age-related callosal decline in women (genu and body) but not men. However, this difference can probably be explained by the different demographics of these studies. Whereas the previous two studies had assessed only men mostly younger than 70 years of age, Salat et al. tested fewer participants but with a mean age of 77.7 years.

As a whole, these findings appear to show that callosal changes take place with age and involve increased connectivity at least until middle-age and for highly automatised processes. A decline in old-age is reflected by thinning of the CC particularly in the anterior regions. Furthermore, the pattern of decline maybe sex specific and becomes particularly apparent in the seventh decade of life.

Consequently, it would seem that hemispheric interactions are likely to be affected by age and sex, and possibly only through a subtle interactions between these variables.

1.4.6 Behavioural Implications of Callosal Differences

Callosal differences would be of little practical interest were they not to involve behavioural consequences. Some relationships between callosal variability and behaviour (e.g. handedness, functional lateralisation) have been discussed in the previous section and will not be discussed here. Others are more relevant to topics treated in detail in future chapters and will be treated later. Therefore, a limited number of studies showing a relationship between callosal properties and behavioural consequences will be presented here.

1.4.6.1 Split-Brain and Acallosal Individuals

One of the more striking effect callosal differences can have on behaviour have been demonstrated in patients in whom the CC has been cut as a treatment for intractable epilepsy and in individuals with agenesis of the CC (ACC) in whom the CC has developed only partially or not at all. Findings relating to these two groups will be discussed further later, therefore only one example will be given here.

In neurologically normal individuals who fixate their gaze in the middle of the visual field, stimuli appearing in the LVF are perceived by the right hemisphere whereas stimuli presented to the RVF are perceived by the left hemisphere. Since each hemisphere controls the contra-lateral hand, responding with one hand (by pressing a button) to a stimulus presented on the same side as the responding hand (direct route) is faster than if it is presented on the other side (crossed route) because information need not be transferred to the other hemisphere to elicit a motor response. The difference in response between the crossed and direct conditions is called the crossed-uncrossed difference (CUD). In normal individuals the CUD averages 2-6 ms. In split-brain individuals and ACCs, however, this measure is dramatically lengthened to around 20 ms in ACCs and 40 ms in split-brain patients (Berlucchi, Aglioti, Marzi, & Tassinari, 1995; Forster & Corballis, 1998; Iacoboni, Fried, & Zaidel, 1994). Thus the integrity of the CC is clearly essential for the fast transfer of information between the hemispheres even when this information can be transferred via other channels.

1.4.6.2 Functional Lateralisation

Most callosal fibres are excitatory, however the functional effect of the information relayed through these fibres can be excitatory or inhibitory in nature depending on the type of inter-neurons being activated (see Saron, Foxe, Simpson, & Vaughan, 2002, pp. 208-209). Consequently, larger CCs can potentially increase the cross-activation between the hemispheres or inhibit more the less active hemisphere. Yazgan, Wexler, Kinsbourne, Peterson, & Leckman (1995) conducted an experiment to clarify this issue. They were also interested in determining whether functional lateralisation was related to CC size. They hypothesised that if callosal function was mostly excitatory in nature, individuals with a larger CC should demonstrate a smaller lateralisation bias on task known to be functionally lateralised, than those with a smaller CC, because activation in one hemisphere would more easily spread to the other in the first group. Alternatively, if the CC had mostly an inhibitory function, individuals with a larger CC should show a greater lateralisation bias since inhibition would be spread more efficiently from the more active to the less active hemisphere. Yazgan and colleagues administered four tasks known to be lateralised to eleven individuals in whom the size of the CC was measured by MRI. They found that callosal size was significantly negatively correlated with lateralisation of a dichotic listening task ($r = -.70$), with a line bisection task ($r = -.61$), and with a leftward turning bias ($r = -.70$), suggesting that greater callosal size produced a greater spread of activation to the less active hemisphere and thus decreased the laterality bias in these tasks. Consistent with these findings, they also found that greater CC areas were associated with less interference in a dual task paradigm where the two tasks were presented to the same hemisphere ($r = -.62$) or not ($r = -.73$). Manually connecting sequential numbers was slowed less in individuals with larger CCs when a verbal task, consisting in conjugating irregular verbs in their past tense, was introduced. These results were interpreted as showing that interference was decreased in individuals with larger CCs because resources in the contralateral hemisphere were more efficiently recruited in these individuals.

1.4.6.3 Development and Age

In pre-term babies, the CC has been shown to be thinner than in full-term babies. Nosarti et al. (Nosarti et al., 2004) assessed seventy-seven individuals, aged 14-15 years, and born before 33 weeks of gestation, as well as age-matched controls. Total callosal areas of the pre-term adolescents were 7.5% smaller than those of the controls. This size difference mostly affected posterior callosal regions and in boys was related to decrease in verbal IQ and verbal fluency.

In younger but not older adults the integrity of the CC (splenium) as measured by diffusion tensor imaging has been shown to be related to response time in a visual detection task consisting in pressing a button when a target (filled circle) was presented or another button when a familiar stimulus (filled square) or a novel stimulus (photograph of varying everyday objects) were presented (D. J. Madden et al., 2004). This suggests that behavioural performances related to CC properties are not uniformly affected across ages.

1.4.6.4 Sex

Davatzikos & Resnick (1998), mapped MRI images of the midsagittal callosal surface of 114 individuals aged 56-85 years onto templates of "typical" CC sections in order to quantify their deviation from the norm. They found that females had a larger and more bulbous CC (splenium) and that in females but not males the shape of all sections of the CC was significantly associated with cognitive performance, which was assessed with card rotation, object identification, letter fluency, and recognition memory tasks.

1.4.6.5 Plasticity of the Corpus Callosum: Morphology and Behaviour

In musicians, callosal connectivity appears to be affected by behaviour since a group of thirty professional pianists and string instruments players has been shown to have larger CCs, probably because the extensive practice of bimanual motor skills, which require interhemispheric transfer, has affected the development of their CC and their functional lateralisation (Schlaug, Jancke, Huang, Staiger, & Steinmetz, 1995). However, it has not been excluded yet that this effect might be at least partly due to a predisposition of certain individuals to play music because they possess a larger CC, and are functionally less lateralised. This view appears to be supported by twin studies showing that 94% of the variance in CC size can be explained by genetic factors (Scamvougeras, Kigar, Jones, Weinberger, & Witelson, 2003) and that this genetic influence remains strong throughout the lifespan (Pfefferbaum, Sullivan, & Carmelli, 2004). However, a study (Juraska & Kopcik, 1988) of rats reared in enriched environments has also shown that these rats develop a larger CC than rats reared in isolated environments. Other environmental effects on the size and shape of the CC have been demonstrated in relation to social interaction (Sanchez, Hearn, Do, Rilling, & Herndon, 1998), and pre-natal alcohol exposure (Bookstein, Sampson, Steissguth, & Connor, 2001; Riley et al., 1995). Furthermore, bilingual individuals have been shown to have a larger anterior midbody than non-bilinguals (Davatzikos & Resnick, 1998). Since none of the bilinguals tested in this study had a familial bilingual upbringing it appears that at least in certain conditions, callosal differences may be only due to environmental factors (bilingual education at school). It may be that under "normal" circumstances (e.g. typical environment, no intensive musical training) genetic influences prevail and that environmental factors only have a noticeable effect under atypical circumstances. It is more likely that genetic and environmental factors interact. Interestingly, the relationship between CC size and musical practice seems to be only present in males and not in females and might reflect the fact that women are functionally less lateralised and, as discussed previously, might also on average have a larger CC than males (Lee, Yi, & Schlaug, 2003).

1.5 Summary

The evidence presented in this chapter suggests that hemispheric interactions are powerful mechanisms affecting most processes involved in complex cognitive tasks. Some variables affecting hemispheric interactions are relatively well understood. It is known that hemispheric interactions are more beneficial for more complex and demanding tasks. It is also known that hemispheric interaction is a mechanism used to maximise the efficient use of limited cognitive resources spread across the cerebral hemispheres and that this applies to all modalities and a large variety of tasks. It is also understood that hemispheric interactions are modulated by, and interact with, complex attentional processes and might provide a gating mechanism to isolate the hemispheres when interactions would not be beneficial.

However, it is not well understood how interhemispheric transfer and certain factors affecting transfer might affect hemispheric interactions. Since complex cognitive processes require more hemispheric interaction and callosal transfer is necessary for sharing complex information between the hemispheres, it is particularly important to investigate how variables affecting callosal function influence the efficiency of hemispheric interactions. Differences in callosal connectivity suggest that variables such as functional lateralisation, handedness, sex, and age could affect callosal transfer and hemispheric interactions. Yet, past studies have often failed to show such effects or have produced contradictory results. The effects of practice and hemispheric arousal on interhemispheric interaction are also mostly unexplored.

One possible reason for the failure to detect consistently the effects of these variables is that they are likely to interact with each other. Thus certain sex effects might only be evident at certain ages and effects of handedness and functional lateralisation might be more evident in males. Hemispheric arousal effects might also affect these relationships in unknown ways since this variable has seldom been researched. Consequently, it is important to use designs and statistical analyses that are particularly suited to detecting small differences in performance, and able to account for multiple interactions. This is likely to require large sample sizes, large numbers of experimental trials, and tasks complex enough so that a sufficient spread of performance is available, without ceiling effects. The statistical analysis used should also be adequate to detect and define the types of interactions expected.

Based on these findings, the following chapters will attempt to better define the relationship between hemispheric interaction, callosal efficiency, and other factors known to vary in different individuals.

The second Chapter will discuss two tasks that measure some aspects of callosal efficiency and hemispheric interaction respectively, and argue that these tasks are well suited to better define the relationship between these variables. Methodological issues relating to the validity of these tasks will also be presented.

In Chapters 3, 4, and 5 a clear link between hemispheric interaction and callosal efficiency will be shown using behavioural measures, and their association with sex and age will be discussed. Chapter 3 will demonstrate that in right-handed individuals the efficiency of hemispheric interaction is inversely related to interhemispheric transfer. Chapter 4 will focus on the effects of handedness and functional lateralisation on hemispheric interaction, and in Chapter 5, the effects practice has on hemispheric interaction will be scrutinised.

Chapter 6 will test whether individuals with dyslexia, who are known to show atypical interhemispheric transfer, also demonstrate a hemispheric interaction deficit, and will investigate how attentional factors might be related to performance.

Finally, Chapter 7 will show that hemispheric interaction is influenced by the lateralisation of hemispheric activation.

A new measurement method capable of assessing cerebral activity in typical psychological studies will be presented in Chapter 8, and its validity and sensitivity demonstrated.

Finally, Chapter 9 will synthesise the present findings and outline certain unresolved issues and how future research might address them.

CHAPTER 2

2.1 Methodology

This chapter will scrutinise methodological issues related to the measurement of variables used in the following chapters. As discussed in Chapter 1, it is expected that the efficiency of interhemispheric transfer would affect the efficiency of hemispheric interactions and that both these variables are likely to be modulated by factors such as age, sex, handedness, functional lateralisation, and attention. Therefore the practical aspects of measuring the efficiency of interhemispheric transfer and hemispheric interactions will be discussed first. The results of two pilot studies will be presented to demonstrate the effect certain experimental variations (shape of display and type of response) have on the measure of hemispheric interaction.

The assessment of interhemispheric transfer and hemispheric interaction requires equipment allowing high measurement accuracy. Interhemispheric transfer through the corpus callosum varies between 2 and possibly as much as 30 ms or more depending on the type of callosal fibres participating in the transfer. Hemispheric interaction measurements usually require the detection of timing variations between two different conditions, which typically amount to tens of milliseconds. It is therefore important to ensure that the measurement equipment used is sensitive enough to detect timing variations with close to millisecond accuracy. The timing accuracy of the experimental apparatus that will be used in the present study will be discussed in the last section of this chapter, while a comprehensive audit can be found in appendix A.

2.2 The Measurement of Interhemispheric Transfer Time

In humans, interhemispheric transfer time has usually been measured in one of two ways: with an electro-physiological measure (electroencephalogram, EEG) or with the so-called Poffenberger paradigm, which is a behavioural measure.

The measure based on EEG involves the recording of event-related potentials on the scalp surface while visual stimuli are presented to a single visual field / single hemisphere. Electrical signals associated with the perception of the visual stimuli are compared between different recording sites, positioned either on the same side as the perceiving hemisphere or on the contralateral side. The rationale is that electrical signals associated with stimulus perception (or sometimes motor responses to stimulus perception) will take less time to reach the electrodes on the same side as the perceiving hemisphere than to the same location on the opposite side, which is at a greater distance, and that this time difference reflects the time taken to cross from one hemisphere to the other.

The advantages of this measure are that it is based on measuring neuronal activity that can be clearly associated with one event (e.g., stimulus perception), it can be repeated multiple times under consistent experimental conditions, and because it is based on measuring activity associated with brain processes limited in time, it is less likely to be affected by other cognitive processes (e.g., attention, motivation); therefore, it is assumed to be subject to little variation.

However, this may not be as self evident as assumed. Electrical potentials associated with one specific event do not necessarily cross through one single type of fibres in a single location. Therefore, the positioning of the electrodes on the scalp will be very influential and will partly determine which interhemispheric route is being measured. There is also no guarantee that the efficiency of the route measured relates to the task to be performed (e.g., pressing a button using the motor centres of the non-perceiving hemisphere) since a signal crossing via another route might be used to trigger the response (see Zaidel & Iacoboni, 2002a). Furthermore, when interhemispheric transfer time is compared between different individuals, small differences in electrode position can potentially significantly affect the measure and suggest inter-individual differences that are not necessarily present. Finally, EEG measures are costly, difficult to administer, and analysis of the data is complex and resource intensive.

In contrast, the Poffenberger paradigm (Poffenberger, 1912), is a behavioural measure. Participants are briefly presented with a simple stimulus (e.g., a white circle on a black background) and are asked to press a button as soon as they perceive the stimulus. The participants are asked to focus on a central fixation point, and are presented with a stimulus either in the left or in the right visual field at eccentricities that ensure that the stimulus will initially only be perceived by a single hemisphere. In half of the experimental trials they are asked to respond with one hand, and in the other half with the other. In trials where the responding hand is on the same side as the stimulus, the hemisphere which perceives the stimulus also controls the motor response, therefore no interhemispheric transfer is necessary. This condition is called the direct or uncrossed route. In the other trials the responding hand is opposite to the stimulus and information from the perceiving hemisphere must be transferred to the non-perceiving hemisphere in order to trigger the motor response. This condition is called the indirect or crossed route. Poffenberger hypothesised that when the reaction times using the direct route are subtracted from those of the indirect route, the difference (also called the crossed-uncrossed difference or CUD) is a measure of interhemispheric transfer time.

The advantages of this measure are that it has high ecological validity because it is based on observable behaviour, since it assesses differences in conduction representing transfer through fibres that can be shown to be used in the performance of a real task. Moreover, if different populations of fibres are used in different individuals, this measure will reflect this difference since it is not affected by factors such as electrode positioning. It is also a more practical, and less costly measure to use and involves less complex data analysis than the EEG measure. It is also interesting to note that age and sex differences in CUD have been demonstrated, which are consistent with differences in callosal conductivity associated with these variables as discussed in the previous chapter.

But the CUD also has disadvantages. Since it reflects the sum of the variability of multiple processes (perception, attention, motor planning, motor control) it is quite variable across trials. Therefore it requires large numbers of trials and as such, can be dull for participants and challenge both their attentive and motivational processes. It has therefore been argued that the measure it produces might not reflect interhemispheric transfer time but other variables such as functional lateralisation, attention, and stimulus-response compatibility effects. These objections will be discussed in detail in the next section.

Since the present thesis is interested in the relationship between interhemispheric transfer and hemispheric interaction it is particularly important to use a measure of callosal transfer that reflects the influence of multiple variables on behaviour. In this sense, a more variable measure that is more likely to be ecologically valid might also provide the advantage of being influenced by subtle differences between individuals such as sex, age, functional lateralisation, and age. This would suggest that the Poffenberger paradigm might be better suited to the aims of this thesis.

Another important factor to consider in choosing a measure of interhemispheric transfer is where the transfer takes place. This is particularly critical here because if a task assessing interhemispheric transfer targets channels different from those used during a task assessing hemispheric interactions, failure to detect a relationship between these variables would not necessarily mean that none would be found if the efficiency of relevant channels was assessed. Since, as will be shown further on, the Poffenberger paradigm involves transfer of information through multiple channels or pathways, it is less likely that the channels being assessed do not mediate interhemispheric signals used during the task measuring hemispheric interactions, at least in part.

2.2.1 Validity of the CUD as a Measure of IHTT

A fundamental criticism of the Poffenberger paradigm and its CUD is that it does not measure interhemispheric transfer time, either because it is too variable or because it reflects spatial compatibility effects, individual differences in functional lateralisation, or attentional bias. It is argued that if the CUD is a valid measure of interhemispheric transfer reflecting hardwired properties, this measure should not be modulated by the manipulation of experimental variables such as stimulus size, luminance, type of hand response (e.g., position, responding finger), or attention. Since such effects have been found, these criticisms will be evaluated in turn.

2.2.1.1 CUD and Perceptual Factors

Several studies have attempted to modulate the CUD by varying the perceptual qualities of the stimulus used in order to demonstrate that the CUD was not a measure of hemispheric interaction but reflected properties of perceptual processes. Results of such studies failed to show that the CUD was influenced by luminance, size, contrast, or eccentricity of the stimulus (Braun, 1993; Forster & Corballis, 1998; Miniussi, Maravita, & Marzi, 2002). This has reinforced the view that the CUD is a valid measure of interhemispheric transfer and that the transfer does not involve perceptual information, since signals carrying information about stimuli of different eccentricity or varying in other ways would not be transferred by the same neural pathways, and therefore, should have produced different CUDs.

2.2.1.2 Spatial Compatibility Effects

Experiments relying on responses more complex than that initially used by Poffenberger have demonstrated that when different responses have to be made based on a cue presented before each trial (choice RT or go/no-go tasks instead of simple RT) spatial compatibility effects can be found (see Bashore, 1981; Braun, Larocque, & Achim, 2004 for a review). Crossing the hands over the midline modulated the CUD such that responses were faster when the responding hand was on the same side as the visual stimulus even though this condition involved interhemispheric transfer. This suggested that the CUD in complex reaction time tasks was not a measure of hemispheric transfer. However, other studies using the original simple RT design failed to produce similar findings (e.g., Aglioti, Dall'Agnola, Girelli, & Marzi, 1991; Anzola, Bertoloni, Buchtel, & Rizzolatti, 1977; Berlucchi, Crea, Di Stefano, & Tassinari, 1977). Hommel (1996) suggested that this might be due to responses being triggered so rapidly in simple RT tasks that they occur before a spatial code has been established. However, Hommel also showed that spatial compatibility effects could be demonstrated under specific conditions in simple RT tasks, for instance, when the response made was changed before every trial.

Braun, Larocque, and Achim (2004) further investigated spatial compatibility effects by systematically varying motor responses during a simple RT task, by asking participants to press the response button multiple times, alternating the responding finger or the responding hand at short (every trial) or longer intervals, using central or lateral responses, or by crossing the hands or not. They showed that spatial compatibility effects were present under these conditions but this effect was independent of the CUD measure. They argued that the spatial compatibility effects were mostly due to a shift of attention to the hemispace on the side of the new response triggered by the changed stimulus-response mapping. They concluded that although spatial compatibility effects were present, they occurred only under very specific conditions (e.g., changing the responding hand before every trial), and that these effects did not interact with the CUD component of the measure. Therefore the CUD remained a valid behavioural index of interhemispheric transfer.

2.2.1.3 CUD and Attention

Since attentional processes appear to be involved in some of the spatial compatibility effects present in simple RT and because attention allocation can vary substantially between individuals, it is important to examine the effect of attention on the CUD.

Braun, Daignault, Dufrensne, Miljours, and Collin (1995) manipulated attentional parameters of a simple RT task by providing valid or invalid spatial cues before the appearance of the visual stimulus. They were able to produce non-significant CUDs in participants who had previously demonstrated typical CUDs using the Poffenberger task. However, this effect was reliably demonstrated in only one of four studies. The authors proposed that invalid cues activated the responding hand in the crossed condition producing a priming effect. In contrast, valid cues in the crossed condition would not produce faster responses because the perceiving but not the responding hemisphere would be primed. An effect of attention consistent with these findings was also found in another study where the proportion of uncrossed and crossed trials was manipulated (Weber et al., 2005).

Zaidel and Iacoboni (2002a) reported an unpublished study (Aziz-Zadeh, Iacoboni, & Zaidel, submitted) in which a simple RT task using complex stimuli consisting of images of left or right hands (which are known to activate lateralised pre-motor areas) or of neutral stimuli produced negative CUDs. Since the CUD must be positive to be a valid measure of interhemispheric transfer, this suggested that the involuntary processing of complex stimuli interfered with the CUD measure. Furthermore, when the motor responses were manipulated (by crossing the hands), only responses to hand images produced spatial-compatibility effects. This was interpreted by the authors as demonstrating an effect of attention on motor decision.

These findings indicate a possible effect of attention on the CUD. However, the conditions in which such an effect could be demonstrated were very specific and suggest that these effects are unlikely to be a strong influence in the usual Poffenberger task.

2.2.2 Variability of the CUD

It has been argued that the CUD is not a valid measure of interhemispheric transfer because it is too variable (Saron & Davidson, 1989; Swanson, Ledlow, & Kinsbourne, 1978). Although it appears that the CUD might be more variable than event-related potential measures, it is also likely, as discussed above, that the source of this variability, that is, involvement of a greater number of processes in this task, could make this measure better suited to exploring the effects of subtle individual differences in interhemispheric transfer on hemispheric interaction. This is only likely to be the case, however, if this measure is sufficiently stable and reliable.

Iacoboni and Zaidel (2000) tested three participants in a typical simple RT task comprising between twelve and sixteen thousand trials and compared their performance to that of fifteen participants tested in one session of 560 trials. They found that individual variability on this task for the three participants tested over a larger number of trials was similar to that of the larger group of participants tested on fewer trials but with an equal total number of trials. They also found that the CUD measure stabilised after around 2000 trials and concluded that reliable measures of interhemispheric transfer time could be obtained with 2000 trials for single individuals but that for large groups experiments involving 600-800 trials were likely to be adequate.

In another study, StJohn, Shields, Krahn, and Timney (1987) tested six participants over twenty sessions for a total of 5760 trials each and found that the CUD was a reliable measure, with a reliability coefficient of .8.

Meta-analyses of interhemispheric transfer measures using simple RT have also shown that the CUD is remarkably stable across studies, despite methodological differences in response type, presentation times, and eccentricities used, with most studies reporting CUDs in the range of 2 to 6 ms (Bashore, 1981; Braun, 1993).

Overall, these findings suggest that the CUD is stable enough to be used as an index of interhemispheric transfer, at least when large numbers of trials and large sample sizes are used.

2.2.3 Pathways Underlying Interhemispheric Transfer in the Poffenberger Paradigm

In this thesis a case will be made for an influence of interhemispheric connectivity on hemispheric interactions. More specifically, it is being argued that individual variations in callosal connectivity are likely to affect the efficiency of hemispheric interactions. Consequently, it is important to clarify where the interhemispheric transfer involved in the Poffenberger paradigm takes place but also to show that the task assessing hemispheric interactions is likely to rely, at least in part, on the same interhemispheric pathways as those used in the task assessing interhemispheric transfer. The localisation of interhemispheric transfer in the Poffenberger paradigm will be reviewed in this section while that involved in the task used to assess hemispheric interactions will be reviewed in a later section.

Since a number of findings have shown that both individuals with agenesis of the CC (ACC) and callosotomised patients can perform the Poffenberger task, it could be argued that the CUD is not a measure of callosal transfer. Although this is a reasonable hypothesis, it is not a proof in itself that in neurologically normal individuals transfer measured with the CUD does not take place via the CC.

First, it has been shown that interhemispheric transfer time is dramatically increased in callosotomised and ACC individuals. ACC individuals typically present with interhemispheric transfer times in the order of 15 to 20 ms while callosotomised patients usually have CUDs in excess of 30 ms. Furthermore, since agenesis of the CC is a prenatal neurological abnormality, it is likely, given the plasticity of the central neural system, especially in early development, that acallosals have a pattern of cerebral wiring different from normal individuals (Sauerwein, Lassonde, Cardu, & Geoffroy, 1981), and it is unlikely that findings in acallosals can be generalised to intact individuals. For example, it has been shown in acallosals that interhemispheric transfer might occur through the anterior commissure or subcortically, and that acallosals with larger anterior commissures might demonstrate a more efficient level of hemispheric interactions (Barr & Corballis, 2002).

It is possible that changes in neuronal connectivity also occur in callosotomised individuals after section of the CC, to maximise the efficient use of interhemispheric resources. Nonetheless, it has been shown in a callosotomised patient tested before and after surgery, that, although the CUD was normal before surgery it was significantly lengthened after surgery (Iacoboni et al., 1994). These findings strongly suggest that callosal transfer is the norm in the Poffenberger task. A recent fMRI study (Tettamanti et al., 2002) also confirmed the role of the CC in the CUD of intact individuals by showing that the crossed condition (but not the uncrossed) was associated with increased activation in the genu of the CC. These findings were also replicated in another study (Weber et al., 2005). Moreover, Schulte, Pfefferbaum, and Sullivan (2004) have shown that interhemispheric transfer time measured using the Poffenberger paradigm was negatively correlated with the crossectional surface area of the body of the CC while a diffusion tensor imaging study has shown that structural properties of the body of the CC were associated with the CUD (see Gazzaniga, 2005, pp 655-656).

It appears therefore that multiple routes, callosal and non-callosal, can mediate interhemispheric transfer involved in the CUD, but that the faster callosal routes are favoured in neurologically normal individuals. Thus, transfer might occur through multiple channels, but, as in a horse-race metaphor, the first horse past the post is the winner (see Weber et al., 2005).

There is substantial uncertainty about which callosal fibres are used for the transfer of information in simple RT tasks. The above fMRI findings suggest that pre-frontal pathways crossing through the genu might be involved[1]. However, studies of partially callosotomised patients paint a more complex picture (Tassinari, Aglioti, Pallini, Berlucchi, & Rossi, 1994). Patients with either anterior or posterior callosotomies performed similarly on a simple RT task, and demonstrated normal CUDs compared to controls. Consequently, it seems that the CUD can be mediated by both anterior and posterior fibres. The argument that this might be the case only for callosotomised patients with substantial changes due to neural plasticity occurring over time can also be rejected, since Tassinari and colleagues tested one partially callosotomised individual only five days after surgery, and showed similar performance to long term callosotomised individuals.

Behavioural findings suggest that interhemispheric transfer in the Poffenberger paradigm occurs before the motor stage response. Cavina-Pratesi, Bricolo, Pellegrini, and Marzi (2004) showed, in a simple RT task, that stop signals given to participants after perception of the trigger stimulus produced a pattern of performance consistent with interhemispheric transfer occurring before the motor stage. Since, as discussed

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[1] Despite their findings showing greater activation in the genu during the crossed condition, Weber et al. (2005) suggest that information transfer is likely to occur through different anterior and posterior callosal fibres but that limitations in the detection of activation in highly myelinated fibres with fMRI makes it more difficult to demonstrate hemispheric transfer through larger, myelinated posterior fibres.

above, the CUD is unaffected by perceptual variables such as eccentricity, size, or luminance it is most likely that transfer occurs through associative/pre-motor fibres. Findings in a recent PET scan study (Marzi et al., 1999), showing bilateral activation of parietal areas in the crossed, but not the uncrossed condition, are also consistent with this view since the parietal cortex is densely connected through the posterior mid-body of the CC, and is involved in the processing of complex cognitive information beyond sensory representations.

In summary, it appears that multiple pathways, callosal and non-callosal, are capable of transferring information necessary to perform the Poffenberger task. It is also likely that information is transferred simultaneously through different callosal channels. However, in neurologically normal individuals, the available evidence suggest that non-sensory associative fibres crossing in the posterior mid-body of the CC are most likely to be assessed by the CUD.

2.3 The Measurement of Hemispheric Interactions

A wide variety of tasks have been used to assess the degree of hemispheric interaction, ranging from simple reaction time tasks employing basic shapes to complex bi-manual motor tasks.

In experiments using visual stimuli, hemispheric interactions have been usually assessed by comparing the performance of a task (such as matching of stimuli) in two conditions, where stimuli were either presented to a single visual field/hemisphere, or across the two visual fields/hemispheres. It was assumed that stimuli in the within hemifield condition were predominantly processed in a single hemisphere, and involved relatively low levels of hemispheric interactions, if at all. In contrast, in the across hemifield condition, stimuli were thought to be processed by the two hemispheres, and would necessarily involve hemispheric interactions in order to perform the task. It has recently been shown that, under certain circumstances, high levels of hemispheric interaction also take place in the within visual field condition but that the efficiency of such interactions may not be as high as that in the across-visual field condition (Pollmann et al., 2003a). Consequently, tasks assessing hemispheric interactions may not compare a condition where no interaction takes place to another in which hemispheric interaction does take place. Instead, such tasks contrast conditions in which relatively less or more efficient interactions take place.

A large number of studies investigating hemispheric interactions have used a tachistoscopic, split visual field letter-matching task. There is considerable advantage in using such a task. The brain processes involved have been extensively studied and large amounts of data are available to build hypotheses. Moreover, this task is known not to be strongly lateralised, and is therefore ideal to compare performance across conditions in regardless of which hemisphere controls the task.

Initial versions of this task used displays containing only two letters. In the within-visual field condition the two letters were presented either to the left or to the right of a fixation point, while in the across-visual field condition, one letter was presented in each of the two visual fields. Although experiments using this task demonstrated an advantage of hemisphere interactions in the across-visual field condition (the bilateral distribution advantage or BDA), it was correctly argued that the perceptual load of the two hemispheres was different in the two conditions (Banich & Shenker, 1994). To remove this confounding factor, Banich & Belger (Banich & Belger, 1990) used a display containing three letters so that in each condition one hemisphere perceived one letter while the other perceived two. The across-visual field advantage found using this new display could therefore not be attributed to a difference in perceptual load.

The following sections will discuss the parameters affecting the assessment of hemispheric interaction using this type of letter-matching task.

2.3.1 Number of Stimuli

As stated above, the number of stimuli presented to each visual field could potentially affect the size of the BDA. This could occur for three reasons. Firstly, because one experimental condition (e.g., the across-visual field condition) is presented with a lighter perceptual load than the other (the within-visual field condition). Secondly, because one hemisphere is presented with a lighter perceptual load than the other. Or, thirdly, because displays with a greater number of stimuli are harder to process and require more cognitive resources than displays with fewer stimuli.

To my knowledge, no study has specifically compared BDAs in a two or in a three letter-matching task. However, since it could be argued that a BDA found in a two-letter task might be due to a difference in perceptual load, it is preferable for to use a display with at least three letters.

It could also be argued that the perceptual load is different for each hemispheres in a three-letter task. To assess the effect of hemispheric perceptual load asymmetry on the BDA, Weissman, Banich, and Puente (2000) tested participants in three- and four-letter-matching tasks. They found that although the absolute size of the BDA did not differ between these conditions, the advantage of processing the matching letters across visual fields was smaller when it was considered as a proportion of overall RT. They concluded that hemispheric interactions are more beneficial when one hemisphere's load is lighter thus enabling this hemisphere to use its spared processing capacity to perform processes that the other hemisphere cannot conduct, due to its higher perceptual load.

Another possibility, not necessarily mutually exclusive, is that the modulation of attentive processes underlies the change in BDA between asymmetrical and symmetrical displays. In the three-letter task, the bottom letter is inevitably part of the match if one is present whereas in the four-letter match either of the two lower letters could participate in a match. It is therefore possible that the increased attentional requirements needed either to perform a greater number of comparisons in the four-letter task or necessary to shift attention between two possible bottom targets, may explain the difference in BDA.

Belger and Banich (1992) tested participants on a three- and five-stimuli shape letter-matching task, in which the bottom letter always participated in the match, and found a significant BDA in the five-letter condition but not in the three-letter condition. They interpreted these findings as supporting the theory that more demanding tasks benefit most from hemispheric interactions. It is unlikely that the increased number of comparisons required in a symmetrical four-letter task decreases the efficiency of hemispheric interactions when the hemispheric perceptual load is equal in the two hemispheres, since this should also have been the case in the five-letter task (see also Merola & Liederman, 1990).

An alternative explanation is that a symmetrical display requires a greater number of shifts in attention between the two hemispheres since in a match, the bottom target can be located in either visual field. Shifts in attention between visual fields have been shown to be more costly than shifts in attention within visual fields. Furthermore, in a symmetrical display, the attentional effect each letter stimulus has on the other stimuli is likely to be magnified. It has been shown that simple RT to two symmetrically presented stimuli, one in each visual field, is faster than that to a single stimulus (redundancy gain). A similar effect has also been demonstrated between the upper and lower quadrants of each visual field (Murray, Foxe, Higgins, Javitt, & Schroeder, 2001). Thus, it is possible that in an asymmetrical display this redundancy gain benefits the across-visual field condition but that these effects are more matched for each visual field condition in a symmetrical display.

For these reasons, it appears preferable to use a symmetrical display to assess hemispheric interactions in the present research. The fact that the BDA produced by a symmetrical display is likely to be smaller than that of an asymmetrical display is unimportant because the studies described in the next chapters do not require a particularly strong BDA, instead they require a broad spread in performance across participants. This is also most likely to be achieved by a more demanding task such as the four-stimulus letter-matching task.

2.3.2 Stimulus Eccentricities

Most studies that have used a letter-matching task to assess hemispheric interactions have presented stimuli at eccentricities of two to three degrees of visual angle. This was done partly to ensure that the stimuli were not projected onto the fovea but were perceived either by the left or the right hemisphere, and partly to diminish the effects of perceptual degradation of stimuli at greater eccentricities.

Few studies have researched the effect of stimuli's eccentricities on the BDA. Lavidor and Ellis (Lavidor & Ellis, 2003) tested participants on a shape and a name letter-matching task under two stimulus eccentricity conditions. In the first condition the stimuli were presented at para-foveal eccentricities (2.8 degrees of visual angle) while in the second condition they were presented foveally (less than 1 degree of visual angle). They found that both conditions produced similar pattern of hemispheric interaction with foveal presentation producing somewhat faster RTs. These findings were interpreted as showing that the fovea, like the peripheral visual field, is also divided into two hemifields that are each projected to a separate hemisphere.

No studies investigating stimulus-matching across visual fields at larger eccentricities were found in an extensive literature search. It is unclear whether the eccentricity of stimuli should affect performance in one visual field condition more than the other, although it would seem that variables such as decreased perceptual resolution at higher eccentricities should affect each visual field condition in similar ways.

Nevertheless, in order to make results more comparable, similar eccentricities to those used in past studies will be used here.

2.3.3 Type of Match

Two types of letter-matches have been used in past studies investigating hemispheric interactions. Letter-matching based on shape has been shown to produce less efficient hemispheric interactions than letter-matching based on identity (name). This was initially thought to be due to the name letter-matching task requiring an extra processing step (retrieving letter names) and therefore being more demanding than the shape letter-matching task. This difference in task complexity has been demonstrated in numerous experiments showing that RT to shape-matches are significantly faster than RT to name-matches.

Recent findings have shown that it is not only a difference in task complexity that produces a bilateral advantage in the name letter-matching task but not in the shape letter-matching task. An fMRI study showed that in the name letter-matching task, cortical areas are activated bilaterally both in the within- and across-hemisphere conditions suggesting that, in this task, certain processes are overloaded within a single hemisphere and that additional processing resources are recruited in the other hemisphere (Pollmann et al., 2003a; Pollmann, Zaidel, & Cramon, 2003b). In the shape letter-matching task, however, this bilateral pattern of activation was not present in the within-hemisphere condition. Therefore, it appears that it is the greater efficiency of hemispheric interactions, and a better use of bi-hemispheric resources that produces an advantage in the across-visual field condition of the name letter-matching task.

Since the present study is interested in assessing variations in hemispheric interactions in association with other variables, a task that requires a high degree of hemispheric interaction must be used, and the name letter-matching task seems particularly suited to assess hemispheric interaction in the following studies.

2.3.4 Shape of the Display

Most studies (e.g., Banich & Belger, 1990; Belger & Banich, 1992; Weissman et al., 2000) using stimulus-matching tasks to assess hemispheric interactions have used a display of three stimuli positioned in a V-shape with the two top stimuli being presented at equal eccentricities from the midline and slightly above the centre of the screen while the bottom stimulus was positioned below the centre of the screen and in one visual field, but closer to the midline than the top stimuli. The rationale for this was that in order to diminish the effect of scanning habits (related to reading direction) the matching letters in the across-visual field condition were presented on the diagonal and not on the horizontal axis. One consequence of this choice was that the distance between matching letters would be shorter in the within-visual field condition than in the across-visual field condition if two letters were presented exactly above each other in the within-visual field condition. Since a difference in distance between matching stimuli might advantage the within-visual field condition, the bottom stimulus was displaced towards the midline making the angle between matching stimuli in the within- and across-visual field condition more equal.

Similar displays were also used when four-letter stimuli were used, with both bottom letters presented closer to the midline.

Although controlling for such effects is laudable, one study comparing displays with the bottom stimulus presented at different eccentricities failed to demonstrate any significant effect of this manipulation (see Banich & Shenker, 1994, p. 272).

Unfortunately, breaking the horizontal or the vertical symmetry of a display may have unintended consequences. The brain's architecture is organised in very symmetrical ways especially in early, low-level cognition. Furthermore, intra- and interhemispheric connections are also mostly symmetrical. Thus there is a possibility that less symmetrical displays might lead to unexpected interactions with other variables and affect results.

For example, it has been shown that spatial attention is not evenly spread across the visual fields and that it varies both with eccentricity and direction (from central fixation) (Hagenbeek & Van Strien, 2002). In addition, the allocation of attention is not equal in the two visual fields and each hemisphere's attentional capacity is not equal to the other's, and can be modulated by both the level of arousal in each hemisphere and the type of stimulus being processed, or the type of task being performed (e.g., Fink et al., 1996; Fink et al., 1997; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001). Moreover, at least in low-level vision, aligned flanker stimuli influence the detection of target stimuli and this effect has been shown to be modulated both by the eccentricity of the stimuli and attention (Shani & Sagi, 2005).

Little is known about how such factors (spatial attention, stimuli's properties, type of task, hemispheric arousal) interact with handedness, functional lateralisation, sex or age. Consequently, the possibility that the shape of the display interacts with other variables in a letter-matching task cannot be discounted. Therefore, I intend to use a symmetrical display in the following studies. However, since a four-letter display will be used it is important to assess how the display shape affects the BDA. The following experiment set out to answer this question prior to the major studies in Chapters 3 to 8.

2.3.5 Experiment 1

2.3.5.1 Method

Participants. Twenty right-handed subjects (10 females, 10 males) with normal or corrected-to-normal vision completed this study (one participant's data were excluded because despite stating that he was right-handed during the interview his responses to the handedness questionnaire suggested otherwise). They were students who either participated to fulfil undergraduate psychology course requirements, or were recruited on the Australian National University campus, and received 10 dollars as compensation for their time and travel. Handedness was assessed with a questionnaire based on the Edinburgh Handedness Inventory (Oldfield, 1971, see Appendix B). Participants who reported a history of neurological or motor disease were excluded from the study. The study received approval from the Human Research Ethics Committee.

Stimuli and procedure. The stimuli were 7 capital letters and their lower case counterparts ("Aa", "Bb", "Ee", "Ff", "Gg", "Hh", "Tt") displayed in Arial 34-point bold font. Arrays of four letters were displayed with the top two letters in upper case, and the lower two letters in lower case. Stimuli subtended a maximum of 1.0° of visual angle and were displayed as white letters on a black background to decrease eyestrain. There were two display conditions: a V-shaped display and a square-shape display. In the V-shape display condition the top two letters were presented 3.5° of visual angle to the left or right of a central fixation cross while the bottom two letters were presented 2.0° of visual angle to the left or right of the central fixation cross. In the square-display condition all four letters were presented 2.0° of visual angle to the left or right of the central fixation cross. In both conditions, the top letters were 2.0° above, and the bottom letters 2.0° below the central fixation cross. In the "match" condition 2 letters were matching, whereas in the "no match" condition none of the letters matched. The match always occurred between a lower case letter in the lower part of the visual field and an upper case letter in the upper part of the display. For half of the "match" trials the match occurred within the left or right half of the visual field (within-hemisphere condition), and for the other half, across the two hemifields (across-hemisphere condition). In the across-hemisphere condition, matches always occurred on one of the diagonals (upper left and lower right letters or lower left and upper right letters). In half of the trials the stimuli were presented in the V-shaped display while for the other half they were presented in the square-shaped display. The subject's task consisted in deciding whether two letters in the display were matching. In the match condition (half of the trials), a mouse button had to be pressed with the index finger, whereas in the no match condition, no response was to be made. A fixation point first appeared in the middle of the screen for 700 ms, after which the stimuli were presented for 200 ms. Trials timed out after 2400 ms if no response was made. Each trial was followed by a 500 ms inter-trial pause. The type of match, and the responding hand and display type were randomised across blocks of trials. Feedback (average RT and % correct) was given at the end of each block, and after each trial with a wrong response ("wrong") to encourage higher accuracy. Subjects were tested in one session while seated in a dimly lit room, with their chins in a chinrest, and positioned 40 cm from the computer screen with their eyes focused on a fixation cross. They were first presented with 32 practice trials followed by four blocks of 48 experimental trials.

2.3.5.2 Results

Participants'variables. Participants had a mean age of 25.6 years (SD = 8.6), and an average handedness coefficient (in an adapted version of the Edinburgh Inventory, see Appendix B) of 0.87 (SD = .14), where +1 denotes complete right-handedness and –1 denotes complete left-handedness.

RT measures. Average response time to matching-letter pairs were computed for two display (V-shaped and square-shaped) conditions and two visual field (within-visual field, and across-visual field) conditions, and are presented in Table 2-1. RT smaller than 250 ms, considered to be anticipatory responses, or larger than 1500 ms, considered to be due to attentional lapses, (2.8 % of all responses) were excluded.

The differences between the within- and across-visual field measures were also computed as indexes of hemispheric interaction. They ranged from –103 ms (a bilateral disadvantage to 186 ms (a bilateral advantage) with an average of –11 ms (SD 70) for the V-shaped display condition. In the square-shaped condition they ranged from –89 ms to 77 ms with an average of –25 ms (SD 45).

Table 2-1. Average response times to matching letters in the within- and across-visual field conditions for the two display types. Standard deviations are presented in brackets.

Display type	Within	Across
V-shaped	855 ms (103)	866 ms (78)
Square-shaped	861 ms (119)	886 ms (108)

A 2 visual field (within/across) x 2 display shape within-subject analysis of variance with sex as across-subject variable, and age and handedness as covariates was computed to determine whether display shape influenced the relationship between within- and across-visual field performance. No main effects were present, but a visual field by sex interaction reached significance, F(1,15) = 9.086, p < .01. Post hoc contrasts showed that females performed equally well in the within- (892 ms, SD 96) and across-visual field (893 ms, SD 86) conditions, F(1,9) = .698, ns, whereas males performed significantly better in the within- (119 ms, SD 115) compared to the across-visual field (871 ms, SD 110) condition, F(1,8) = 23.148, p < .01.

Accuracy measures. Average accuracy to matching-letter pairs were computed for two display (V-shaped and square-shaped) conditions and two visual field (within-visual field, and across-visual field) conditions, and are presented in Table 2-2.

The differences between the within- and across-visual field measures were also computed as indexes of hemispheric interaction. They ranged from –10.42% (a bilateral advantage) to 12.50% (a bilateral disadvantage) with an average of –0.44 % (SD 5.96) for the V-shaped display condition. In the square-shaped condition they ranged from –8.33 to 13.54% with an average of 1.43% (SD 5.70).

A 2 visual field (within/across) x 2 display shape within-subject analysis of variance with sex as across-subject variable, and age and handedness as covariates was computed to determine whether display shape influenced the relationship between within- and across-visual field performance. No main effects were present, but three interactions between visual field and age, $F(1,15) = 17.360$, $p < .01$, visual field and sex, $F(1,15) = 10.482$, $p < .01$, and visual field and handedness, $F(1, 15) = 6.897$, $p < .05$, were detected.

In order to better describe these interactions, the two covariates were split into two groups. Participant aged below 25 years were assigned to a younger group (mean age 19.45 years, n = 11) and the rest to an older group (mean age 34.13, n = 8). With regard to handedness, participants were assigned to a mildly right-handed group (mean .74, n = 9) if they handedness coefficient was below .8, and to a strongly right-handed group (mean .99, n = 10) otherwise. The accuracy measures were also collapsed over display types since no main effect of this variable was found.

Table 2-2. Average accuracy to matching letters in the within- and across-visual field conditions for the two display types. Standard deviations are presented in brackets.

Display type	Within	Across
V-shaped	80.87 % (20.50)	81.30 % (20.91)
Square-shaped	80.70 % (20.78)	79.28 % (19.68)

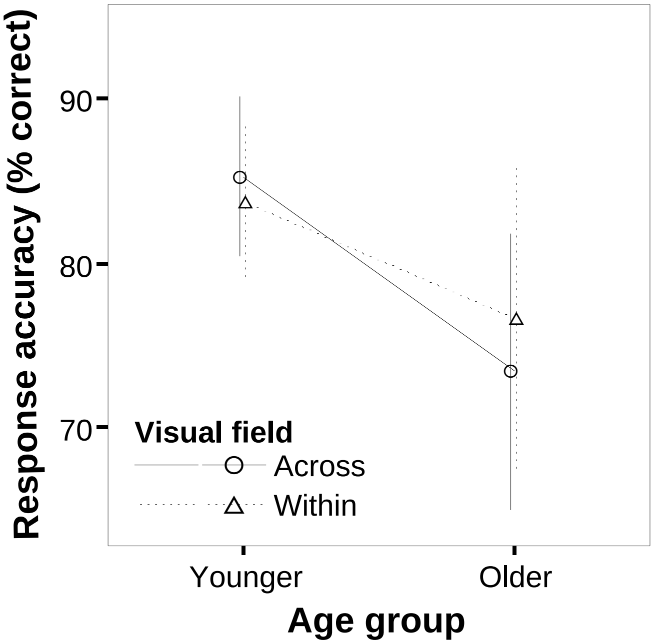

Figure 2-1. Visual field (within/across) by age group (younger/older) interaction for the accuracy measure. Error bars represent the standard error of the mean.

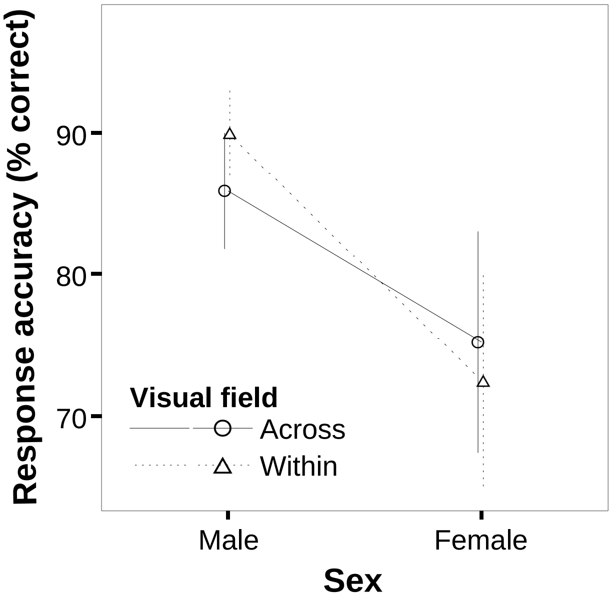

Figure 2-2. Visual field (within/across) by sex (male/female) interaction for the accuracy measure. Error bars represent the standard error of the mean.

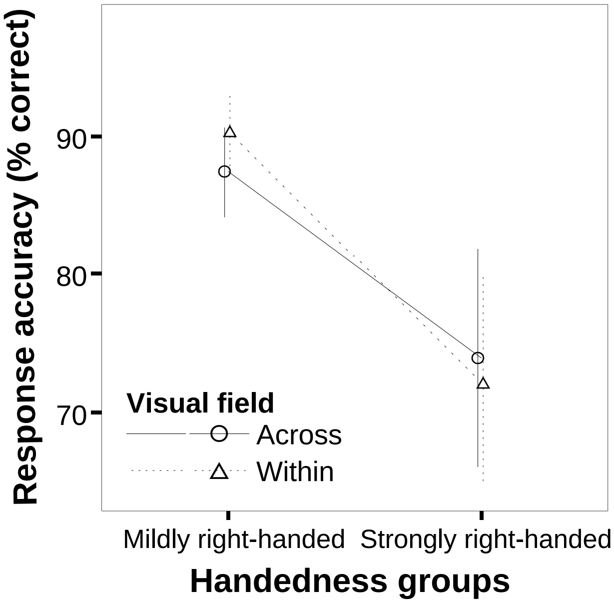

Figure 2-3. Visual field (within/across) by handedness group (mildly/strongly right-handed) interaction for the accuracy measure. Error bars represent the standard error of the mean.

A 2 visual field x 2 age group x 2 sex x 2 handedness group ANOVA was conducted. It revealed a significant interaction between visual field and age group (Figure 2-1), F(1,11) = 10.642, p < .01. None of the follow-up contrasts were found to be significant, suggesting that this effect is weak[2]. A second visual field by sex interaction was also detected (Figure 2-2), F(1,11) = 12.924, p < .01, indicating that in males within-visual field performance was significantly more accurate than across-visual field performance, t(1,8) = 3.571, p < .01, but not in females, t(1,9) = 1,995, ns. A third interaction was detected between visual field and handedness (Figure 2-3), F(1, 11) = 5.663, p < .05. Post hoc contrasts revealed a trend suggesting that in mildly right-handed individuals within-visual field performance might be more accurate than across-visual field performance, t(1,8) = 2.151, p = .064, but not in strongly right-handed individuals, t(1,9) = 1.008, ns.

Within-across performance and speed-accuracy trade-off. Correlations between the within- minus across-visual field performance of the RT and accuracy measure were computed to determine whether participants who demonstrated a positive bilateral distribution advantage (BDA) in the response time measure also demonstrated a positive BDA in the accuracy measure. Correlations presented in Table 2-3 show that the RT BDAs of the two response-type conditions were negatively correlated with the accuracy BDAs. Since a bilateral advantage is indicated by a positive RT BDA but a negative accuracy BDA, this indicates that more efficient hemispheric interactions in the RT measure were associated with more efficient hemispheric interactions in the accuracy measure.

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[2] In addition, correlational analysis of within- and across-visual field performance and age (continuous variable), which would not suffer from the same loss of power as that produced by categorising continuous variables, did not reveal any significant results.

Table 2-3. Correlations between RT BDAs and accuracy BDA of the two display conditions (V-shaped, square-shaped).

	V-display RT BDA	Square-display RT BDA	V-display accuracy BDA	Square-display accuracy BDA
V-display RT BDA	1	0.394	-0.534*	-0.487*
Square-display RT BDA	0.394	1	-0.462*	-0.472*
V-display accuracy BDA	-0.534*	-0.782**	1	0.545*
Square-display accuracy BDA	-0.487*	-0.472*	0.545*	1

*. Correlation is significant at the 0.05 level (2-tailed).

2.3.5.3 Discussion

This experiment was designed to replicate the findings of another study (see Banich & Shenker, 1994, p. 272) showing that the shape of the display (V-shaped vs square-shaped) did not affect the relative performance in the within- and across-visual field conditions of a letter-matching task when the display contained four instead of three letters.

As expected, the present results show that the shape of the display had no effect on the letter-task performance, and particularly on the relative performance in the two visual field conditions. They also showed that no interaction was present between display shape and variables of interest such as age, sex, and handedness.

Contrary to expectations, overall, across-visual field performance was slower and less accurate than within-visual field performance. It is unclear why this was the case. It may be due to variability associated with this particular sample or to design differences between this experiment and previous experiments. The latter seems less likely because experimental parameters were closely matched to those of previous studies. In any case, this difference is not of major concern because, since the research to be reported in this thesis is interested in studying hemispheric interaction differences in different individuals, it is more important to use a task that produces a good spread of hemispheric interaction pattern across individuals. The present results show that such a spread is produced by the present task, with performance varying between a bilateral disadvantage of 89 ms and 13% and a bilateral advantage of 77 ms and 8%.

Interestingly, although this study was not specifically designed to discover these effects, interactions between visual field conditions (within/across) and age, sex, and handedness were detected. These effects were not strong and therefore their importance should not be overemphasised. Nevertheless, it is encouraging that variables which were theoretically likely to influence hemispheric interaction (as discussed in the introductory chapter), significantly influenced the relative performance of within- and across-visual field processes.

It is particularly interesting to note that females performed relatively better than males in the across-visual field condition when compared to the within-visual field condition. This is consistent with females being, on average, less functionally lateralised, and therefore more likely to benefit from hemispheric interactions (e.g., Shaywitz et al., 1995).

Another point of interest is the finding that participants who produced more efficient RT hemispheric interactions also demonstrated more efficient accuracy interactions. This suggests that variability in these two measures is affected, at least in part, by the same neurophysiological substrates.

In conclusion, this study was conducted to determine how a square-display, which was chosen for the present research to control for potential interactions between spatial attention and stimuli's properties, would differentially affect hemispheric interactions compared to a v-display. Since, no hemispheric interactions were found between conditions using these two types of display, the use of the square-display was deemed appropriate for the present research.

2.3.6 Motor response

Some studies investigating hemispheric interactions using matching tasks similar to those used by Banich and colleagues (Eviatar & Zaidel, 1994; Weissman et al., 2000), have used two alternative forced-choice responses, where participants had to respond by pressing one button if they thought that two letters were matching, or another button if they thought that none of the letters were matching. Other studies have used go/no-go responses (Banich et al., 1990; Banich, Passarotti, & Janes, 2000; Banich, Passarotti, Nortz et al., 2000; Belger & Banich, 1992; Reuter-Lorenz & Stanczak, 2000). The advantage of using go/no-go responses is that because this type of response is less complex, its use should decrease the variability of the performance in a task known for its high variability.

Another expected consequence is that go/no-go responses should be faster and/or more accurate than forced-choice responses. Since it has been argued that task complexity is a determinant of the efficiency of hemispheric interactions, it should follow that the relative within- and across-visual field performance would be modulated by the type of response used. This is unlikely, however, because it has also been shown that it is the overloading of specific processes in a single hemisphere which makes recruiting additional resources in the opposite hemisphere so beneficial and that the excessive load seems to occur at the perceptual/decisions making stages and not at the motor stage (Pollmann et al., 2003a, 2003b).

To my knowledge, the influence of response type on within- and across-visual field performance has not been previously investigated. The next experiment will clarify this issue.

2.3.7 Experiment 2

2.3.7.1 Method

Participants. Twenty-four right-handed subjects (12 females, 12 males) with normal or corrected-to-normal vision completed this study. They were students who either participated to fulfil undergraduate psychology course requirements, or were recruited on the Australian National University campus, and received 10 dollars as compensation for their time and travel. Handedness was assessed with a questionnaire based on the Edinburgh Handedness Inventory (Oldfield, 1971). Participants who reported a history of neurological or motor disease were excluded from the study. The study received approval from the Human Research Ethics Committee.

Stimuli and procedure. The stimuli were identical to those of experiment 1 except only one, square, display was used where each letter was presented 2.0° of visual angle to the left or right and 2.0° above or below the central fixation cross. The participants' task was to determine whether two of the four letters were matching. In half of the trials, participants used a forced-choice response while in the other half they used a go/no-go response. In the forced-response condition, a mouse button had to be pressed with the index finger, whereas in the no match condition a second mouse button had to be presed with the middle finger of the same hand. In the go/no-go condition, a mouse button had to be pressed with the index finger, whereas in the no match condition, no response was to be made. A fixation cross first appeared in the middle of the screen for 700 ms, after which the stimuli were presented for 200 ms. Trials timed out after 2400 ms if no response was made. Each trial was followed by a 500 ms inter-trial pause. The type of match was randomised across trials. The responding hand was randomised across blocks of trials. Feedback (average RT and % correct) was given at the end of each block, and after each trial with a wrong response ("wrong") to encourage higher accuracy. Subjects were tested in one session while seated in a dimly lit room, with their chins in a chinrest, and positioned 40 cm from the computer screen, with their eyes focused on a fixation cross. Half of the participants started with the forced-response condition followed by the go/no-go condition while the other half did the reverse. Participants were presented with 32 practice trials before each response condition, followed by two blocks of 80 experimental trials (for each response condition).

2.3.7.2 Results

Participants'variables. Two participants (one male, one female) were excluded from the data analysis because their average accuracy on the letter task was below 70% correct. The remaining 22 participants had a mean age of 24.0 years (SD = 6.4), and an average handedness coefficient (adapted version of the Edinburgh Inventory) of 0.90 (SD = .13).

RT measures. Average response time to matching-letter pairs were computed for two response (forced-choice and go/no-go) conditions and two visual field (within-visual field, and across-visual field) conditions, and are presented in Table 2-4. RTs smaller than 250 ms, considered to be anticipatory responses, and larger than 1500 ms, considered to be due to attentional lapses, (3.6 % of all responses) were excluded.

The differences between the within- and across-visual field measures were also computed as indexes of hemispheric interaction. They ranged from –94 ms (a bilateral disadvantage) to 83 ms (a bilateral advantage) with an average of –17 ms (SD 53) for the forced-choice condition. In the go/no-go condition they ranged from –209 ms to 109 ms with an average of –29ms (SD 77).

A 2 visual field (within/across) x 2 response type (forced-choice/go no-go) within-subject analysis of variance with sex as across-subject variable, and age and handedness as covariates was computed to determine whether response type influenced the relationship between within- and across-visual field performance. No main effects were present, but three two-way interactions were detected. Response type interacted with sex, F(1,18) = 11.817, $p < .01$, with age, F(1,18) = 8.851, $p < .01$, and with handedness, F(1,18) = 5.499, $p < .05$. Post hoc contrast showed that males performed equally well in the forced-response (915 ms, SD 138) and go/no-go (920 ms, SD 133) conditions, F(1,10) = .038, ns, whereas females responded significantly slower in the forced-response (943 ms, SD 90) compared to the go/no-go (881 ms, SD 148) condition, F(1,10) = 13.424, $p < .01$. Correlations between age and RT in each visual field and response type conditions were computed to clarify the effect of this variable. A single correlation between age and RT to across-visual field matches in the forced-choice response condition reached significance, r = .548, p < .01, indicating that older participants tended to respond more slowly in this condition. The third interaction between response type and handedness was not further analysed because participants were very homogenous on this variable. All participants except two had a handedness coefficient equal or greater than .8 and consequently it was thought that this variable was too restricted in range to produce a meaningful interpretation.

Table 2-4. Average response times to matching letters in the within- and across-visual field conditions for the two response types. Standard deviations are presented in brackets.

Response type	Within	Across
Forced-choice	921 ms (124)	937 ms (107)
Go/no-go	886 ms (124)	915 ms (91)

Accuracy measures. Average accuracy to matching-letter pairs were computed for two response (forced-choice and go/no-go) conditions and two visual field (within-visual field, and across-visual field) conditions, and are presented in Table 2-5.

The differences between the within- and across-visual field measures were also computed as indexes of hemispheric interaction. They ranged from –22.50% (a bilateral advantage) to 16.25% (a bilateral disadvantage) with an average of 1.25 (SD 9.84) for the forced-choice condition. In the go/no-go condition they ranged from –16.25 to 17.50% with an average of 1.02% (SD 9.30). A 2 visual field (within/across) x 2 response type (forced-choice/go no-go) within-subject analysis of variance with sex as across-subject variable, and age and handedness as covariates was computed to determine whether display shape influenced the relationship between within- and across-visual field performance. No main effects or interactions reached significance.

Table 2-5. Average accuracy to matching letters in the within- and across-visual field conditions for the two response type conditions. Standard deviations are presented in brackets.

Response type	Within	Across
Forced-choice	79.43 % (10.84)	78.18 % (6.81)
Go/no-go	85.17 % (10.82)	84.14 % (6.57)

Within-across performance and speed-accuracy trade-off. Correlations between the within- minus across-visual field performance of the RT and accuracy measure were computed to determine whether participants who demonstrated a positive bilateral distribution advantage (BDA) in the response time measure also demonstrated a positive BDA in the accuracy measure. Correlations presented in Table 2-6 show that the RT BDAs of the two response-type conditions were negatively correlated with the accuracy BDAs. Since a bilateral advantage is indicated by a positive RT BDA but a negative accuracy BDA, this indicates that more efficient hemispheric interactions in the RT measure were associated with more efficient hemispheric interactions in the accuracy measure.

Table 2-6. Correlations between RT BDAs and accuracy BDA of the two response conditions (forced-choice, go/no-go).

	Forced-choice RT BDA	Go/no-go RT BDA	Forced-choice accuracy BDA	Go/no-go accuracy BDA
Forced-choice RT BDA	1	0.588**	-0.613**	-0.581**
Go/no-go RT BDA	0.588**	1	-0.782**	-0.548**
Forced-choice accuracy BDA	-0.613**	-0.782**	1	0.423
Go/no-go accuracy BDA	-0.581**	-0.548**	0.423	1

** Correlation is significant at the 0.01 level (2-tailed).

Variability across participants. In order to determine whether the variability of the RT and accuracy measures varied between response types across participants, average RT and accuracy were computed for each response condition and each visual field condition. Responses below 250 ms and above 1500 were not excluded for this analysis since the occurrence of such RTs might be associated with the type of response being used. Levene's test of equality of variance between response conditions was computed and revealed that the response conditions did not significantly differ in their variability for RT in the within-visual field condition, t(1,42) = .185, $p < .05$, or in the across-visual field condition, t(1,42) = .006, ns. Response variability for the accuracy measure did not differ in the within-visual field, t(1,42) = .024, ns, or across-visual field, t(1,42) = .067, ns, conditions.

Variability within participants. In order to determine whether the variability of the RT and accuracy measures varied between response types within participants, the standard deviations in each response condition, for the RT and the accuracy measures, and for each participant were computed for each visual field condition. Levene's test of equality of variance between the standard deviations of the response conditions were computed and revealed that the response conditions did not significantly differ in their variability for RT in the within-visual field, t(1,42) = 1.582, ns, or across-visual field, t(1,42) = .003, ns, conditions. Response variability for the accuracy measure did not differ in the within-visual field, t(1,42) = 2.517, ns, or across-visual field, t(1,42) = 2.539, ns, conditions.

2.3.7.3 Discussion

This experiment was designed to assess the effect of response type on performance in a letter-matching task containing four stimuli. The predictions were that using a simpler go/no-go response would decrease the response variability and increase response speed. It was also suggested that although increased task complexity is usually associated with a relative improvement of across-visual field performance compared to within-visual field performance, increased response complexity was unlikely to have such an effect because it is the overloading of perceptual and response selection processes in one hemisphere that have been shown to benefit most from the sharing of resources across hemispheres.

It was found that the response variability was not decreased in the go/no-go condition for either the RT or accuracy measures. This is surprising, since it would have been expected that a simpler motor response selection would be associated with less variability. It is possible that the more complex response-mapping in the forced-response condition increases variability but that this is matched in the go/no-go condition by an increased variability due to the withholding of any response.

Contrary to expectations, go/no-go responses did not uniformly produce faster RTs than forced-choice responses. Only females responded significantly faster in the go/no-go condition than in the forced-response condition, although male participants followed the same trend. It is unclear why this should be the case but it may be related to the difference in functional lateralisation found between males and females. In this context, it should be noted that response type also interacted with age, with older participants tending to respond more slowly in the forced-choice condition.

As expected, the increase in response complexity did not improve across-visual field performance compared to within-visual field performance, even in females whose RTs were significantly slower in the forced-choice condition. This is probably due to the fact that motor-response selection and planning processes are not sufficiently taxed in these conditions and therefore do not require the recruitment of additional resources across hemispheres.

In conclusion, this study was conducted to determine whether the use of a go/no go response instead of a forced response would affect the measure of hemispheric interactions. No significant difference was found between these two response conditions in regard to the measure of hemispheric interaction, therefore, either response type could be used for this research. However, because the go/no go response is a simpler motor response that might be associated with lower variability in more demanding conditions, it was deemed more suitable for the present research.

2.3.8 Pathways Underlying Hemispheric Interactions in Letter-Matching Tasks

In the context of this thesis it is important to establish at least two facts in relation to the interhemispheric transfer necessary for proficient performance of letter-matching tasks. Firstly, does it require transfer through the CC, and secondly, if it is the case, does it involve callosal fibres that are likely to also take part in a Poffenberger task, which will be used in this research to assess the efficiency of callosal transfer?

Studies in split-brain patients have shown that very limited perceptual information can be transferred in the absence of the CC (Corballis & Corballis, 2001) and that subcallosal transfer of complex perceptual or semantic information in the split-brain can probably be mostly attributed to adaptive strategies (Corballis, 1994), ispsilateral control of the hand (Kingstone & Gazzaniga, 1995; Miller & Kingstone, 2005), or to the incomplete section of the CC (Funnell et al., 2000a).

Consequently, it is unlikely that demanding tasks which require the transfer of letter information could be conducted without an intact CC. Eviatar and Zaidel (1994) tested three patients with complete commissurotomy with shape- and an name-letter-matching tasks to clarify this question. They found that while one patient could respond slightly above chance (69% correct) in the shape letter-matching task but not in the name letter-matching task; the other two patients could not perform any of these tasks above chance. This suggests that the CC is essential for matching letters across visual field, and even more so when the match is based on letter-name.

In a fMRI study, Pollmann, Zaidel and Cramon (2003) investigated the neural correlates of typical shape- and name-letter-matching tasks. They found that the anterior and posterior cingulate areas seemed to be particularly involved in the transfer of information between the hemispheres. Furthermore, the name-letter-matching task produced greater activation, lateralised to the left hemisphere in posterior cortex, but distributed bilaterally in the anterior cortex.

Pollmann and colleagues interpreted this pattern as showing that left lateralised activation in the inferior occipital gyrus was probably due to the greater perceptual demands of the name-matching task, since this region has been shown to be specifically involved in letter processing (Puce, Allison, Asgari, Gore, & McCarthy, 1996). Moreover, Pollman and colleagues concluded that it was the overloading of perceptual processes involved in letter discrimination that were at the base of the bilateral distribution advantage found in the name-letter-matching task.

The frontal bilateral activation, on the other hand, was thought to be due to greater executive demands necessary to complete the more difficult name letter-matching task.

Taken together these findings suggest that the cost of callosal transfer taking place between the posterior cingulate regions via the posterior mid-body of the CC and the splenium are most likely to account for the bilateral distribution advantage found in the name but not in the shape letter-matching task.

Earlier discussion of the possible locus of callosal transfer in Poffenberger tasks suggested that transfer occurred in the posterior mid-body (e.g.,Marzi et al., 1999). Therefore, the assumption that the Poffenberger task and the letter-matching task rely on an overlapping population of callosal fibres seems justified. In addition, it is possible that the difference in transfer speed of specific callosal fibres between individuals also predicts the relative efficiency of other callosal fibres in the same individuals. To my knowledge this has not been demonstrated but, nevertheless, should not be ignored.

2.4 Experimental Design and Timing Accuracy

The types of studies that will be reported in the following chapters involve two main technical requirements in relation to timing accuracy. Firstly, visual stimuli need to be presented at specific times for precise durations. Secondly, motor responses need to be recorded with high temporal accuracy. To meet these requirements in a practical and cost-effective fashion, a combination of a standard Pentium grade PC running MS Windows operating system, a cathode ray tube monitor, a mouse response device, and the Inquisit psychological testing software package (Draine, 2003) were selected.

A difficulty in choosing these components is that psychological experiments have conflicting requirements. It is normally suitable to use a multi-tasking operating system to simplify the development of experimental tasks and stimuli. However, multi-tasking operating systems tend to share their processing power between a number of computing tasks that are not all related to the experimental parameters being measured. This has the unwanted consequence of limiting the timing accuracy of the system.

The use of off-the-shelf cathode ray tube monitors is also suitable since these monitors are widely available and cheap. Unfortunately, the display on these monitors is typically refreshed only every 10 to 16 ms. Thus, if presentation of the stimulus is not synchronised with the refresh rate of the monitor, a stimulus that should be presented for 50 ms might be presented for a period varying between 34 and 66 ms. It is therefore particularly important to choose a software package that links the presentation of stimuli on screen to the start of the monitor refresh cycle. It is also important for the testing software to use every possible avenue to limit the sharing of processing resources with unnecessary processes during the timing of experimental trials.

Finally, there are also advantages in using standard input devices (mouse, keyboard). This facilitates the transfer from one computer to another or the ability to test in different and/or multiple locations. However, the way in which information is transferred between these input devices and the computer is not well known by most users and can dramatically influence the accuracy of the measures. Data transmitted by certain input devices may only be "read" by the computer relatively infrequently, and the input device itself may buffer inputs for significant periods of time. These technical variables may induce measurement errors amounting to tens of milliseconds. Furthermore, these errors may be random or follow a pattern and therefore they may not only overestimate measurements but also add significant noise to them which may hide subtle experimental effects which could otherwise have been detected.

To address these issues, a systematic audit of the selected hardware and software has been conducted and is presented in detail in Appendix A. The main conlusions were that the hardware and software selected were near millisecond accurate but that response times tended to be systematically overestimated and that the mouse hardware added some variability to the response time measure. This was not deemed an important factor as all experimental conditions would be affected in a similar fashion.

2.5 Summary

This chapter was concerned with methodological issues and specifically interested in determining whether the Poffenberger task was an adequate paradigm to assess interhemispheric transfer time; whether a four-stimulus name letter-matching task was a suitable task to assess hemispheric interaction; and to determine whether the timing accuracy of the software and hardware planned for the present research were sufficiently accurate.

The Poffenberger task, although not perfect, was found to be suitable and to have a number of advantages over other techniques. Of particular importance was the fact that the Poffenberger paradigm assesses interhemispheric transfer time in the context of real behaviour and therefore is more likely to reflect subtle individual differences over a wide range of neural processes; processes that may be differentially affected by variables which are of particular interest to this research such as sex, age, handedness, and functional lateralisation.

The letter-matching task was also found to be highly suited to assessing hemispheric interaction and to reveal differences between experimental groups of interest. It was particularly encouraging to find that two methodological experiments which were not specifically designed to study variations in individual variables, uncovered such differences. Furthermore, this task was found to produce important variations in the level of hemispheric interactions between individuals which makes its data ideal for use in regression analyses involving independent variables whose influence might be very subtle.`

Finally, the audit of the experimental apparatus revealed that it was extremely accurate and well suited to the type of tasks and experiments that will be conducted.

Based on the above findings, the following chapter will investigate whether a clear link can be established between the efficiency of hemispheric interaction and interhemispheric transfer time and if present, how this relationship is modulated by other variables such as sex, age, and handedness.

CHAPTER 3

3.1 Callosal Transfer and Hemispheric Interaction

Associations between callosal variables and tasks requiring hemispheric interaction habe been shown in a number of studies. For instance, the size of specific sections of the CC was related to accuracy of performance in a verbal task requiring callosal transfer (Hellige, Taylor, Lesmes, & Peterson, 1998) and to response time in a visual detection task (D. Madden et al., 2004). Thinning of the CC related to aging has been associated with decreased performance of tasks which typically require bi-hemispheric processing (Sullivan, Pfefferbaum, Adalsteinsson, Swan, & Carmelli, 2002b). Evidence presented in Chapter 1 also shows an association between CC size and handedness, sex and cerebral laterality (Aboitiz, Scheibel, Fisher, & Zaidel, 1992b; Luders et al., 2003), which in turn are related to functional lateralisation (Jancke & Steinmetz, 2002). These findings suggest that CC properties might significantly modulate hemispheric interaction, and do so differently depending on age, handedness, and sex.

To my knowledge, only five studies have attempted to investigate a direct link between CC properties and behavioural measures of hemispheric interaction. Hellige, Kristen, Taylor, Lesmes & Peterson (1998) found an association between the size of the mid-sagittal section of the CC and performance of a consonant-vowel-consonant triagram identification task but only when stimuli were presented to the left visual field and right hemisphere, and therefore requiring transfer to the left hemisphere. In this condition, individuals with a larger mid-sagittal CC made more errors. The other four studies attempted to relate inter-hemispheric transfer time (IHTT) to measures of hemispheric interaction.

Two of these studies measured IHTT with evoked potentials (by comparing measures taken over the left hemisphere to those taken over the right hemisphere during the performance of the tasks used to assess IHI) and IHI with a 2-letter matching task (Brown & Jeeves, 1993) as well as a pattern-matching task (Larson & Brown, 1997) and found that left-to-right IHTT were negatively correlated with IHI.

The last two studies used a behavioural measure of IHTT based on the Poffenberger paradigm (Poffenberger, 1912). Braun, Collin & Mailloux (1997) found some association between their measure of IHTT and hemispheric interaction measured with a dot size matching task. However, theirs was an atypical version of the classic Poffenberger paradigm, using a complex reaction time task which is probably not an adequate measure of IHTT (Bashore, 1981; Brysbaert, 1994b, see also Chapter 2). In contrast to the Poffenberger paradigm, in which participants respond to a single light spot, Braun and colleagues used left- or right-hand responses when two circles of identical size were detected in a single visual field. This task is much more likely to be affected by functional lateralisation and by stimulus-response compatibility effects, which are absent in the Poffenberger paradigm (Anzola et al., 1977; Berlucchi et al., 1977). Furthermore, because the same task is used to assess hemispheric interaction, correlation between the two measures may be due to numerous other factors shared by this task. This is much less likely to happen when two independent tasks are used.

Finally, Corballis (2002) used the Poffenberger paradigm but assessed hemispheric interaction using a version of the redundant target effect: in a simple reaction time task, responses are consistently faster when identical targets are presented across visual fields than when single targets are presented to individual visual fields. Corballis hypothesised that if hemispheric interaction is related to IHTT, the redundant target effect would be greater in individuals with slower hemispheric transfer than in those with faster IHTT, but no significant correlation between hemispheric interaction and IHTT was found. However, this negative result might be attributed at least in part to the relatively small number of trials (528) used to measure IHTT which is well below the benchmark (2000+) recommended by Iacoboni & Zaidel (2000), although these authors also suggest that for larger numbers of subjects, 600-800 trials/subject are probably adequate.

In summary, the evidence to date on the relationship between CC efficiency of transfer and IHI is not conclusive. Although the few studies which have tried to assess it have mostly found some association between these two variables, their results are conflicting or are confounded by methodological issues such as the use of a measure unlikely to adequately assess IHTT, low subject numbers, or too few experimental trials.

Nevertheless, a strong case for an association between callosal transfer and hemispheric interaction can be made, as outlined in Chapter 1. Moreover, it appears that this association should be modulated by certain individual variables (e.g., sex, age, handedness, and functional lateralisation), which do not seem to have been specifically scrutinised in previous studies. However, because the influence of each of these variables is likely to be subtle, and because these variables have been shown to interact with each other, assessing the relationship between callosal transfer and hemispheric interaction requires an experimental design sensitive enough to detect small effects. It is also essential that any effect detected should not be attributable to variables not accounted for in this design.

3.2 Experiment 3

The aim of the present study was to determine whether efficiency of callosal transfer was related to hemispheric interaction when large numbers of trials[3] and participants were used, and when the influence of important individual variables was accounted for. Because some variables were expected to interact with each other in subtle ways, and because some of their effects could be small, a design based on multiple regression analysis was chosen. Although this statistical analysis typically requires a large cohort of participants, it can be very powerful when its assumptions are respected, and is most likely to reveal the effect of small variations between participants. IHTT was measured with the Poffenberger paradigm, as a predictor variable, while the efficiency of hemispheric interactions, the dependent variable, was assessed with a variation of the typical name letter-matching task widely used in this field of research. The advantages of using these tasks have been extensively discussed in Chapter 2 and will not be elaborated further here. Other variables (sex, handedness, functional lateralisation, and an index of attention) were also either recorded, assessed, or computed from the experimental data.

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[3] It should be noted that the inclusion of large numbers of trials (in tasks assessing hemispheric interaction) could also have the unintended consequence of decreasing cortical involvement through practice. Practice effects in tasks similar to that used in the present study have been reported (Liederman et al., 1985; Weissman & Compton, 2003). Nonetheless, because this type of practice effect has not been specifically studied, the use of large number of trials will help clarify this issue. For measuring hemispheric transfer time, large number of trials are recommended by Iacoboni & Zaidel (2000).

Based on previous studies, a negative correlation between IHTT and the efficiency of hemispheric interaction (RT measure) was expected, suggesting that individuals with faster callosal transfer demonstrate more efficient hemispheric interactions. In addition to such a relationship between IHTT and the RT measure of the BDA in the letter-matching task, a similar relationship with the accuracy measure of hemispheric interaction might also be expected since Haglethorn, Brown, Amano, & Asarnow (2000) showed that with increasing age and myelination of the corpus callosum, which have been shown to be associated with a faster CUD (Brizzolara, Ferretti, Brovedani, Casalini, & Sbrana, 1994), both the RT and accuracy BDA increased, and were correlated with each other.

3.2.1 Method

3.2.1.1 Participants

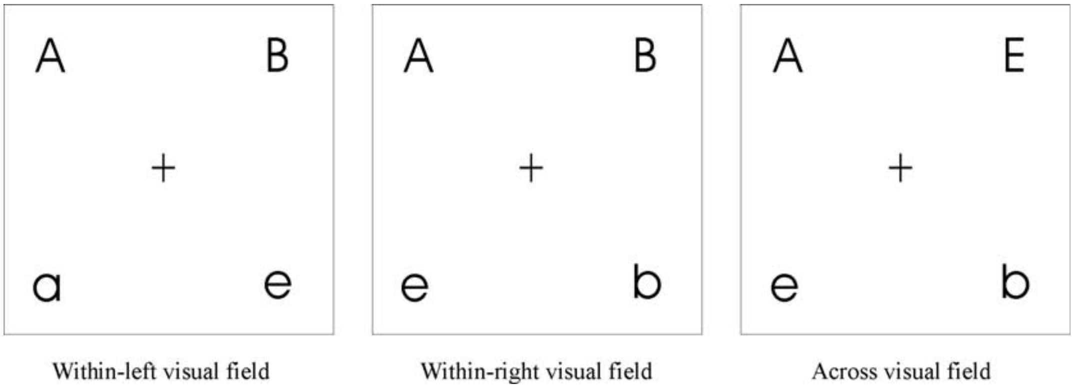
Eighty-six right-handed subjects (42 females, 44 males) with normal or corrected-to-normal vision took part in this study (six participants' data were excluded because they did not complete all sessions). They were students who either participated to fulfil undergraduate psychology course requirements, or were recruited on the Australian National University campus, and received 35 dollars as compensation for their time and travel. Only right-handed participants, with normal or corrected to normal vision were accepted in the study. Handedness was assessed with a questionnaire based on the Edinburgh Handedness Inventory (Oldfield, 1971, see Appendix B). Participants who reported a history of neurological or motor disease were excluded. The study received approval from the Human Research Ethics Committee.

3.2.1.2 Stimuli and Procedure

For each session, participants were seated in a dimly lit room, had their chins in a chinrest, and were positioned 40 cm from a computer screen with their eyes focused on a fixation cross. Stimuli were presented on a Daewoo 17" cathode ray tube monitor controlled by a Pentium III computer. The Inquisit software package (Draine, 2003) was used for stimulus presentation and response recording. Testing was spread over 6 half hour sessions, with the first two sessions dedicated to the Poffenberger task and handedness questionnaires, and the last 4 sessions to the letter task.

Poffenberger task: The stimuli were white dots on a black background, with a size of 0.6° of visual angle and displayed with their centres 4.0° to the left or right of a central fixation cross. Stimuli were presented for 47 ms. During each trial, a fixation cross appeared for 500ms or 800ms (to discourage anticipatory responses) after which a dot was flashed randomly to the left or the right of the cross. The subject's task consisted of responding to detection of the stimulus by pressing with the index finger the button of a centrally positioned computer mouse. Each session consisted of 12 blocks of 50 trials (25 trials per visual hemifield, in random order). Left and right hand responses were randomised across blocks. Subjects were tested in two sessions, for a total of 1200 trials.

Letter task: The stimuli were 7 capital letters and their lower case counterparts ("Aa", "Bb", "Ee", "Ff", "Gg", "Hh", "Tt") displayed in Arial 34-point bold font. Arrays of four letters were displayed in a square format with the top two letters in upper case, and the lower two letters in lower case. Stimuli subtended a maximum of 1.0° of visual angle and were displayed as white letters on a black background to decrease eyestrain. Each letter was presented 2.0° of visual angle to the left or right of the central fixation cross and 2.0° above or below the central fixation cross for 200 ms. In the "match" condition 2 letters were matching, whereas in the "no match" condition none of the letters matched. The match always occurred between a lower case letter in the lower part of the visual field and an upper case letter in the upper part of the display. For half of the "match" trials the match occurred within the left or right half of the visual field (within-hemisphere condition), and for the other half, across the two hemifields (across-hemisphere condition, see Figure 3-1). In the across-hemisphere condition, matches always occurred on one of the diagonals (upper left and lower right letters or lower left and upper right letters). This was done to decrease the influence of scanning habits which would increase for horizontal matches. The subject's task consisted in deciding whether two letters in the display were matching. In the match condition (half of the trials), a mouse button had to be pressed with the index finger, whereas in the no match condition, no response was to be made. A fixation point first appeared in the middle of the screen for 700 ms, after which the stimuli were presented for 200 ms. Trials timed out after 1700 ms if no response was made. Each trial was followed by a 500 ms inter-trial pause. The responding hand was randomised across blocks of trials. Feedback (average RT and % correct) was given at the end of each block, and after each trial with a wrong response ("wrong") to encourage higher accuracy. Subjects were tested in four sessions, for a total of 2304 trials. Each session consisted of 12 blocks of 48 trials, amounting to 288 trials per condition (2 hands (L/R) x 2 match conditions (match/no-match) x 2 hemisphere conditions (within-hemisphere match/across-hemisphere match).



Within-left visual field

Within-right visual field

Across visual field

Figure 3-1. Exemplars of the different visual field conditions (with matching letters): within left visual field, within right visual field and across visual field.

3.2.1.3 Simple RT vs forced-Choice Response Time Estimates of IHTT

In order to assess the relationship between simple RT and complex RT estimates of IHTT in the present study, response times were also recorded for 'match' conditions, by hand, an by visual field in the complex (letter-matching) RT task. The complex RT CUDs were computed by subtracting average response times of the hand contra-lateral to the visual field in which the matching letter pairs were detected (indirect route) from the average response time of the hand ipsilateral to the visual field detecting the matching letters (direct route).

3.2.2 Results

3.2.2.1 Participants' Variables

Participants had a mean age of 22.5 years (SD = 6.9), and an average handedness coefficient (adapted version of the Edinburgh Inventory, see Appendix B) of 0.88 (SD = .16) where 1 denotes extreme right-handedness, and –1 extreme left-handedness.

3.2.2.2 Inter-Hemispheric Transfer Time (IHTT) using the Poffenberger Paradigm

Reaction times (RT) to the presentation of a dot in the left or right visual field (VF) were measured for the two hands, and an estimate of IHTT or crossed-uncrossed difference (CUD) was computed by subtracting RTs for the direct route (VF ipsilateral to responding hand) from RTs for the indirect route (VF contralateral to responding hand). Reaction times smaller than 100ms, considered to be anticipatory responses, and larger than 1000 ms, considered to be due to attentional lapses, were excluded (2.3%). The average RT in the Poffenberger task in all conditions ranged from 205 ms to 337 ms with average accuracy rates of 98%. The average CUD was 3.02 ms (SD = 3.83).

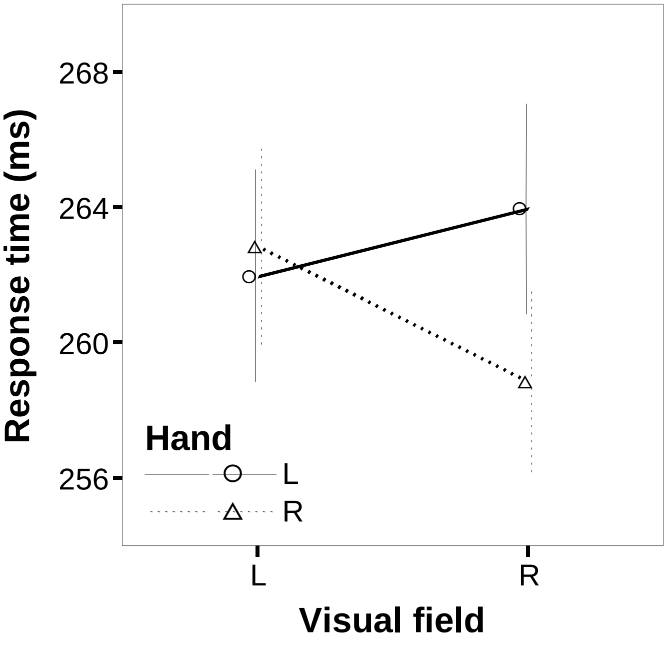


Figure 3-2. Response times for the Poffenberger task show an interaction between visual field of presentation of the dot (left/right visual field) and responding hand (left/right). Error bars represent the standard error of the mean.

A repeated-measures analysis of variance applied to the reaction time measures confirmed an expected hand by VF interaction, F(1,78) = 49.87, p < .001. This is usually interpreted as a test of validity of the CUD, confirming faster responses for the direct route compared to the indirect route (Figure 3-2). A main effect of hand was also found, F(1,78) = 4.51, p = .037, with right hand responses (261 ms) being faster than left hand responses (263 ms).

3.2.2.3 Hemispheric Interaction in a Letter-Matching Task

RT and accuracy for matching letter pairs were measured for four visual field/hemisphere conditions: within left visual field (LVF), within right visual field (RVF), and across visual fields (across up, when the matching letters are located in the lower left and upper right positions; or across down, when the matching letters are located in the upper left and lower right positions) and are presented in Table 3-1; the differences between averaged within visual field and across visual field conditions were calculated as indexes of hemispheric interaction. RTs smaller than 250 ms and larger than 1500 ms (2.3% of all responses) were excluded.

Table 3-1. Accuracy and RT Measures for the Different Conditions of the Letter-Matching Task. Standard deviations are presented in brackets.

	Within Left	Within Right	Across Up	Across Down
Response Time	829 ms (94)	849 ms (112)	876 ms (99)	870 ms (93)
Accuracy	92.4 % (5.9)	91.5 % (6.3)	92.5 % (5.6)	90.5 % (6.0)

Average response times to matching letter pairs were 839 ms (SD = 88) for the within visual field conditions and 873 ms (SD = 80) for the across visual field condition (Figure 3-3A). The difference between within and across visual field conditions, the latency BDA (-34.7 ms, SD = 34.7), was significant, t(1,79) = 8.94, p < .001.

Average accuracy rates were 92% (SD = .05) for the within-hemisphere conditions and 91.5% (SD = .05) for the across-hemisphere condition (Figure 3-3B). The difference between within and across visual field conditions, the accuracy BDA (0.45%, SD = 2.74), did not reach significance, t(1,79) = -1.47, ns. Since these results differed from those of previous studies and could be due to a learning effect, the analysis was repeated for the first session data alone, which showed no difference between within and across-hemisphere performance for the reaction time measure, t(1,79) = 1.37, ns, or for the accuracy measure, t(1,79) = .97, ns. (see Chapter 5 for further discussion of this practice effect).

The correlation between the accuracy and RT measure of hemispheric interaction was significant, r = -.527, p < .001, and a greater within-hemisphere accuracy advantage was associated with a greater within-hemisphere RT advantage. Most participants (87.5%) showed a within-hemisphere advantage over the across-hemisphere condition for the RT measure; but for the accuracy measure, only 60 % of participants showed a within-hemisphere advantage.

To determine whether one hemisphere was more proficient at the letter task than the other, t-tests were conducted, but no significant difference was found for the RT measure, t(1,79) = 1.67, ns, or for the accuracy measure, t(1,79) = 1.72, ns.

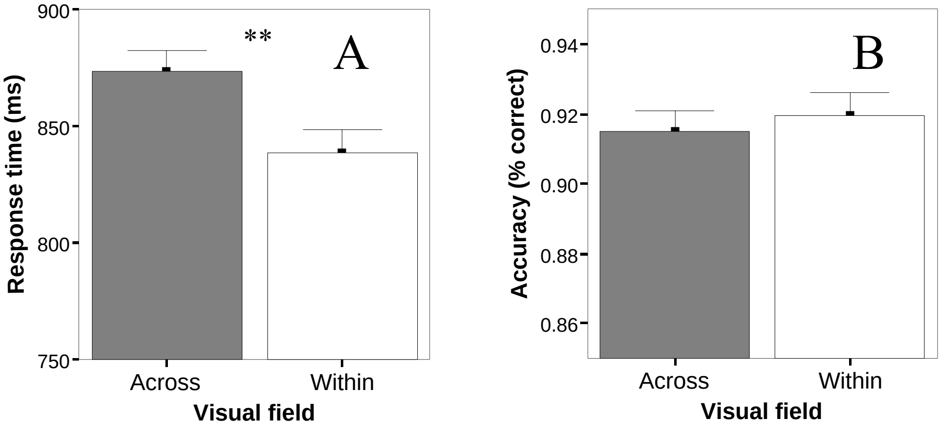


Figure 3-3. Average response time (A), and accuracy (B), of the letter task in the two visual field conditions (within, across). Across and within-hemisphere performance was significantly different RT for but not for accuracy. Error bars represent the standard error of the mean.

3.2.2.4 IHTT – Hemispheric Interaction Relationship

A correlational analysis showed that IHTT and BDA were significantly correlated for the accuracy measure, r = .354, p < .001, but not for the RT measure of hemispheric interaction, r = -.078, ns. Theoretically, variability of these parameters could also be explained by other factors such as sex, age, handedness, hemispheric lateralisation, or attention, and a multiple regression analysis was conducted using these variables. Lateralisation indexes for the letter task were computed with the following formula, (RVF – LVF)/(RVF + LVF), for the RT and accuracy measures. Correct RT and accuracy rates of the Poffenberger task were used as indexes of attention. This analysis showed that neither sex, age, handedness coefficient, hemispheric lateralisation of the letter task, or attention significantly accounted for the variability in hemispheric interaction, leaving IHTT as the only significant variable, F(1,78) = 11.17, p = .001, accounting for 12.5% of the variance in hemispheric interaction (accuracy measure), 95% confidence interval (7-50).

Because this relationship could be due to differences in overall accuracy between participants, the regression analysis was re-run with total accuracy as a predictor variable. Total accuracy did not significantly predict the accuracy BDA but enhanced the effect of the CUD (r^2 = .147).

Contrary to previous studies, no significant RT and accuracy BDAs were found at the group level. To further ensure that the relationship between IHTT and BDA was indeed reflecting increased interaction efficiency associated with faster transfer, data from twenty-one participants who demonstrated better performance in the across-hemisphere than in the within-hemisphere condition for both the RT and the accuracy measures were analysed separately. In this sub-group, the average CUD was 3.43 ms, the average accuracy rate of the letter task was 89.1% and the average RT was 865 ms. The RT BDA was 28 ms (SD = 25) and the accuracy BDA was –4.12% (SD = 3.47). When correlations between IHTT and BDAs for the four sessions of the letter task were analysed, both accuracy BDA, r = .681, p = .001, and latency BDA, r = -.559, p < .01, were significantly correlated with IHTT.

Since the subgroup of 21 participants with better bilateral than unilateral performance on both the accuracy and the response time measure showed greater correlation between IHTT and accuracy performance it is possible that the performance of this subgroup is responsible for the significant IHTT-BDA relationship at the group level. Therefore, the analysis was re-run using the data of the remaining 59 participants. The correlation between IHTT and accuracy BDA was reduced for this group but still significant, $r = .270$, $p < .05$.

3.2.2.5 Simple RT vs Forced-Choice Response Time Estimates of IHTT

CUDs in simple reaction time tasks have been used extensively to assess IHTT and are recognised as a valid measure, despite high variability. However, the use of complex reaction time to calculate the CUD has not been validated. Since Braun and colleagues (1997) have attempted to use this method to demonstrate a link between IHTT and hemispheric interaction, the relationship between simple reaction time (simple RT) CUD and complex reaction time (complex RT) CUD was assessed here to determine whether this approach was valid, at least for this task.

The complex RT CUD was computed by subtracting response times to correct within-visual field "match" trials of the letter task with contralateral hand response (indirect route) from those with ipsilateral hand response (direct route). The average CUD found was 16 ms (SD = 20.19) compared to 3.02 ms (SD = 3.83) for the simple RT measure of the Poffenberger task. The correlation between these two variables was computed but did not reach significance ($r = -.013$, ns). Since even small differences in functional lateralisation of the letter task in different individuals could have a great influence on the CUD measure, a multiple regression analysis was conducted to determine whether lateralisation of the complex RT task (for the latency and accuracy measures) and handedness coefficient could predict the variance in complex RT CUD. Both the latency measure ($\beta = .326$) and the accuracy measure ($\beta = .343$) of hemispheric lateralisation, but not handedness, were significant predictors of the complex RT CUD measure, $F(2,77) = 3,92$, $p = .024$, $r = .304$.

3.2.3 Discussion

Only a handful of studies, until now, have attempted to determine whether hemispheric interaction efficiency is directly related to callosal transfer speed, but these have produced unclear or contradictory results. Two studies used evoked potential measures of IHTT and found that only faster left-to-right IHTT was associated with more efficient hemispheric interaction (Brown & Jeeves, 1993; Larson & Brown, 1997). Braun et al. (1997) found significant correlations between only four pairs (out of 16) of measures of IHTT and hemispheric interaction but since they used a measure of IHTT based on complex RT, which may or may not assess callosal transfer (see Bashore, 1981; Brysbaert, 1994b, for a discussion), the meaning of these results is unclear. A fourth study (Corballis, 2002) did not find a significant relationship between IHTT and hemispheric interaction.

The present study was able to demonstrate a direct relationship between IHTT and a widely used measure of hemispheric interaction.

IHTT was measured with the Poffenberger paradigm which yielded an average transfer time of 2.73 ms, which is in accord with past findings of 2-5 ms (Bashore, 1981; Brysbaert, 1994a; Iacoboni & Zaidel, 2000). The validity of the measure was demonstrated by a significant hand by visual field interaction confirming that in trials where no inter-hemispheric transfer was required, RTs were shorter than in those that did require inter-hemispheric transfer.

IHI measured in the letter-matching task produced a negative latency BDA (- 34.7 ms) and a non-significant accuracy BDA (0.45%) at the group level. This means that most participants performed better on the task when the two matching letters were presented either in the left or right visual fields compared to processing the matching letters across visual fields. However, 13.5% of participants responded faster, and 40% more accurately, when matching letters were presented to different hemispheres.

A correlation of .354 was found between IHTT and accuracy BDA suggesting that individuals with faster hemispheric transfer showed more efficient hemispheric interaction than those with slower hemispheric transfer. However, a significant correlation between IHTT and BDA could also be explained by other variables such as functional lateralisation, handedness, sex, age, or attention. First, with respect to functional lateralisation, hemispheric interaction relies on the sharing of processing between the two hemispheres. Consequently the relative capacity of each hemisphere to perform the different processes involved in each task might influence performance in both simple RT and complex RT tasks. If one hemisphere were less proficient at some sub-processes necessary to complete the task and the other hemisphere were over-loaded for these sub-processes, a less efficient hemispheric interaction would be expected. Second, handedness has been shown to be associated with functional lateralisation and callosal structural differences (Westerhausen et al., 2003) and might also affect hemispheric interaction and transfer. With regard to sex, males tend to be more lateralised than females morphologically and functionally (e.g., Aboitiz, Scheibel, & Zaidel, 1992; Allen et al., 2003; Siegel-Hinson & McKeever, 2002; Weiss et al., 2003). Consequently, men might differ in hemispheric interaction and be more affected by the efficiency of callosal transfer. With respect to age, as individuals get older, they tend to be less functionally lateralised compared to younger individuals (Cabeza et al., 2002) or, at least, present with a different pattern of hemispheric lateralisation compared to younger populations (Hausmann, Güntürkün, & Corballis, 2003), and different brain regions are affected differently by the ageing process (Driesen & Raz, 1995; Sullivan et al., 2002b). As a consequence, if functional lateralisation significantly influences hemispheric interaction, age could modulate this relationship. Finally, although there are no strong indications suggesting that attention should affect measures of IHTT and hemispheric interaction in a systematic way, nevertheless, because attentional processes seem to be more lateralised to the right hemisphere (Davidson, Cave, & Sellner, 2000; Doty, 2002; Ernest, 1998; Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Siegel-Hinson & McKeever, 2002; Vogel, Bowers, & Vogel, 2003; Weekes & Zaidel, 1996), there is a possibility that IHTT and hemispheric interaction could be affected.

A multiple regression analysis showed that none of the above variables was a better predictor of the accuracy BDA than IHTT. Further analysis showed that varying performance levels between participants could not account for this finding either. Therefore, it is most likely that individuals with faster inter-hemispheric transfer have a more efficient (as measured by accuracy) hemispheric interaction, at least on this type of task.

It should be noted that in a recent study, Singh and O'Boyle (2004) found that mathematically gifted children (age 13 years) demonstrated increased hemispheric interaction compared to age-matched controls of average ability, and college students. They suggest that the increased hemispheric interaction in these children might be due to differences in brain organisation and possibly to increased callosal connectivity. This explanation would be consistent with the present findings. At this stage, however, it is not possible to discount the possibility that this relationship between cognitive abilities and hemispheric interaction is unrelated to callosal connectivity. In my view, it is unlikely that the present findings are due to differences in cognitive ability since most participants were undergraduate students and thus the spread in cognitive ability would have been much smaller than that present in Singh and O'Boyle's study. Nonetheless, since data on cognitive ability were not collected in the present study, an effect of this variable cannot be excluded and should be controlled for in future research.

Other studies, especially those based on behavioural measures of IHTT, have generally failed to demonstrate a direct relationship between callosal transfer speed and hemispheric interaction. This is likely to be due to small sample sizes and small numbers of trials used, or the use of a measure which may not be a reliable index of IHTT (Bashore, 1981; Brysbaert, 1994b). In this study, using 1200 trials for the Poffenberger task and 2304 trials for the letter task, the relationship between IHTT and hemispheric interaction stabilised once approximately 20 participants were tested, with correlations (always significant) oscillating between .3 and more than .5 until testing was completed.

Based on previous findings using a task very similar to that used in this study, (Weissman et al., 2000) an across visual field advantage for both RT and for accuracy was expected. It was therefore somewhat surprising to find a within-hemisphere advantage for RT. This discrepancy may be due to a practice effect that is more prominent in the within visual field condition and which has been described elsewhere (Liederman et al., 1985; Weissman & Compton, 2003). To determine whether an RT and accuracy BDA would be present if a number of trials similar to previous studies had been used, the data of the first session were analysed separately but neither an across nor a within-hemisphere advantage (or disadvantage) was found. It is unclear why this is the case. Although a display of different shape (square vs v-display) was used, results from Experiment 1 (Chapter 2), have shown no difference between these two types of displays. It may be that since Weissman, Banich, & Puente (2000) tested participants on a 3 item display and a 4 item display (although it is unclear whether these two tasks were mixed or counterbalanced) and since Pollman, Zaidel, and Cramon (2003) used a 4 item display but cued the matching letters, these differences improved across-hemisphere performance.

The lack of RT and accuracy BDA at group level could be interpreted as showing that there is no difference in the level of hemispheric interaction in the within- and across-hemisphere condition. If this were the case, the meaning of a correlation between IHTT and the BDA measures would be unclear. To address this concern, the data of a subgroup of participants (n = 21) who all showed a RT and accuracy advantage in the across-visual field condition were analysed. Even when only the first session of the letter task was considered, the correlation between accuracy BDA and IHTT was larger (r = .587) than that found in the whole group, and again larger when all four sessions were considered (r = .681) strengthening an interpretation of the present results as an association between IHTT and BDA.

A relationship between CUD and hemispheric interaction for accuracy but not for RT was somewhat surprising, particularly since accuracy and response time BDA were strongly correlated (r = -.527) which suggests that individuals who have higher accuracy BDAs also have more efficient latency BDAs. Other factors such as hemispheric organisation may underlie this relationship or, at least, mask the influence of IHTT. This hypothesis is supported, at least in part, by the finding that in participants who show both a latency and accuracy BDA during the first session, a significant relationship was found not only between the accuracy BDA and IHTT for the first and for all four sessions, but also between the overall latency BDA and IHTT (r = -.559). Therefore the latency measure might be "noisier" than the accuracy measure, and more sensitive to uncontrolled experimental variables. Furthermore, in the entire participant group as well as in the sub-group who demonstrated positive BDAs (21 participants who responded faster and more accurately in the across hemisphere condition) a more efficient accuracy interaction was associated with a more efficient response time interaction. This is consistent with a developmental study showing that as the CC matures, both response time and accuracy BDAs increase (Hagelthorn et al., 2000).

A second CUD measure was computed using RT to letter-matches to determine whether complex RT CUD was a valid measure of IHTT. No significant correlation was found between simple RT CUD (3 ms, SD 3.83) and complex RT CUD (16 ms, SD 20.19). The difference between the two types of CUDs was not unexpected as it is probable that the type of information transferred between the cerebral hemispheres during the simple RT task (pre-motor) (Tettamanti et al., 2001) and during the complex RT task (high-level cognitive) is quite different and therefore mediated by different types of fibres with different conduction times. The complex RT transfer time of 16 ms found is consistent with the transfer speed of callosal fibres (19-25 ms) that transfer high-level cognitive information (Aboitiz et al., 2002). The lack of correlation between the two CUD measures can therefore be interpreted in two ways. There may be no relationship between the transfer speed of discrete callosal channels in different individuals, in which case the complex RT CUD might be a valid measure of IHTT for specific channels, and unrelated to those conveying simple RT information. Alternatively, since I have shown that the simple RT CUD is related to the hemispheric interaction measured by the complex RT task, which suggests a relationship between different callosal channels, the complex RT CUD might simply not be a ‘pure’ measure of IHTT but also reflect the effects of other variables such as functional lateralisation. The latter explanation seems more likely but others cannot be excluded at this stage.

In summary, these results demonstrate that individual speed of hemispheric transfer (a behavioural measure) is related to the efficiency of hemispheric interaction (accuracy) so that individuals with faster IHTT tend to have more efficient hemispheric interaction. This relationship cannot be explained better by other variables such as functional lateralisation, handedness, sex, age, or attention. This relationship seems to be strongest between IHTT and the accuracy BDA although a significant correlation was also found between IHTT and RT BDA.

CHAPTER 4

4.1 Interhemispheric Transfer, Hemispheric Interactions, and Left-Handedness

Small but significant differences between left-handed and right-handed individuals have been demonstrated in numerous neuroanatomical (e.g., Westerhausen et al., 2004), morphological (Amunts, Jancke, Mohlberg, Steinmetz, & Zilles, 2000; Tuncer, Hatipo, & Özate, 2005) and behavioural studies (Haude, Morrow-Thucak, Fox, & Pickard, 1987; Schmidt, Oliveira, Rocha, & Abreu-Villaca, 2000; Tremblay, Monetta, & Joanette, 2004). But other studies have failed to show any handedness effects (Beaton, 1997; Piccirilli, Finali, & Sciarma, 1989; Steinmetz et al., 1992). As a whole, the results suggest that slight neuroanatomical differences between handedness groups may nevertheless be indicative of differences in interhemispheric conductivity and in patterns of functional lateralisation which are likely to affect hemispheric interactions.

At least five morphological studies have shown that left-handed individuals differ from right-handed individuals in the size of their corposa callosa. Witelson (1985; 1989) found, in two postmortem studies, that left-handed and mixed-handed individuals had a larger corpus callosum (CC) than right-handed individuals. This difference was mainly present in the isthmus which connects regions of the parietal association cortices that are known to be involved in asymmetrical brain processes (e.g., language). In an MRI study, Habib and colleagues (1991) confirmed that nonconsistent right-handers (including left-handed participants) had larger CCs, although this time it was demonstrated for the anterior part. Further support for such a difference was provided by Tuncer, Hatipolu, and Özate (2005) who found that left-handers had larger areas of the anterior body, posterior body and the isthmus. Finally, Moffat, Hampson, and Lee (1998) found in a MRI study that left-handed participants with left-hemisphere speech functions had a larger CC (isthmus, splenium, and genu) than both left-handed participants with right-hemisphere speech functions or right-handed participants.

An interaction of sex and handedness was also found in three of these studies (Habib et al., 1991; Tuncer et al., 2005; Witelson, 1989) suggesting that males tend to have a larger CC than females (although Jancke and Steinmetz (2002) have argued that these findings might be methodological artefacts), with left-handed males having a larger CC than right-handed males, whereas females do not seem to differ in CC size as a function of handedness.

A larger CC size in left-handed individuals is not in itself proof that interhemispheric connectivity is greater in this group, since fibre density and size could vary between handedness groups. However, a recent diffusion-tensor MRI study (Westerhausen et al., 2004) indicates that fibre density might be greater in the CC of left-handed people suggesting a greater interhemispheric conductivity in this group, particularly in the posterior third of the CC (isthmus and splenium).

These findings are consistent with the results of three behavioural studies. Fagard and Corroyer (2003) showed that in small children, handedness is associated with interhemispheric transfer, with less right-handed children performing better on a bimanual coordination task. Another study, in adults (Potter & Graves, 1988), also showed that non-right-handed participants performed significantly better than right-handed participants in a motor task (drawing a line with each hand while blindfolded) and on a tactile task (determining whether left and right hands were touched in the same location). Finally, Schmidt, Oliveira, Rocha, and Abreu-Villaça (2000) showed that left-handed men benefited most from learning transfer between hands in a fine motor task.

Left-handed individuals have also been shown to differ from right-handed individuals in measures of anatomical and functional lateralisation. Left-handers tend to have more anatomically symmetrical hemispheres and specifically, a more symmetrical planum temporale (see Beaton, 1997 for a review; Sequeira et al., in press) as well as a reversed pattern of asymmetry of the motor cortex (Amunts et al., 2000). Since more symmetrical brains have been shown to be associated with a greater number of callosal fibres, these findings are also consistent with greater interhemispheric connectivity in left-handers (Rosen et al., 1989). This view is supported by an electro-physiological study showing that event-related potentials across the CC are faster and have a greater amplitude in left-handed compared to right-handed individuals (Hoffman & Polich, 1999).

It has also been demonstrated that left-handed individuals vary in their pattern of functional lateralisation. More left-handed individuals (15% compared to 1-8% in right-handers) present with bilateral or reversed representation of the language centres (Knecht et al., 2000; Tzourio, Crivello, Mellet, Nkanga-Ngila, & Mazoyer, 1998). Left-handers have also been shown to be less functionally lateralised than right-handers (e.g., Eviatar et al., 1997).

As a whole, the findings presented above suggest that left-handed individuals have a greater interhemispheric connectivity which may be associated with a more efficient level of hemispheric interaction in this population but tests of this hypothesis have produced mixed results. Two studies using digit- and letter-matching tasks (Banich et al., 1990) or mental calculation tasks (Hatta & Yoshizaki, 1996) failed to find significant differences in hemispheric interaction between left- and right-handers. A third study found that left-handed participants did not benefit from hemispheric interactions in a task involving matching letters across- and within-visual fields (Eviatar et al., 1997), whereas right-handed participants demonstrated a significant across-visual field advantage in this task.

A fourth study (Belger & Banich, 1998) found that handedness affected hemispheric interaction but that this effect was modulated by an interaction with hemispheric arousal. In this study, Belger and Banich assessed asymmetric hemispheric activation (AHA) with a chimeric face test consisting of indicating a preference for one of two chimeric faces, of which one half was smiling, and the other not. According to Belger and Banich, this test has been shown to predict perceptual asymmetries in various tasks thought to engage processing by one hemisphere more than the other. No effect of AHA was found for left-handed participants, but right-handed individuals with a right hemisphere bias demonstrated a significant across-hemisphere advantage in a rhyming task, whereas those with left hemisphere bias demonstrated a significant within-hemisphere advantage. Belger and Banich suggested that in right-handed individuals with a right hemisphere bias, the greater activation of the right hemisphere counterbalanced the left hemisphere lateralisation of the rhyming task, thus favouring across hemisphere processing. In contrast, in right-handed individuals with a left hemisphere bias, the greater activation of the left hemisphere further biased processing towards the already specialised hemisphere and thus favoured within (left) hemisphere processing. Interpretation of the left-handed group results is speculative but the decreased level of functional lateralisation in left-handed individuals suggests that in this group the BDA might have been less influenced by both comparatively smaller functional lateralisation and AHA.

The above four studies' inconsistent findings cannot be attributed to a lack of power since they all used large numbers of participants (86, 66, 106, and 57 respectively), nor can they be attributed to obvious differences in the type of tasks used since they were very similar, particularly the tasks used by Banich et al. and Eviatar et al. (letter- and digit-matching) and used comparable parameters (e.g., eccentricity, presentation time, stimulus size).

These findings are particularly surprising because, as reviewed earlier, morphological, neurophysiological, and behavioural data point to left-handed individuals having greater interhemispheric connectivity. Furthermore, the findings of Experiment 3 show that greater interhemispheric connectivity (interhemispheric transfer time measured with the Poffenberger paradigm) is associated with more efficient hemispheric interactions (measured with a letter-matching task similar to that used by Banich et al. and Eviatar et al.). It is possible that some limitations of previous studies might have obscured subtle differences between handedness groups. For instance, three of the four studies reported did not take into account the magnitude of left- or right-handedness. Rather, they relied on direction only, although Hatta et al. have split the left-handed group into familial and non-familial left-handers. This is important because there is substantial evidence that handedness is probably a continuous measure and certainly not a homogeneous one (see Beaton, 1997). It is also possible that the task used by Banich et al. might not have been difficult enough to reveal differences between handedness groups. This possibility is supported by the fact that Eviatar et al., using a similar but more complex task (name rather than shape letter-matching task) have demonstrated a handedness group difference, while Hatta et al. have found trends suggesting a difference between familial and non-familial left-handers in their more complex task but not in the simpler one.

4.2 Experiment 4

Based on this evidence, the aim of this study was to assess the efficiency of hemispheric conductivity and of hemispheric interactions in left-handed individuals and to compare them with right-handed individuals using identical measures. Since it was shown in Chapter 3 that interhemispheric connectivity is related to the efficiency of hemispheric interactions the first aim would be to test whether this is also the case in a left-handed population using a identical design. Secondly, the findings in right-handed participants (Chapter 3) were compared with those of this experiment to determine whether handedness differences were present. This was done by merging the two data sets so that a multiple regression could be conducted based on left- and right-handed participants' measures. Conducting a multiple regression analysis has the advantage of enabling the assessment of not only the direction but also the strength of handedness measures, and to determine whether other factors such as age, sex, attention, and overall performance also influence hemispheric interactions.

4.2.1 Method

4.2.1.1 Participants

Twenty left-handed subjects (10 females, 10 males), aged between 18 and 42 years old with normal or corrected-to-normal vision completed this study (two participants' data were excluded because they did not complete all sessions). They were students who either participated to fulfil undergraduate psychology course requirements, or were recruited on the Australian National University campus, and received 35 dollars as compensation for their time and travel. Handedness was assessed with a questionnaire adapted from the Edinburgh Handedness Inventory (Oldfield, 1971, see Appendix B). Participants who reported a history of neurological or motor disease were excluded from the study. The study received approval from the Human Research Ethics Committee.

4.2.1.2 Stimuli and Procedure

The stimuli and procedure used in this experiment were identical to those used in Experiment 3.

4.2.2 Results

4.2.2.1 Participants' Variables

Participants had a mean age of 25 years and 4 months (SD = 7.2 years), and an average handedness coefficient (Edinburgh Inventory) of -0.72 (SD = .26).

4.2.2.2 Inter-Hemispheric Transfer Time (IHTT) using the Poffenberger Paradigm

Reaction times (RT) to the presentation of a dot in the left or right visual field (VF) were measured for the two hands, and an estimate of IHTT or crossed-uncrossed difference (CUD) was computed by subtracting RTs for the direct route (VF ipsilateral to responding hand) from RTs for the indirect route (VF contralateral to responding hand). Reaction times smaller than 100 ms and larger than 1000 ms (2.3%) were excluded. The average RT in the Poffenberger task in all conditions ranged from 231 ms to 321 ms with average valid response rates of 98%. The average CUD was 1.56 ms (SD = 2.99).

A 2 Hand x 2 VF within subject ANOVA was applied to the reaction time measures to confirm that responses by the hand contralateral to the hemisphere perceiving the stimulus were faster than those of the ipsilateral hand. A significant Hand by VF interaction, $F(1,19) = 5.428$, $p < .05$, supported this premise Figure 4-1.

4.2.2.3 Hemispheric Interaction in a Letter-Matching Task

RT and accuracy for matching letter pairs were measured for four visual field/hemisphere conditions: within left visual field (LVF), within right visual field (RVF), and across visual fields (up or down) and are presented in Table 4-1; the differences between the averages of the within-visual field and across-visual field conditions were calculated as an index of IHI. RTs smaller than 250 ms and larger than 1500 ms (3.3% of responses) were excluded.

Average response time and accuracy for the within- and across-hemisphere condition and the difference between these conditions, the RT and accuracy BDAs are presented in Table 4-2. The RT BDA was not significant, $t(1,19) = .76$, n.s., but the accuracy BDA was significant, $t(1,19) = 2.495$, $p < .05$, indicating that participants performed more accurately in the across visual field trials.

The correlation between the accuracy and RT measure of IHI was not significant, $r = -.032$, n.s.

To determine whether one hemisphere was more proficient at the letter task than the other, paired sample t-tests were conducted, but no significant difference was found for the latency measure, $t(1,19) = .997$, n.s., or for the accuracy measure, $t(1,19) = .037$, n.s.

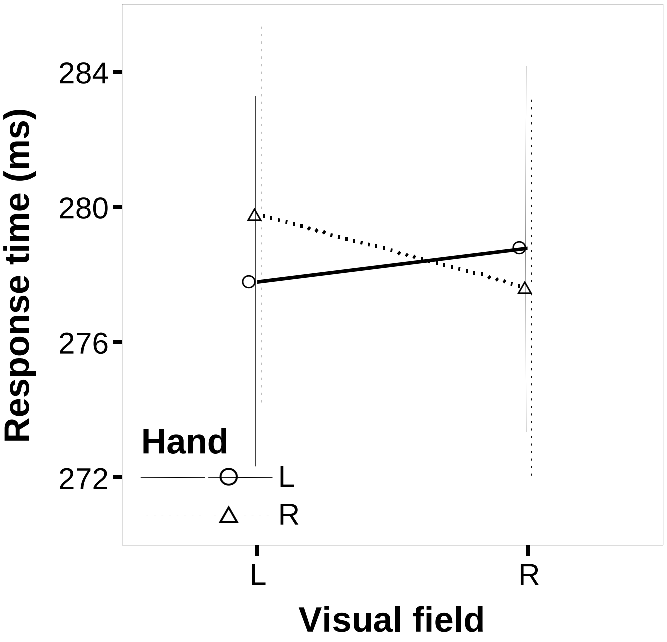


Figure 4-1. Response times for the Poffenberger task show an interaction between visual field of presentation of the dot (left/right visual field) and responding hand (left/right). Error bars represent the standard error of the mean.

Table 4-1. Accuracy and RT measures for the different conditions of the letter-matching task for the left-handed participants (Experiment 4) and right-handed participants (experiment 3). Standard deviations are presented in brackets.

Group	Measure	Visual field conditions			
		Within left	Within right	Across up	Across down
Left-handed	RT	879 ms (109)	899 ms (90)	915 ms (94)	942 ms (70)
	% correct	90.6 % (7.2)	90.8 % (6.8)	89.3 % (8.6)	89.4 % (6.4)
Right-handed	RT	829 ms (94)	849 ms (112)	876 ms (99)	870 ms (93)
	% correct	92.4 % (5.9)	91.5 % (6.3)	92.5 % (5.6)	90.5 % (6.0)

Table 4-2. Accuracy and RT measures for within visual field matches (within), across visual field matches (across), and for the BDA of the letter-matching task for the left-handed participants (Experiment 4) and right-handed participants (experiment 3). Standard deviations are presented in brackets.

	Measure	Within	Across	BDA
Left-handed	RT	888 ms (88)	878 ms (62)	10 ms (60)
	% correct	91.0 % (7.0)	89.0 % (7.0)	1.5 % (2.7)
Right-handed	RT	839 ms (88)	873 ms (80)	-35 ms (34)
	% correct	92.0 % (5.0)	91.5 % (5.0)	0.5 % (2.7)

4.2.2.4 IHTT – Hemispheric Interaction Relationship

In the previous chapter it was shown that in right-handed individuals, IHTT and the accuracy BDA were significantly correlated ($r = .354$, $p < .001$), whereas IHTT and response time BDA were not ($r = -.078$, n.s.). A correlational analysis between IHTT and BDA was conducted to determine whether these variables were also associated in left-handed individuals. IHTT was not found to be significantly correlated with the response time BDA, $r = .041$, n.s., but a correlation of magnitude similar to that found in right-handed individuals was found between IHTT and the accuracy BDA, $r = .401$, $p = .08$, although this relationship was marginally insignificant.

4.2.2.5 Handedness Effect in the Relationship between IHTT and CUD

In order to further investigate the effect handedness has in the relationship between IHTT-CUD the data of the present study were pooled with those of right-handed individuals collected during Experiment 3.

Since the variability of the BDA could, apart from the CUD and possibly handedness, also be explained by other factors such as sex, age, hemispheric lateralisation, or attention, a multiple regression analysis was conducted on these variables. Lateralisation indexes for the letter task were computed with the following formula, (RVF – LVF)/(RVF + LVF), for the latency and accuracy measures. Correct RT and accuracy rates of the Poffenberger task were used as indexes of attention. Since both handedness coefficients and age were negatively skewed, these variables were transformed with an inverse function. Average accuracy rate for the letter-matching task was also included in the analysis to exclude the possibility of an effect of overall performance.

The regression analysis showed that sex, age, lateralisation, attention, and overall performance did not significantly predict the accuracy BDA. The analysis was rerun without these variables and confirmed that the CUD, $t(1,99) = 3.901$, $p < .001$, and (inverse) handedness, $t(1,99) = -2.503$, $p < .05$, were significant predictors of the accuracy BDA, $F(2, 99) = 9.338$, $p < .001$, accounting for 16.1 % (14.4% adjusted) of its variance. Correlations between these variables, the standardised regression coefficients (β), and the semi-partial correlations (sr_i^2) are presented in Table 4-3.

In order to better describe how handedness affects the accuracy BDA, the combined sample was split into four groups: extreme left-handed (handedness coefficients between –1.0 and -.8), left-handed (handedness coefficients between -.8 and 0), right-handed (handedness coefficients between 0 and .9), extreme right-handed (handedness coefficients between .9 and 1.0). Because left-handed individuals live in a right-handed world and are therefore biased towards using their right hand more than the right-handers would use their left, the cut-off chosen for extreme left-handedness was lower than that for extreme right-handedness. The proportions of males and females, and ages, of these groups are shown in

Table 4-4. Figure 4-2 shows the accuracy BDA for each group. To determine whether differences between the handedness groups were significant a one-way ANOVA with handedness category as independent variable and accuracy BDA as dependent variable was conducted but no main effect was detected, F(3,96) = 1.010, n.s.

Table 4-3. Correlations between the CUD, handedness, and accuracy BDA and standardised regression coefficients (β) and semi-partial correlations (sr_i^2) of the final regression analysis.

	Correlations			Coefficients	
	CUD	Handedness	BDA (Accuracy)	β	sr_i^2
CUD	1	.172	.328	.368	.363
Handedness	.172	1	-.173	-.236	-.233

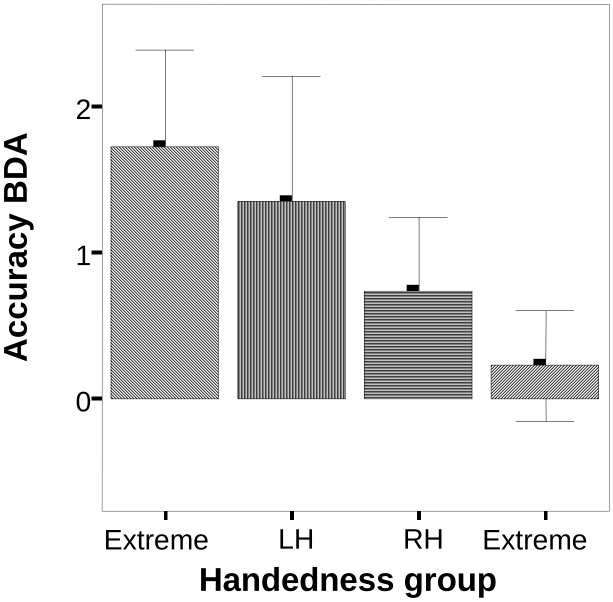


Figure 4-2. Accuracy BDA for the four handedness groups. Results show no significant difference between the handedness groups. Error bars show the standard error of the mean.

Table 4-4. Handedness, sex ratio, and average age for the four handedness groups. Standard deviations are presented in brackets.

	Hand. coef.	Male / Female ratio	Age
Extreme left-handed	-1.0 >< -.8	4 / 3	25.0 years (8)
Left-handed	-.8 >< 0.0	6 / 7	25.5 years (7)
Right-handed	0.0 >< .9	23 / 12	21.3 years (5)
Extreme right-handed	.9 >< 1.0	17 / 28	23.4 years (8)

4.2.2.6 Handedness and Response Time BDA

Since no significant correlation was found between CUD and response time BDA there was no rationale for analysing this relationship further. However, this does not exclude the possibility that handedness is a significant predictor of the response time BDA. Therefore a regression analysis similar to that conducted on the accuracy BDA was conducted on the response time BDA. The same variables were included, with the exception of the CUD and the average accuracy measure of the letter-matching task, which was replaced with the average response time measure of this task (i.e. overall performance).

The regression analysis showed that sex, age, and the latency measure of attention did not significantly predict the latency BDA. The analysis was rerun without these variables and revealed that (inverse) handedness, $t(1,99) = -3.758$, $p < .001$, overall performance (RT of the letter-matching task), $t(1,99) = 3.490$, $p < .01$, and attention (average RT of the Poffenberger paradigm), $t(1,99) = -1.997$, $p < .05$, were significant predictors of the response time BDA, $F(3, 96) = 9.928$, $p < .001$, accounting for 23.7 % (21.3% adjusted) of its variance. Correlations between these variables, the standardised regression coefficients (β), and the semi-partial correlations (sr_i^2) are presented in Table 4-5. The handedness groups used in the previous analysis were used to further describe the effect of handedness on the RT BDA. Figure 4-3 shows the differences in RT BDA between these groups. To determine whether differences between the handedness groups were significant, a one-way ANOVA with handedness category as independent variable and latency BDA as dependent variable was conducted. A significant effect of handedness category was detected, $F(3,96) = 9.785$, $p < .001$. Post hoc contrasts showed that the latency BDA of the extreme left-handed group was significantly larger than all other handedness groups and that the difference between the left-handed group BDA and the extreme right-handed group BDA almost reached significance ($p = .077$). A trend analysis also revealed that the relationship between handedness category and response time BDA was linear, $p < .001$.

Finally, because of the different relationships found between CUD, handedness, and accuracy and response time BDAs, a correlational analysis between accuracy and response time BDA was conducted to exclude the possibility of a speed-accuracy trade-off. The correlation between accuracy and response time BDA was significant, $r = -.275$, $p < .01$, indicating that participants who had more efficient interhemispheric interactions based on the accuracy measure also had more efficient response time interactions based on the response time measure.

Table 4-5. Correlations between handedness, overall performance, attention and RT BDA and standardised regression coefficients (β) and semi-partial correlations (sr_i^2) of the final regression analysis.

	Correlations				Coefficients	
	Handedness	Overall performance	Attention	BDA (RT)	β	sr_i^2
Handedness	1	-.094	-.113	-.347	-.338	-.335
Overall performance	-.094	1	.139	.322	.315	.311
Attention	-.113	.139	1	-.099	-.181	-.178

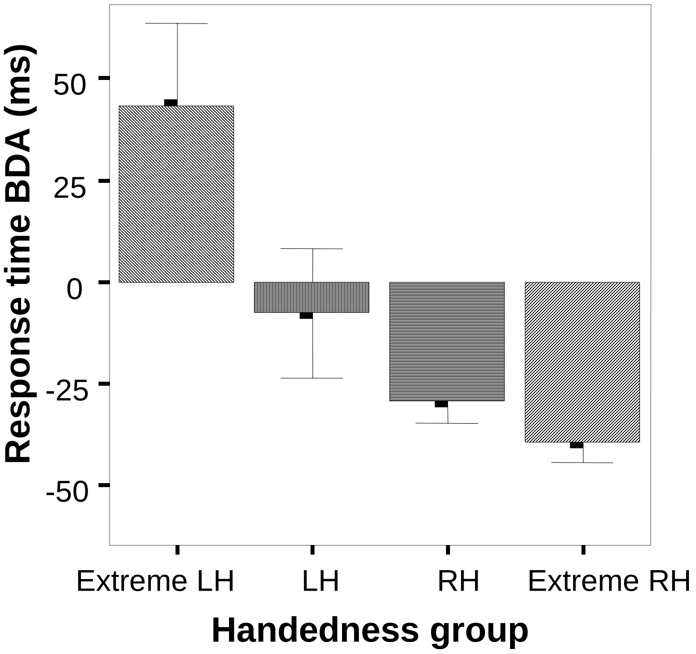


Figure 4-3. RT BDA for the four handedness groups. Results show a significant difference between the extreme left-handedness group and all other group and a near significant difference between the left-handed group and the right-handed group. Error bars show the standard error of the mean.

4.2.3 Discussion

The aims of this study were twofold. First, to establish whether the positive relationship between efficiency of interhemispheric transfer and hemispheric interactions found in Experiment 3, in a right-handed population, was also present in left-handed participants. Secondly, to determine whether left-handed individuals differed from right-handed individuals in the efficiency of their hemispheric interactions. The latter hypothesis was based on findings showing that left-handed individuals tend to differ in their cerebral morphology and asymmetry as well as in their functional asymmetry from to their right-handed counterparts, and that these variations are thought to indicate greater interhemispheric connectivity in left-handed people.

The present findings show that, as in right-handers (r = .354), the measure of inter-hemispheric connectivity (interhemispheric transfer time measured with the Poffenberger paradigm) was significantly correlated with a measure (accuracy) of hemispheric interaction (letter-matching within and across visual field) in left-handed individuals (r = .401), such that individuals with faster interhemispheric transfer time demonstrated a greater degree of hemispheric interaction.

The effect of direction and degree of handedness was examined by merging the dataset of the present experiment with that in right-handed participants of Experiment 3. This analysis revealed that handedness was significantly associated with both the latency and accuracy measure of hemispheric interaction. Surprisingly, left-handedness was associated with reduced hemispheric interaction efficiency when the accuracy measure was considered but with a greater hemispheric interaction efficiency when the response time measure was considered. This suggests the presence of a dissociation between neural substrates underlying accuracy and response time performance across the hemispheres.

To further define the relationship between handedness and hemispheric interaction, participants were allocated to four handedness groups. Post hoc tests showed that at least for the response time BDA, handedness category was a significant predictor of hemispheric interaction efficiency. Furthermore, the relationship between handedness category and response time BDA was shown to be linear, with greater efficiency of hemispheric interaction being associated with more extreme left-handedness. Opposite trends were found for the accuracy BDA.

It is difficult to explain the opposite direction of the relationship between accuracy and response time BDA and handedness, particularly because, in the whole sample, those participants who demonstrated an across-hemisphere advantage for the accuracy measure also demonstrated an across-hemisphere advantage for the response time measure. One possibility is that one of these relationships is mediated by one factor, perhaps some properties of interhemispheric transfer, whereas the other might be mediated by another factor such as the degree of anatomical/functional lateralisation. One finding lending some support to this hypothesis is the fact that the measure of interhemispheric transfer was a significant predictor of the accuracy BDA but not of the response time BDA. Thus it appears that the response time BDA must be mediated by other factors, most likely, the varying degree of individuals' cerebral lateralisation.

In any case, the positive relationship between handedness and response time BDA was strong, with extreme left-handed individuals presenting an across visual field advantage of 43 ms while extreme right-handed individuals performed better in the within-visual condition by 39 ms. In contrast, the handedness – accuracy BDA relationship was much weaker with extreme left-handed individuals performing slightly better (1.7 %) in the within-visuals field condition compared to the across-visual field condition, whereas extreme right-handers performed equally well in the within- and across-hemisphere conditions.

A surprising result is that no effect of sex was found. A number of studies discussed in the introduction reported handedness effects in males but not in females. It might therefore have been expected that an interaction between sex and handedness would be found. The fact that it was not emphasises the importance of using large sample sizes, controlling covariates, and replicating studies involving heterogeneous variables. It is also important to treat handedness as a continuous variable or at least to use more than two handedness groups since subtle differences are often found between strongly and mildly left-handed individuals or between strongly and mildly right-handed individuals.

In conclusion, these findings confirm the prediction of an increasing efficiency of hemispheric interactions with increasing left-handedness. Furthermore, they reinforce the view that hemispheric interactions are mediated by a number of subtly interacting factors. Finally, they replicate findings in Experiment 3 showing that greater hemispheric interaction efficiency is associated with faster inter-hemispheric transfer.

CHAPTER 5

5.1 Hemispheric Interaction and Practice Effects

While many variables affecting hemispheric interaction have been studied in detail, the effect practice may have on hemispheric interaction has been mostly ignored. Two reports of practice effects in a letter-matching task similar to that used in the present thesis have been made (Liederman et al., 1985; Weissman & Compton, 2003). It appears that initially performance of a complex task, such as the name letter-matching task, is faster and more accurate in the across-visual field condition. However, with practice, fewer regions need to be recruited as processing becomes more efficient, and a decrease in BDA (that is, an increase in within-hemisphere advantage) is observed. This view is consistent with the results of Experiment 3. Weissman and Compton have found that this increased efficiency, due to practice, was only observable in the within-hemisphere condition and interpreted it as a qualitative shift in strategy due to learning (Logan, 1988). They suggest that, initially, an algorithmic strategy, in which letter pairs are compared sequentially, might be used to solve the task but that with practice, a strategy based on direct memory retrieval might be favoured. Based on the assumption that algorithmic solutions involve more processing steps than direct memory retrieval, Weissman and Compton suggest that the decrease in BDA with practice might be due to a decrease in task complexity and therefore, an increase in single-hemisphere processing.

In order to better define the effect practice has on within- and across-hemisphere performance, Weissman and Compton (Weissman & Compton, 2003) reanalysed two studies of hemispheric interaction. The first study (Weissman et al., 2000) used a letter-matching task where three (or four) letters were presented in a V-shaped display, with two letters presented in one visual hemifield and the third (or the other two) letter(s) in the other hemifield. The task consisted of detecting whether two letters were matching, with matches occurring either within the same hemifield (unilateral condition) or across hemifields (bilateral condition). Participants were tested in two consecutive blocks. As participants practiced physical- and name-identity versions of the letter-matching task, performance improved more in the within-visual-field condition than in the across-visual-field condition for both versions of the task. The significant BDA for the name-identity task was eliminated, and led to an even larger within-visual-field advantage for the physical-identity task. The second study (Weissman & Banich, 1999) was based on a similar design but involved assessing the effect of interference, using a global-local perception paradigm, on IHI. The global matching letters to be detected were made up of local smaller letters which could either be congruent with the global letter they were part of, or not. A global-local interference index could then be computed for the unilateral and the bilateral conditions by contrasting performance using congruent or incongruent global-local matching letters. In the initial analysis, it was found that interference decreased when targets were divided between the hemispheres. As in the first study (Weissman et al., 2000), however, this BDA disappeared in the second half of the experiment, with interference decreasing for the unilateral condition but remaining the same for the bilateral condition.

These results are surprising in that if a strategy shift occurs, it would seem that it should also influence, although possibly to a lesser extent, performance on the bilateral trials. Furthermore, as Weissman and Compton acknowledge but discount, other theories such as differential priming levels in the unilateral and bilateral conditions could also account for this pattern of results. One potential difficulty associated with the reanalysis of these studies is that data were gathered in a single (though two-block) session, and using a relatively small number of trials. It would therefore be interesting to assess how within-, compared to across-hemisphere performance, behaves over a longer period of time, using multiple sessions/blocks and large numbers of trials. If a shift in strategy is indeed the cause of the disappearance of the BDA, performance in the unilateral trials would be expected to plateau over subsequent sessions. On the other hand, if performance continues to improve, a different explanation is needed, at the least, that a strategy shift and another practice effect act together. Such a combination of learning effects has been demonstrated by Kirsner and Speelman (1996). They found that results obtained by Logan (1988) were better explained by a combination of repetition priming and general practice than by repetition priming alone.

It is also possible that in addition to the improvement in within-hemisphere performance with practice, performance of two hemispheres working together does improve over time, but at a slower pace than that of a single hemisphere, and thus could not be observed in the data used by Weissman and Compton, who used only a limited number of trials divided into two (study 1) and four (study 2) blocks.

5.2 Supplementary Analysis of Experiment 3

To answer these questions I conducted a further analysis of the data from experiment 3, which used a paradigm similar to that used by Weissman et al. (1999; 2000) but where relevant data were collected over four sessions taking place on separate days, and totalling 2304 trials for each of eighty participants.

It would be expected that, if the practice effect is best explained by Logan's model (1988), responses to first presentations of unique stimuli should be markedly slower than responses to second and later presentations. This improvement in response speed should rapidly decrease and plateau, following a power function. This effect should be present within and across sessions but responses to first presentations of different stimuli in different sessions should not differ, since no memory trace would have been laid, and therefore one cannot be retrieved. In contrast, if a general practice effect is also present (Kirsner & Speelman, 1996) first presentations of unique stimuli in later sessions should be faster than those in earlier sessions. According to Kirsner and Speelman, a general practice effect should also follow a power function (or an exponential function which has a very similar shape).

Finally, if, as suggested by Weissman and Compton's findings (Weissman & Compton, 2003), an effect of practice occurs only in the within-hemisphere condition, no such pattern of results should be observable in the across-hemisphere condition.

5.2.1 Method

See Experiment 3.

5.2.2 Results

Response-time and accuracy measures for matching letter pairs were measured for three visual field/hemisphere conditions (within-left-visual field (wl), within-right-visual field (wr), and across visual fields (ac)) with the aim of computing the differences between average within-visual-field and average across-visual-field conditions as an index of hemispheric interaction. Response times less than 250 ms were considered to be anticipatory responses and were excluded.

Average response times to matching letter pairs averaged over the four sessions were 839 ms (SD, 88 ms) for the within-visual-field condition and 873 ms (SD, 80 ms) for the across-visual-field condition. The difference between “within” VF and “across” VF conditions, the response-time BDA (-34.7 ms; SD, 34.7 ms), was significant, t(1,79) = 8.94, p < .001.

Average accuracy rates were 92% (SD, .05%) for the within-hemisphere condition and 91.5% (SD, .05%) for the across-hemisphere condition. The accuracy rate difference between within- and across visual field conditions, the accuracy BDA (0.45%; SD, 2.74%), did not reach significance, t(1,79) = -1.47, ns.

Next the performance for each session was computed for the wl, wr and ac conditions (Figure 5-1) and for the BDA (Figure 5-2).

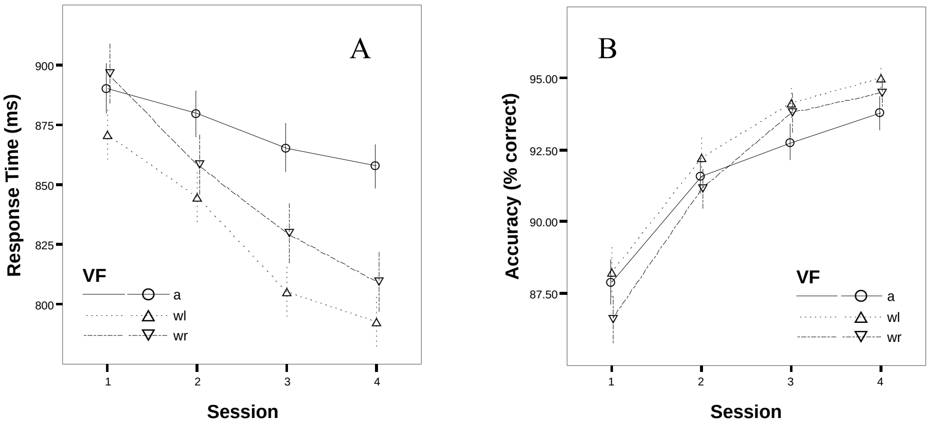


Figure 5-1. Improvement in letter-matching detection over 4 sessions for different visual-field conditions: within-left-visual field (wl), within-right-visual field (wr), and across-visual fields (a) for A) the response time measure and B) the accuracy measure. Error bars represent the standard error of the mean.

Repeated measures ANOVAs were conducted on accuracy and response-time data to determine whether left- and right-hemisphere performances were different across the four sessions. No main effect of hemisphere was found for accuracy, F(1,79) = 2.949, ns, or for response time, F(1,79) = 2.790, ns. However, a significant session effect was found for accuracy, F(1,77) = 57.72 , p < .001, and for response time, F(1,77) = 33.253, p < .001, reflecting a learning effect over the four sessions. Since left- and right-hemisphere performances did not differ, they were averaged and further repeated measures ANOVAs were computed to determine whether within-hemisphere performance differed from across-hemisphere performance over the four sessions. For accuracy, no difference was found between within- and across-hemisphere performance, F(1,79) = 2.155, ns, but a session effect was again present, F(1,77) = 58.989, p < .001, as well as an interaction between hemisphere conditions and testing sessions, F(1,77) = 4.179, p < .01, reflecting a slightly greater learning effect for the within- than for the across-hemisphere condition. For response time, in contrast to prior reports, but consistent with a practice-related reduction of the BDA, a significant within-field advantage was observed for the letter-matching task, F(1,79) = 79.973, p < .001. A main effect of testing session, F(1,79) = 20.529, p < .001, as well as an interaction between hemisphere conditions and testing session, F(1,77) = 32.191, p < .001, were also detected showing that within-hemisphere performance was faster, and improved more over time, than across-hemisphere performance. To determine whether a significant learning effect occurred in the within- as well as the across-hemisphere conditions between the first and the fourth sessions, paired-sample t-tests were conducted, and showed that significant improvement in response speed occurred over time in the within-, t(1,79) = 9.951 , p < .001 , as well as in the across-hemisphere conditions, t(1,79) = 4.144, p < .001.

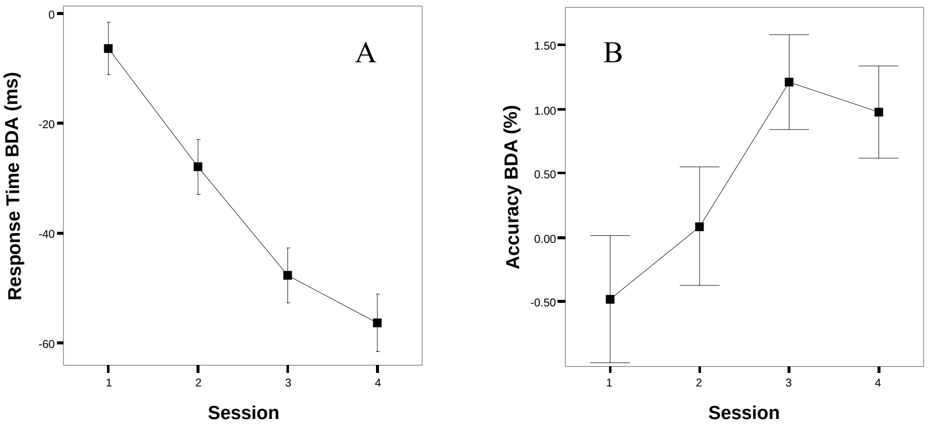


Figure 5-2. Change in BDA (within - across-hemisphere performance) over 4 sessions for A) response time and B) accuracy. For the response-time measure, a positive BDA denotes a bilateral advantage whereas for the accuracy measure a negative BDA denotes a bilateral advantage. Error bars represent the standard error of the mean.

In order to determine whether the present data were consistent with a strategy-shift theory (Logan, 1988) or a combination of repetition priming and general practice (Kirsner & Speelman, 1996), each presentation of a unique stimulus for all sessions for each participant was ranked. For example, the first time the letters A, B, a, g (clockwise, starting from top left corner of the display) were presented to a specific participant, this trial was ranked as 1. The second time this stimulus was presented it was ranked as 2 (although other, different stimuli, are likely to have been presented in-between), and so on. This was repeated for each combination of letters used during a session. The change in response times as a function of the number of presentations of unique stimuli (for the first three presentations) for all participants and each session is shown in Figure 5-3. Presentations were limited to three to make performances in different sessions more comparable, given that only a small number of stimuli were presented four times or more in the first session. A practice effect can be observed, since items which were presented for the first time in sessions 2, 3, and 4 were responded to faster than those presented in previous sessions (Figure 5-3). On the other hand, no obvious repetition priming effect was observed in any of the sessions since no sharp improvement in response time was observed between the first, second, and third presentations of identical stimuli as would be predicted by Logan's model.

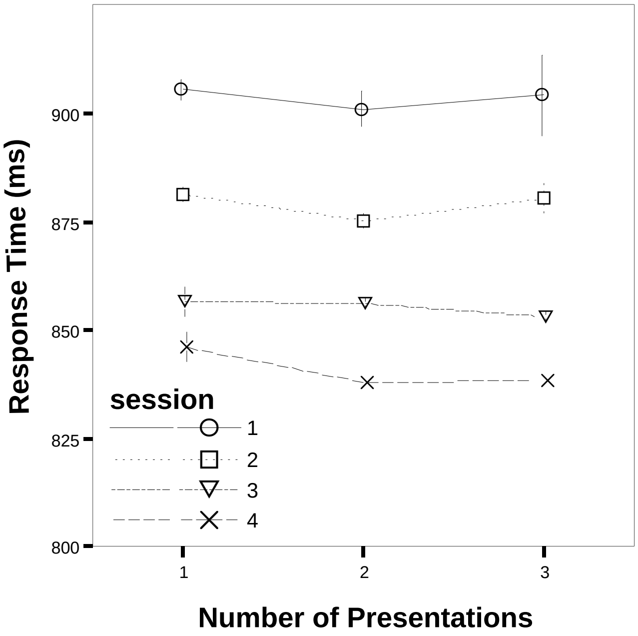


Figure 5-3. Change in response time as a function of the number of presentations of unique combinations of letters (in identical positions) for each session. Error bars represent the standard error of the mean.

In order to further define the quality of the practice effect across the four sessions, response times to first presentations of all stimuli in each block of each session were computed. Because Kirsner and Speelman (1996) showed that a power function better described the practice effect in group data whereas exponential functions better describe individual data, different curves were fitted to determine which of these functions best described the present data. For the accuracy measure, the best fit was attained using a power function of the type $F(x) = a – b * x^C$ with $r^2 = .797$ (linear, $r^2 = .628$; exponential, $r^2 = .272$). The same procedure was repeated for the response-time performances of first presentations. The best fit was attained using a power function, $r^2 = .777$ (linear, $r^2 = .741$; exponential, $r^2 = .745$), and is shown in Figure 5-4. To determine whether improved accuracy scores were closely related to improved response times, the correlation between these two measures was computed. A highly negative correlation, r = -.758, between response time and accuracy was found.

Since it is possible that a failure to detect a repetition priming effect may be due to a large general-practice effect occurring across the four sessions, hiding a smaller repetition-priming effect, performance in the first session was further analysed. Response times to first, second and third presentations in the sixth and twelfth blocks of session one were computed (Figure 5-5) but did not show a repetition priming effect consistent with that described by Logan (i.e. a power function with a rapid decrease in response time, followed by a plateau, and significant differences between first, second, and third presentations).

To determine whether the above practice effect occurred in the within- as well as in across-hemisphere conditions, response times were plotted as a function of block of presentation for the two conditions (Figure 5-6). Linear, power, and exponential functions were fitted for each condition. The best fit was attained with an exponential function for the within-hemisphere condition, $r^2 = .764$ (linear, $r^2 = .760$; power, $r^2 = .742$), and with a power function for the across-hemisphere condition, $r^2 = .399$ (linear, $r^2 = .367$; exponential, $r^2 = .369$).

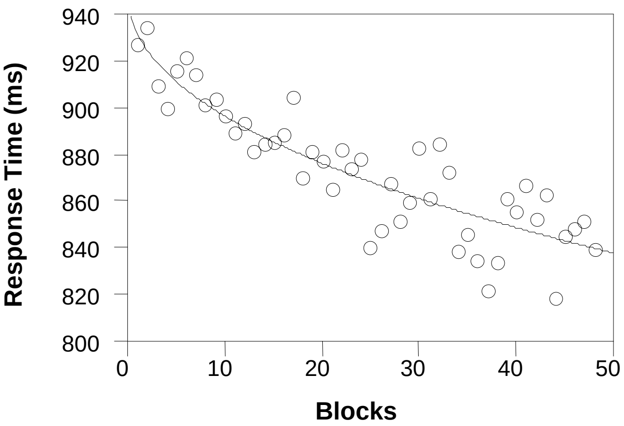


Figure 5-4. Response time as a function of presentation block for first presentations of unique stimuli.

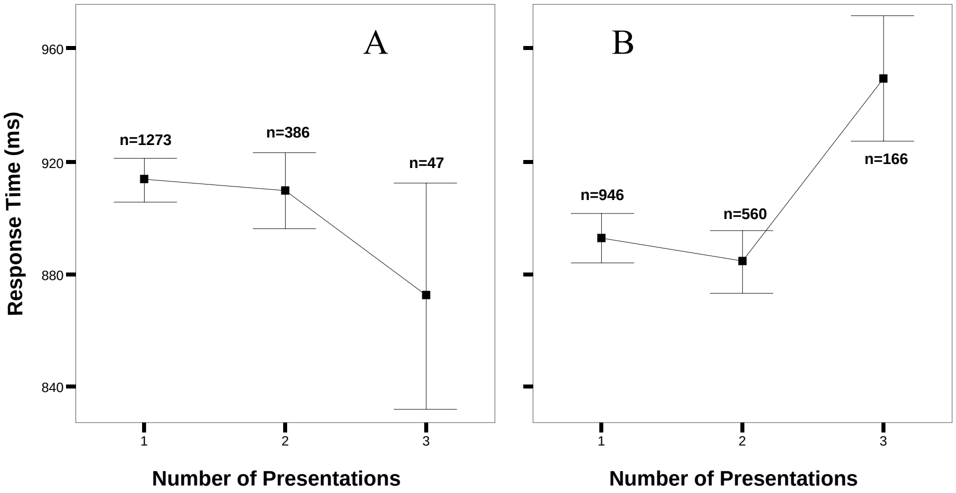


Figure 5-5. Response times to first, second, and third presentations of unique stimuli in block 6 (A) and block 12 (B). Error bars represent the standard error of the mean.

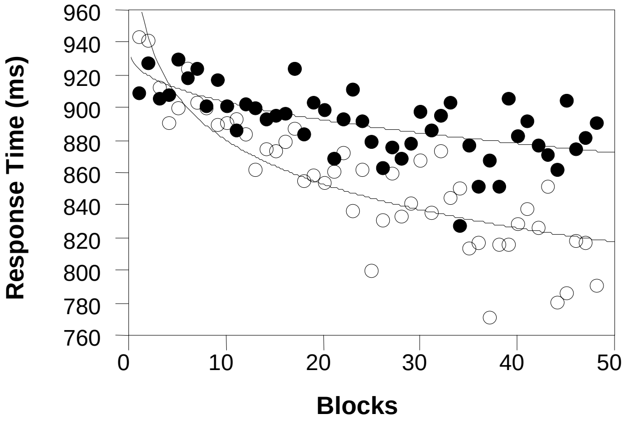


Figure 5-6. Response times as a function of presentation block for first presentations of unique stimuli for the within-visual-field condition (open circles) and for the across-visual-field condition (closed circles).

5.2.3 Discussion

Weissman & Compton (2003) found, in two separate studies that over time, the performance advantage afforded by processing a letter-matching task across two hemispheres instead of using single-hemisphere processing, disappeared. Their data suggested that with practice, single-hemisphere performance improved, whereas performance of two hemispheres working together remained the same.

The present data suggest that this is not entirely the case. Like Weissman & Compton (Weissman & Compton, 2003) I found a very strong practice effect, with the BDA present in the initial blocks of trials rapidly decreasing over time and becoming a within-hemisphere advantage. This decrease was due to a substantial, almost linear, improvement in performance across four sessions when matching letters were presented to a single hemisphere. After four sessions and 2304 trials, within-hemisphere performance was 83 ms faster, and more than 7% more accurate. Across-hemisphere performance also improved substantially with practice, becoming 32 ms faster, and 6% more accurate over the four sessions (see Figure 5-1).

Weissman and Compton hypothesised that a shift in strategy, from algorithmic processing to memory retrieval, as proposed by Logan (1988), could best explain the relative improvement in performance of within-hemisphere processing compared to across-hemisphere processing. The present results do not support this hypothesis. According to Logan, each presentation of a unique stimulus would create a new memory trace, and multiple presentations of the same stimulus produce multiple memory traces. As a consequence, the response to a stimulus that has previously been presented becomes faster due to “competition” between the different memory traces in a race model. Based on Logan’s model, two predictions can be made. Response times to multiple presentations of the same stimulus should decrease following a power function, although an exponential function has since been shown to provide a better fit for individual data (Heathcote, Brown, & Mewhort, 2000). As well average response speeds to stimuli that have been presented only once should not improve between different blocks or between different sessions. This latter prediction has been shown not to be supported by experimental data (Kirsner & Speelman, 1996) and to account for this difference, Kirsner & Speelman proposed a new model suggesting that a combination of both general practice and repetition priming, each following a power function, influences response time.

In order to determine whether the present data were consistent with a practice effect, a repetition priming effect, or a combination of the two, response times to the first, second, and third presentations of unique stimuli in the four experimental sessions were compared. Response times to first presentations (in any session after the first) became progressively faster over the four sessions, which clearly shows a general practice effect. To better define this effect, response times for first presentations of unique stimuli were plotted as a function of the experimental blocks in which they took place. Curves following linear, power or exponential functions were then fitted to determine which function best predicted the data. The power function provided the best fit, explaining over 78% of the variance in response time as a function of practice. To determine whether a repetition priming effect was taking place concurrently, response times to first, second, and third presentations were compared for each session. The comparison was limited to three presentations because few items were repeated more than three times in the first session. Furthermore, both Logan's and Kirsner and Speelman's models would predict the largest improvement in response time between the first and second repetitions. No improvement in response time was detected as a function of the number of repetitions except, possibly, for the first session; but this slight improvement could also be due, at least in part, to differences in general practice between first presentations, which by their nature occurred on average earlier in the first session, and repetitions, which occurred later. Thus, to dissociate the effect of general practice and repetition priming, response times to first presentations taking place in the sixth and twelfth blocks of the first session and the second and third presentations taking place in the same blocks were compared. Blocks 6 and 12 were chosen because all identical stimuli shown previously had been presented within that session, substantial training had taken place (240 trials per participant at the beginning of block 6, and 528 trials at the beginning of block 12), and the effect of practice was approximately equivalent for first, second, and third presentations occurring in these blocks. No improvement following either a power or exponential function, with a sharp decrease in response time between the first repetitions, was present in either block. Logan's model cannot account for the results of the present study since a general practice effect not predicted by this model was found. As well, I failed to find the predicted repetition priming effect.

It is not surprising that no effect of repetition priming was found. The task used in the present study used a combination of letters that could produce a large number of different combinations such that novel stimuli would occur almost as often as repetitions (approximately one in three). Furthermore, stimuli were presented tachistoscopically and consequently were unlikely to leave memory traces of a quality similar to those left by stimuli in the lexical decision tasks used by Logan (1988) and by Kirsner and Speelman (1996), where stimuli stayed on screen until a response was made. Furthermore, the varying duration between repetitions of unique stimuli, sometimes quite long, might have decreased the magnitude of any repetition priming effect since longer intervals between repetitions produce weaker repetition priming effects (Kirsner & Speelman, 1996). Finally, the nature of the task, determining whether two letters were matching, did not rely on identifying all letters but could be terminated once two matching letters were found. Consequently, partial or degraded memory traces might have been generated, and such traces would be unlikely to produce the same priming advantage. If this were the case, it would be predicted that response times to mismatch trials might show a significant priming effect, since all stimuli needed to be perceived. Unfortunately, such an analysis could not be performed in the present study because a go/no go response was used and therefore no response times were available for mismatch trials. Future studies should specifically test this possibility.

It is interesting to note that the practice effect found in the response-time measure was also present in the accuracy measure and was approximately equivalent, with a correlation between the two measures as a function of time (blocks) of -.758, which suggests that as response times become faster with practice following a power function, as predicted by Kirsner and Speelman (1996), responses become more accurate following the same function.

The neurophysiological origins of the general-practice effect are hypothetical at this stage but it seems likely that some kind of gradual neuronal tuning, probably across multiple processes and cerebral areas could underlie the learning effects described in this study. Such neuronal tuning or cortical plasticity has been demonstrated in monkeys in the tactile (Jenkins, Merzenich, Ochs, Allard, & Guíc-Robles, 1990) and visual modalities (Yang & Maunsell, 2004) and has been shown to be related to behavioural performance in the auditory modality (Recanzone, Schreiner, & Merzenich, 1993). In monkeys, these effects have been demonstrated after relatively long training periods ranging from days to months. In a recent study, however, cortical plasticity has also been shown in human musicians who listened to musical stimuli for sessions lasting only three hours (Pantev, Engelien, Candia, & Elbert, 2001). Such plasticity could be comparable to the type of learning effect observed in this study.

It is also possible that, with practice, the sub-processes of the letter-matching task are dealt with more efficiently due to better timesharing between them. Oberauer and Kliegl (2003) and others (Meyer et al., 1995) have shown that with extended practice, the response-time costs of performing two tasks concurrently can disappear completely. In the letter-matching task, it is therefore possible that different sub-processes are synchronised more efficiently with practice and thus, central executive bottlenecks can be avoided. Another possibility is that central bottlenecks due to the competition of simultaneous processes for limited executive resources cannot be avoided (Ruthruff, Pashler, & Klaassen, 2001) but that, with practice, those bottleneck stages can be shorten. Alternatively, some of the neuroanatomical areas used for the unpractised task may be different from those used after training (Petersen, van Mier, Fiez, & Raichle, 1998). Peterson et al. use the analogy of “scaffolding-storage”. During the initial performance of a task, a set of regions might be used to cope with the novel task demands, whereas, with practice, associations are made and processes are more efficiently stored (in neurophysiologically different areas) and can be used as programs rather than single instructions.

Unfortunately, the present findings do not allow us to distinguish between these different hypotheses. It is important to assess, however, whether these hypotheses would predict decreased task complexity or decreased task difficulty with practice. Banich and colleagues (e.g., Banich & Belger, 1990; Banich & Karol, 1992; Belger & Banich, 1992; Passarotti et al., 2002; Weissman & Banich, 2000) have argued that the increased complexity of a task, and not its difficulty, leads to improved performance in the across-hemisphere compared to the within-hemisphere condition; thus it would be expected that a relative improvement in within-hemisphere compared to across-hemisphere performance would be associated with a decrease in task difficulty. The present data cannot categorically answer this question. It would seem that explanations based on neural tuning, better timesharing, and decreased bottlenecks are more consistent with a decrease in task difficulty since the number of steps required to perform the tasks remain the same but efficiency is improved. In contrast, an explanation relying on the recruitment of different cortical areas could be consistent with a decrease in either task complexity or task difficulty depending on whether processes performed in the newly recruited areas with practice are simply more efficient or constitute of a smaller number of processing steps.

Another aim of the present analysis was to contrast within- and across-hemisphere performance, which did not differ for accuracy: response times, however, differed between the two conditions. Response times were faster and improved more quickly in the within- compared to the across-hemisphere condition. In order to determine whether within- and across-hemisphere performance showed the same type of practice effect, response times for the two conditions were plotted as a function of presentation block and different curves were fitted. For the within-hemisphere condition, an exponential function provided the best fit, although the r^2 difference between exponential and power or linear functions was small. Nonetheless, the power function seemed to account better for an initial sharp decrease in response time. For the across-hemisphere condition, the best fit was achieved with a power function; r^2 differences between exponential and linear functions were also small. Although both exponential and power curves fitted the data well in the within-hemisphere condition ($r^2 = .764$), this was not the case in the across-hemisphere condition ($r^2 = .399$). This suggests that the practice effect differs not only quantitatively (as shown by the faster learning curve for the within-hemisphere condition), but also qualitatively between the within- and across-hemisphere conditions, although data in both conditions are consistent with the model proposed by Kirsner and Speelman (1996).

The different strengths and qualities of the learning effect when the within- and across-hemisphere conditions are compared, may be due to less efficient neuronal tuning when processing takes place across the two hemispheres, or to the possibility that the cost of information transfer can be decreased in the within-hemisphere condition but not, or only to a lesser extent, in the across-hemisphere condition. Indeed, in a fMRI study, Pollman, Cramon & Zaidel (2003) found that complex tasks such as those used by Weissman and colleagues, and in this study, require the recruitment of cortical areas in both hemispheres, even when the matching stimuli are initially presented to a single hemisphere. It is therefore possible that, with practice, within-hemisphere conditions rely less or not at all on areas located in the contralateral hemisphere, thus decreasing or even eliminating the transfer cost associated with the recruitment of such areas. On the other hand, in the across-hemisphere condition, some of the transfer costs are fixed, since the two hemispheres must exchange information in order to resolve the task.

The implications of these findings in the broader field of hemispheric interaction still need to be assessed. It would appear that hemispheric interaction might be of most benefit to processes that are only conducted a limited number of times, while within-hemisphere performance might most benefit processes that are highly rehearsed. If these findings can be confirmed in future research, they may lead to interesting implications. Thus, in children and young adults, in whom the corpus callosum continues its development at least until the second decade (Giedd et al., 1996; Hagelthorn et al., 2000; M. Keshavan et al., 2002; Rajapakse et al., 1996), initial learning of a task might be slowed due to less efficient hemispheric interaction. Extended practice, however, may lead to significantly better performance due to an improvement in within-hemisphere performance. In older adults, who have been suggested to rely more on hemispheric interaction as a mechanism to use decreasing resources more efficiently (Cabeza et al., 2002; Reuter-Lorenz & Stanczak, 2000), initial learning of a task might be faster than subsequent improvements. Although these hypotheses are speculative at this stage, further investigations should clarify these issues.

In summary, Weissman and Compton (2003) proposed that the relative performance improvement of the within-hemisphere condition compared to the across-hemisphere condition, and the associated decrease in BDA over time might be due to a shift in strategy from algorithmic processing to memory retrieval with practice and that, as a consequence, tasks become easier and favour single-hemisphere processing. This hypothesis is not well supported by the present findings since no repetition priming, as defined by Logan's (1988), or Kirsner and Speelman's (1996) models, has been detected. This suggests that a memory-retrieval strategy is unlikely to be a major factor affecting performance of this task, if at all. But it has to be recognised that the effects of some variables, which were not controlled for (length of duration between repetitions), or known (the effect of tachistoscopic presentation) in the present study, should be specifically investigated in future research, in order to conclusively refute a repetition-priming effect.

In contrast, a strong general practice effect following a power function and consistent with that described by Kirsner and Speelman (1996) has been demonstrated. This practice effect is more prevalent in the within-hemisphere than in the across-hemisphere condition and may be due to progressive neuronal tuning, better timesharing between processes, a shortening of bottleneck stages of processing, or the recruitment of different network areas which are likely to occur more efficiently in the within-hemisphere condition and which, over time, lead to optimal use of within-hemisphere processes and less and less reliance on processes located in the other hemisphere. In the across-hemisphere condition, potential gains in efficiency are smaller because certain costs associated with callosal transfer cannot be decreased.

CHAPTER 6

6.1 Interhemispheric Transfer, Hemispheric Interactions, and Dyslexia

It is widely recognised, as discussed in Chapter 1, that in normal individuals interhemispheric transfer is affected by callosal properties. Since it is also well known that interhemispheric transfer and hemispheric interactions are abnormal in certain clinical populations (e.g., in those affected by schizophrenia, Alzheimer's disease, multiple sclerosis, or dyslexia) it would be interesting to determine how these variables are associated in a clinical syndrome. The aim of this chapter is, therefore, to study how the relationship between interhemispheric transfer and hemispheric interaction is affected in dyslexia.

Although dyslexia is not a homogeneous syndrome, individuals with dyslexia have been shown to vary significantly from non-dyslexic individuals on measures of callosal size and shape (Robichon & Habib, 1998; von Plessen et al., 2002), interhemispheric transfer (Davidson, Leslie, & Saron, 1990; Fabbro et al., 2001), anatomical and functional lateralisation (Robichon et al., 2000), and attention (Mather, 2001), as well as on measures assessing the efficiency of hemispheric interactions (Estil & Whiting, 2002; Moore, Brown, Markee, Theberge, & Zvi, 1995). This makes this group particularly suited to exploring the relationship between interhemispheric transfer and hemispheric interactions.

Individuals with dyslexia, particularly men, tend to have a larger corpus callosum particularly in the isthmus region (Robichon & Habib, 1998; Rumsey et al., 1996), although a larger genu and splenium have also been reported (Duara et al., 1991; Hynd, Hall, Novey, & Eliopulos, 1995). The shape of their CC also tends to be more curvilinear and thicker compared to that of controls (von Plessen et al., 2002). These differences in callosal size have been interpreted as a possible consequence of decreased neuronal pruning during early development of the CC (Robichon & Habib, 1998), which would be consistent with abnormalities in anatomical lateralisation observed in this population.

Research in anatomical lateralisation in individuals with dyslexia has usually shown that dyslexic brains were either less lateralised or symmetrical, or, in a few studies, that the pattern of hemispheric asymmetry was reversed (see Habib, 2000; Hynd, 1995 for a review). This was particularly the case for the planum temporale, which includes a number of important language regions, and for posterior cortical regions. Since more symmetrical brains have been shown to be linked to greater callosal size and connectivity, an association of decreased anatomical asymmetry and greater callosal size, particularly in the posterior midbody, which connects auditory and associative cortices required for language processing, is unsurprising.

The functional consequences of these differences are not completely clear. However, functional lateralisation differences have been found in individuals with dyslexia (Boles & Turan, 2003; Heim, Kissler, Elbert, & Rockstroh, 2004; Walker, Spires, & Rastatter, 2001) and functional lateralisation of a lexical task has been shown to be associated with performance on language tasks (Weems & Zaidel, 2004). Furthermore, callosal differences and decreased typical lateralisation in individuals with dyslexia have been shown to be associated with impaired phonological and reading abilities (Hynd et al., 1995; Robichon & Habib, 1998). This suggests an interaction between anatomical and functional lateralisation, callosal structure, and dyslexia.

Because of the association between dyslexia and changed callosal morphology, the speed and efficiency of interhemispheric transfer has been investigated in people with dyslexia. The assumption was that abnormal callosal structure would lead to abnormally slow or abnormally fast transfer of information through the CC, which, in turn, might disrupt interhemispheric processing. Davidson, Leslie, and Saron (1990) showed, using the Poffenberger paradigm, that interhemispheric transfer time was significantly faster in a dyslexic group compared to controls and that faster IHTT was associated with poorer reading and language functions. Other tasks involving transfer of tactile information (Fabbro, Libera, & Tavano, 2002), and synchronisation of left and right hand movements (Moore et al., 1995) also demonstrated interhemispheric transfer deficits. It would seem that a larger CC in an individual with dyslexia is associated with a shorter, maybe too short, IHT which appears to disrupts the sharing and coordination of information between the hemispheres. This interpretation is also consistent with an extensive analysis of behavioural data in split-brain patients, supporting the view that dyslexia might be, at least in part, due to a kind of disconnection syndrome between the cerebral hemispheres resembling certain symptoms observed in split-brain patients (Mather, 2001). It is also supported by computer modelling showing that impaired interhemispheric transfer would produce phonological deficits consistent with those found in dyslexia (Monagahan & Shillcock, submitted).

Attention also appears to be impaired in dyslexia. Wijers, Been and Romkes (2005) showed that, unlike controls who showed a right hemisphere specialisation for the control of visual spatial attention in a cued target detection task (using peripheral cues), individuals with dyslexia did not show a hemispheric bias This was thought to indicate an abnormal pattern of hemispheric lateralisation in this group. In contrast, a second (peripherally) cued target detection study (Facoetti, Turatto, Lorusso, & Mascetti, 2001) found similar orienting of attention in controls and individuals with dyslexia for valid cues; but no hemispheric asymmetry in controls for invalid cues while individuals with dyslexia responded significantly slower to invalid cues in the left-visual field than in the right-visual field. This asymmetric control of attention was interpreted by Facoetti and colleagues as showing a possible deficit in right-hemisphere attention allocation, an interhemispheric dysfunction, or an impairment in cerebellar function. In a third study, using event-related potentials in 9- to 12-year-old children, Jonkman, Licht, Bakker, and Van den Brock-Sandmann (1992) found that non-dyslexic children were more reactive to invalid than to valid cues (using central presentation), whereas children with phonological dyslexia only reacted to valid cues. Although the results of these three studies are difficult to reconcile and may reflect differences in methodology or participants' selection, they do show consistent differences in allocation of attention between controls and individuals with dyslexia.

Attentional abilities have been shown to be associated with interhemispheric transfer (with faster IHTT found in adolescents with attention deficit hyperactivity disorder compared to controls (Brown & Vickers, 2004); and the efficiency of callosal transfer being associated with sustained attention in normal adults (Rueckert et al., 1999)) and with hemispheric interaction (Banich, 1998). It is possible that interhemispheric transfer deficits found in dyslexia at least partly underlie both the reading deficits and the attentional deficits present in these individuals, and may be associated with a breakdown in interhemispheric interaction.

6.2 Experiment 5

The aim of this experiment was to investigate the relationship between interhemispheric transfer, hemispheric interactions, attention, and dyslexia. As in Experiments 3 and 4, the Poffenberger paradigm was used since it has been shown to discriminate between controls and individuals with dyslexia in a previous study (Davidson et al., 1990). The same letter-matching task was also used, since Ellis (1981) showed that dyslexic children were slower to respond to letter-matches involving a name match (e.g., Aa) but not a shape match (e.g., AA).

Since dyslexia is a heterogeneous syndrome with subgroups characterised by deficits which may have a different ethiology, a cohort of adults with phonological dyslexia was chosen because phonological deficits are the most prevalent and longer lasting. As well, differences in cerebral asymmetry, callosal differences, and attentional differences have been specifically associated with phonological deficits (e.g., Boles & Turan, 2003; Habib, 2000; Hynd, 1995; Wijers et al., 2005).

The predictions were that the dyslexic group would show a faster interhemispheric transfer time and lower attentional scores. Findings in previous experiments would suggest that faster IHT should be associated with more efficient hemispheric interactions. However, since, in dyslexia, an abnormally fast IHTT is thought to be associated with disruption of interhemispheric processes it was predicted that individuals with dyslexia would present with less efficient hemispheric interactions. Of particular interest were the relationships between measures of reading abilities and attention, interhemispheric transfer, and hemispheric interactions.

6.2.1 Method

6.2.1.1 Participants

Eight participants with dyslexia (1 female, 7 males), aged between 20 and 55 years old with normal or corrected-to-normal vision, and eight sex- and age-matched controls with no history of reading difficulties completed this study. All participants were recruited on the Australian National University campus and received 50 dollars as compensation for their time and travel. Handedness was assessed with a questionnaire adapted from the Edinburgh Handedness Inventory (Oldfield, 1971, see Appendix B). Participants who reported a history of neurological or motor disease were excluded from the study. The study received approval from the Human Research Ethics Committee.

6.2.1.2 Neuropsychological Assessment

The experimental group met the criteria of dyslexia as determined by the Dyslexic Adult Screening Test (DAST: Fawcett & Nicolson, 1998). The following battery of tests was also administered to all participants. Untimed single word reading and spelling abilities were evaluated using the Wide Range Achievement Test (WRAT: Jastak & Wilkinson, 1984). Intellectual functioning was assessed using the Wechsler Abbreviated Scale of Intelligence (WASI®), while the Test of Everyday Attention (TEA: Robertson, Ward, Ridgeway, & Nimmo-Smith, 1994) was used to provide scores of overt attention in the following 4 categories: visual selective attention/speed, attentional switching, sustained attention and auditory-verbal selective attention.

Visual selective attention was assessed using the Map Search task which requires the participants to search a roadmap to find as many instances as possible of a pre-determined target (e.g., petrol station icon) in two minutes. Auditory selective attention was assessed using the Elevator Counting with Distraction task, in which the participants must listen for and count a particular tone that they are asked to think of as a floor travelled in an elevator, while ignoring other tones (Distraction). Visual selective attention was assessed using the Visual Elevator task with or without reversal, in which the participants must keep track of the floor level they are on while travelling in an elevator. A measure of divided attention, across the visual and auditory modalities, was obtained using the Telephone Search while Counting task. This task requires the participants to systematically search two columns of phone entries from top-to-bottom, marking those that match a pre-determined target while counting tones. Finally, sustained attention was assessed using the Lottery task. In this task participants are given a number consisting of three digits, and are required to listen as lottery ticket numbers, of two letters followed by three digits, are read out. When the digits match they must write down the letters of the lottery ticket.

6.2.1.3 Stimuli and Procedure

The stimuli and procedure used in this experiment were identical to those used in Experiment 3.

6.2.2 Results

6.2.2.1 Participants' Variables

Subject group characteristics are presented in Table 6-1. The dyslexic group did not differ from the control group in age or handedness.

Table 6-1. Age and handedness measures for the control and dyslexic groups. Standard deviations are shown in brackets.

Experimental group	Age (years)	Handedness
Control	30.62 (8.41)	.76 (.08)
Dyslexic	31.88 (12.03)	.72 (.40)

6.2.2.2 Neuropsychological Measures

Measures of cognitive performance, reading ability, and sustained and focused attention for the control and dyslexic groups are presented in Table 6-2. The two groups did not differ in IQ (VIQ: verbal IQ; PIQ: performance IQ). However, they differed on all measures of reading ability and on five of the attention tests (ecd, ve, vet, ecr, l), with individuals with dyslexia performing worse on all these tests compared to the control group.

6.2.2.3 Inter-Hemispheric Transfer Time (IHTT) using the Poffenberger Paradigm

Reaction times (RT) to the presentation of a dot in the left or right visual field (VF) were measured for the two hands, and an estimate of IHTT or crossed-uncrossed difference (CUD) was computed by subtracting RTs for the direct route (VF ipsilateral to responding hand) from RTs for the indirect route (VF contralateral to responding hand). Reaction times smaller than 100ms, considered to be anticipatory responses, and larger than 1000 ms, considered to be due to attentional lapses, were excluded. Average RT for each visual field and hand condition, and the CUDs of the control and dyslexic groups are presented in Table 6-3. Average accuracy in this task was 98.63% (SD 2.33) for the control group and 98.00% (SD 1.85) for the dyslexic group and was not significantly different between the two groups, t(1,14) = .595, ns.

Table 6-2. Measures of cognitive performance (Visual, Performance, and Total IQ), reading ability (Reading, Spelling, and Average Reading Quotient), and focused (Map Search, Ms1 & Ms2; Elevator Counting with Distraction, Ecd; Visual Elevator, Ve; Visual Elevator timed, Vet; Telephone Search, Ts; Telephone Search with Counting, Tsc) and sustained attention (Lottery, L) for the control and dyslexic groups. Standard deviations are presented in brackets.

Assessment category	Measure	Experimental group	
		Control	Dyslexic
Cognitive performance			
	VIQ	120.13 (10.70)	113.88 (6.47)
	PIQ	121.50 (10.09)	127.00 (6.00)
	Total IQ	123.00 (11.06)	123.25 (6.50)
Reading ability			
	ARQ **	0.01 (.03)	1.24 (.45)
	Reading ***	109.50 (5.07)	89.25 (10.82)
	Spelling ***	114 (5.66)	87.63 (11.11)
Attention			
	Ms1	13.00 (1.41)	11.25 (4.03)
	Ms2	10.88 (2.10)	10.13 (3.56)
	Ecd *	12.25 (1.49)	9.00 (3.59)
	Ve **	12.25 (1.98)	9.63 (1.19)
	Vet *	16.00 (1.51)	11.00 (5.01)
	Ecr *	13.75 (1.98)	9.38 (3.62)
	Ts	14.38 (3.11)	11.50 (3.74)
	Tsc	12.25 (2.61)	10.13 (3.72)
	L *	12.63 (.52)	9.50 (3.02)

*significant at the 0.05 level (2-tailed); ** at the 0.01 level; *** at the .001 level

The presence of a significant difference in CUD between the control and dyslexic groups was tested by using a meta-analytic technique (Hedges & Olkin, 1985, see Appendix C). This was done because although a large number of trials had been used in the present design, average RTs across trials only would be used for each participant in a typical ANOVA, thus ignoring important individual variability. Taking individual variability into account is particularly important in the present study because two groups, in which the pattern of response variability is expected to vary, are being compared and because the number of participants is relatively small. Therefore a more sensitive measure was required. Using this technique a significant difference in CUD was found between the two groups, $\chi(15) = 8.608$, $p < .01$, indicating that the dyslexic group had, on average, a faster CUD than the control group[4].

Table 6-3. Response time to left (LVF) and right (RVF) visual field presentation with left- (LH) or right-hand (RH) response, and crossed-uncrossed differences (CUD) in the Poffenberger task for the control and dyslexic groups. Standard deviations are presented in brackets.

	LVF		RVF		CUD
	LH	RH	LH	RH	
Control	261.74 ms (17.98)	264.39 ms (19.61)	264.51 ms (21.52)	261.91 ms (24.06)	+ 2.62 ms (5.00)
Dyslexic	287.66 ms (22.72)	288.19 ms (19.01)	291.52 ms (18.62)	291.72 ms (17.22)	+ 0.16 ms (3.61)

6.2.2.4 Hemispheric Interaction in a Letter-Matching Task

RT and accuracy for matching letter pairs were measured for four visual field/hemisphere conditions: within left visual field (LVF), within right visual field (RVF), and across visual fields (up or down). The differences between averaged within visual field and across visual field conditions (BDA) were calculated as an index of hemispheric interaction. RT smaller than 250 ms and larger than 1500 ms (2.8 % of all responses) were excluded. These measures are presented in Table 6-4 for the control and dyslexic groups.

Table 6-4. RT and accuracy measures for all visual field conditions of the letter-matching task for the control and dyslexic groups. Standard deviations are presented in brackets.

	LVF	RVF	Avg. Within	UP	DOWN	Avg. Across	BDA
RT (ms)							
Control	812.68 (96.67)	863.23 (92.44)	837.96 (82.56)	889.18 (98.47)	841.74 (90.65)	865.46 (78.80)	-.59 (4.38)
Dyslexic	898.45 (69.20)	920.38 (127.4)	909.41 (84.74)	901.84 (74.07)	965.26 (96.65	933.55 (71.96)	1.74 (4.76)
Accuracy (%)							
Control	93.32 (3.57)	90.23 (7.24)	91.77 (5.27)	91.32 (2.98)	93.40 (4.02)	92.36 (2.97)	-27.50 (66.40)
Dyslexic	80.60 (14.44)	85.11 (9.81)	82.86 (11.45)	82.20 (16.30)	80.03 (14.46)	81.12 (15.05)	-24.14 (26.87)

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[4] A typical paired sample t-test would have produced a near significant result, $F(1,7) = 2.254$, $p = .059$.

Response time measure. A 2 visual field (within/across) x 2 group (control/dyslexic) paired samples ANOVA was conducted to determine whether the two groups differed in their efficiency of hemispheric interaction. A near significant main effect of group was detected, F(1,7) = 4.344, p = .076, suggesting that the control group responded faster than the dyslexic group.

Accuracy measure. A 2 visual field (within/across) x 2 group (control/dyslexic) paired samples ANOVA was also conducted to determine whether the two groups differed in their efficiency of hemispheric interaction for accuracy. A significant main effect of group was detected, F(1,7) = 6.147, p < .05, indicating that the control group responded more accurately than the dyslexic group.

6.2.2.5 Functional Lateralisation

A lateralisation index was computed for the RT and accuracy measure of the letter-matching task using the formula (LVF-RVF)/(LVF+RVF) for the control and the dyslexic group. The lateralisation indexes did not differ between the two groups for the RT measure, t(1,7) = 1.600, ns, or for the accuracy measure, t(1,7) = 1.131, ns.

6.2.2.6 Relationships between IHTT, Hemispheric Interactions, Cognitive Abilities, Reading and Language Proficiency, Attention, and Functional Lateralisation

In order to investigate the relationship between IHTT and hemispheric interactions, and cognitive abilities, reading and language proficiency, and attention, correlations between these different variables were computed. They are reported in Table 6-5. A number of results are particularly relevant to this study and need to be noted. IHTT was found to be significantly correlated with all reading measures and three (MS1, TSC, L) of the attentional measures. The accuracy BDA was significantly correlated with the accuracy measure of functional lateralisation and two measures of attention (ECR, TSC), and in addition was mildly correlated with three other measures of attention (ECD, VE, VET,TS) and all measures of reading ability. The non-verbal IQ was not correlated with any of the other measures. All reading ability and attention measures were highly intercorrelated.

6.2.3 Discussion

The aim of this experiment was to replicate earlier findings (Davidson et al., 1990) showing a faster IHTT in a dyslexic group compared to a control group and to investigate whether this difference in callosal transfer was also associated with attentional and hemispheric interaction deficits and determining whether a correlation was present between reading and language skills and IHTT, attention and hemispheric interactions.

Each participant with dyslexia was paired with a sex and aged-matched control to exclude these variables as possible confounds. Because dyslexia is associated with significant co-morbidity it was also important to ensure that the dyslexic and control groups did not differ on IQ and handedness. Both groups scored similarly on these variables confirming a good matching process.

Table 6-5. Correlations between IHTT, hemispheric interactions, cognitive abilities, reading and language proficiency, attention, and functional lateralisation measures. Significant correlations are shown in grey.

	IHTT	RT BDA	Acc. BDA	Cognitive abilities			Reading & Language			Attentional Measures									Lateralisation	
				VIQ	PIQ	IQ	ARQ	Read	Spell.	MS!	MS2	ECD	VE	VET	ECR	TS	TSC	L	Acc.	RT
IHTT	1	.089	-.227	.047	-.012	.023	-.651**	.678**	.644**	.655**	.424	.208	.112	.478	.283	.149	.521*	.644**	.133	.268
RT BDA	.089	1	-.609*	-.209	.167	-.052	-.015	-.118	.084	-.106	-.140	-.301	.190	-.077	-.152	.083	.311	-.144	.267	-.141
Acc. BDA	-.227	-.609*	1	-.187	-.225	-.251	.467	0.379	-.481	-.126	-.077	-.303	-.408	-.472	-.530*	-.442	-.628**	-.101	-.743**	.191
VIQ	.047	-.209	-.187	1	.421	.855**	-.410	.537*	.421	.062	.102	.507*	.358	.371	.469	.419	.138	.130	.373	.115
PIQ	-.012	.167	-.225	.421	1	.784**	.222	-.057	-.112	.109	.104	-.171	-.285	-.128	-.066	.196	.079	-.226	.036	.136
IQ	.023	-.052	-.251	.855**	.784**	1	-.113	.309	.179	.072	.107	.310	.015	.226	.301	.391	.138	-.009	.290	.152
ARQ	-.651**	-.015	.467	-.410	.222	-.113	1	-.935**	-.929**	-.415	-.316	-.585*	-.573*	-.692**	-.668*	-.356	-.526*	-.661**	-.523*	.038
Reading	.678**	-.118	-.379	.537*	-.057	.309	-.935**	1	.936**	.435	.314	.636**	.469	.671**	.661**	.305	.464	.649**	.421	.205
Spelling	.644**	.084	-.481	.421	-.112	.179	-.929**	.936**	1	.319	.101	.531*	.596*	.555*	.611*	.360	.423	.532*	.508*	.108
MS1	.655**	-.106	-.126	.062	.109	.072	-.415	.435	.319	1	.728**	.381	.117	.505*	.265	.373	.489	.792**	-.017	.198
MS2	.424	-.140	-.077	.102	.104	.107	-.316	.314	.101	.728**	1	.313	-.140	.556*	.171	.106	.522*	.614*	.015	-.028
ECD	.208	-.301	-.303	.507*	-.171	.310	-.585*	.636**	.531*	.381	.313	1	.507*	.818**	.807**	.604*	.388	.629*	.546*	-.077
VE	.112	.190	-.408	.358	-.285	.015	-.573*	.469	.596*	.117	-.140	.507*	1	.338	.528*	.466	.138	.291	.406	.064
VET	.478	-.077	-.472	.371	-.128	.226	-.692**	.671**	.555*	.505*	.556*	.818**	.338	1	.855**	.591*	.618*	.660**	.681**	-.155
ECR	.283	-.152	-.530*	.469	-.066	.301	-.668**	.661**	.611*	.265	.171	.807**	.528*	.855**	1	.682**	.366	.428	.762**	-.093
TS	.149	.083	-.442	.419	.196	.391	-.356	.305	.360	.373	.106	.604	.466	.591*	.682**	1	.173	.326	.705**	-.228
TSC	.521*	.311	-.628**	.138	.079	.138	-.526*	.464	.423	.489	.522*	.388	.138	.618*	.366	.173	1	.466	.460	-.267
L	.644**	-.144	-.101	.130	-.226	-.009	-.661**	.649**	.532*	.792**	.614*	.629**	.291	.660**	.428	.326	.466	1	.079	.021
Acc. Lat.	0.133	0.267	-.743**	0.373	0.036	0.290	-0.523*	.421	.508*	-.017	.015	.546*	.406	.681**	.762**	.705**	.460	.079	1	-.441
RT Lat.	0.268	-0.141	0.191	0.115	0.136	0.152	0.038	.205	.108	.198	-.028	-.077	.064	-.155	-.093	-.228	-.267	.021	-.441	1

* Correlation is significant at the 0.05 level ** Correlation is significant at the 0.01 level (2-tailed).

As expected, the dyslexic group had a significantly faster IHTT in the Poffenberger task than the control group. This replicates the only findings I am aware of (Davidson et al., 1990), of a faster interhemispheric transfer time in individuals with dyslexia but the dyslexic group was significantly slower (~ 70 ms) than controls in the letter-matching task. However, no difference in the measure of hemispheric interaction (BDA) was detected between the dyslexic and control groups. On the surface, this appears surprising since other studies have shown hemispheric interaction deficits in dyslexia. An alternative interpretation is that, because both the within- and across-visual field conditions of the letter-matching task require some degree of hemispheric interaction, as demonstrated by Pollman, Zaidel, and Cramon (2003a), the possible disruption in hemispheric interaction caused by an excessively fast IHTT might have affected the two conditions in the dyslexic group equally and thus produced overall slower RTs. Beaton and colleagues (in press, p. 8) made a similar point in relation to findings of two studies (Beaton et al., in press; Moore, Brown, Markee, Theberge, & Zvi, 1996) showing an overall deficit in individuals with dyslexia in a tactile localisation task where across- and within-hemisphere conditions were compared but also did not differ.

The resemblance in the pattern of results of these studies and the present findings is particularly interesting because both also reported a significant correlation between performance on these tasks and a measure of phonological ability (as found in this experiment). However, Beaton et al. concluded that an interpretation of these results in terms of the cognitive processes involved, rather than an interhemispheric transfer deficit would be more parsimonious. Given the consistent reports of IHTT and hemispheric interaction deficits in dyslexia, I do not think that an hemispheric interaction deficit explanation should be overlooked. Nonetheless, the present data cannot confirm this hypothesis and further research will be required to answer this question.

Following expectations, the dyslexic group also performed less well than the control group on measures of both focused and sustained attention. This is consistent with other findings indicating an association between attentional deficits and dyslexia. Moreover, of particular relevance is the large proportion of significant correlations found between the attentional measures (both focused and sustained) and the reading measures. This suggests that for both individuals with dyslexia and controls, attentional abilities are related to language skills. It is also interesting to note that IHTT, which is consistently correlated with reading measures, is not strongly correlated with most attentional measures. This might indicate that the effect of IHTT and attention do not, or only partially, overlap in their possible influence on reading abilities.

There is a large body of literature describing functional lateralisation differences in dyslexia. In this experiment, the functional lateralisation of the letter-matching task appears to be associated with reading abilities and many of the attentional measures. However, this is true only for the accuracy measure and not for RT. This reinforces the notion that accuracy and RT in the letter-matching task might have different underlying neural substrates, as already discussed with respect to the accuracy and latency BDA in Experiments 3 and 4. In the present experiment, while the accuracy BDA was somewhat correlated with a number of the attentional measures, this was not the case for the RT BDA. This further strengthens the previous point.

The strength of correlations between the accuracy BDA and other measures was lower than might have been predicted since an excessively fast IHTT, based on Experiments 3 and 4, would have predicted a decreased efficiency of hemispheric interactions. Nevertheless, the accuracy BDA was correlated with most of the language and attentional measures at levels close or higher than .4, which might suggest that the power afforded by the small sample size was not large enough to demonstrate this relationship.

To some extent, it is surprising that the BDA was not more strongly correlated with IHTT since Experiments 3 and 4 have demonstrated correlations higher than .4 for these variables. On the other hand if an abnormally fast IHTT was associated with a break down of hemispheric interactions, this pattern of results would be expected.

As in any correlational study, it is important to remember that correlation does not imply causation. Nevertheless, it is difficult to ignore the large number of cross-correlations between measures of reading ability, attention, and IHTT found in the present study.

Another surprising finding is that two tests (reading and spelling) assessing different aspects of reading abilities were inversely correlated when controls and individuals with dyslexia were considered. This might refect some compensation mechanism whereby individuals with greater reading difficulties compensate by using single letter rather than whole word processing, and they therefore would be more practiced and efficient in this task.

In summary, this study has shown that IHTT is faster in individuals with dyslexia compared to controls, and suggests that this increase in speed of transfer is associated with increased reading difficulties and attentional deficits. A deficit in hemispheric interaction in dyslexia was not clearly demonstrated; however, trends suggest that decreased interaction efficiency (evidenced in the accuracy measure) is associated with increasing signs of dyslexia (ARQ, spelling).

CHAPTER 7

7.1 Hemispheric Activation and Interaction

Many studies have shown that the degree of activation in each hemisphere changes over time and that this is affected by multiple variables such as the mental tasks being performed (Stephan et al., 2003), the amount of practice (Jantzen, Steinberg, & Kelso, 2002; Kerr, Gusnard, Snyder, & Raichle, 2004; Qin et al., 2003), emotional state (Northoff et al., 2004), and the sex (Jordan, Wüstenberg, Heinze, Peters, & Jäncke, 2002), and handedness (Vogel et al., 2003) of the person being tested. Little is known of how different patterns of hemispheric activation (HA) affect performance of subsequent mental processes but a few studies have been able to demonstrate a relationship between performance of a cognitive task and the relative degree of activation of the two hemispheres prior to this task. For instance, Swift (1991) demonstrated that individuals who had a more active left or right hemisphere produced different patterns of behavioural responses when subsequently performing a face-recognition task. Another study showed that measures of arousal asymmetry were significantly related to individual perceptual asymmetry during a lexical decision task (Green, Morris, Epstein, West, & Engler, 1992). Participants who demonstrated greater left hemisphere activation at rest showed a greater left hemisphere perceptual asymmetry during a lexical decision task. This suggests that greater activation in one hemisphere is associated with increased performance in this hemisphere, at least when the task is lateralised to a specific hemisphere.

It is not completely clear to what degree lateralised changes in hemispheric performance, due to different levels of HA, can affect hemispheric interactions. In tasks where single hemispheres could potentially process all relevant stimuli independently, it has been shown that some degree of hemispheric interaction takes place, sometimes with detrimental consequences, (e.g., Stroop studies, Weekes & Zaidel, 1996). On the other hand, it is also clear that hemispheric interaction is a mechanism adopted to make a more efficient use of limited processing resources (Banich, 1998; Belger & Banich, 1992; Liederman & Meehan, 1986; Weissman & Banich, 1999, 2000). This has led to surprising observations showing that under certain circumstances, performance of two hemispheres which are forced to interact, by presenting stimuli relevant to the task divided across visual fields, is better than that of a single hemisphere perceiving all relevant stimuli, despite the cost of callosal transfer in the former condition.

A split-visual field study (Belger & Banich, 1998) showed that performance of lateralised tasks was improved in the between hemifield condition compared to the within visual field condition when the more active hemisphere was the hemisphere not specialised for this task. This can be explained in two ways. Firstly, when across hemisphere performance is considered, greater activation of the non-specialised hemisphere enables a more equal division of task processing between the hemispheres and leads to more efficient sharing of cognitive resources and better performance. In the within visual field condition, however, activation of the non-specialised hemisphere may give this hemisphere control over the processing of the task even if the other hemisphere could process it more efficiently. Such effects of meta-control have been shown in both split-brain (Levy & Trevarthen, 1976) and intact individuals (Hellige et al., 1988; Urgesi et al., 2005). Thus, in a task more lateralised to the left hemisphere and in within-visual field conditions, greater left hemisphere activation would lead to improved right and left visual field performance whereas greater right hemisphere activation would decrease performance in both visual fields, because the "wrong" hemisphere takes control over the task. These two types of effect could therefore have an additive influence on hemispheric interaction by decreasing within visual field performance and increasing across visual field performance when the more active hemisphere is not specialised for the task at hand.

While past studies have measured the latent pattern of HA (Morgan, MacDonald, & MacDonald, 1971; Resnick, Lazar, Gur, & Gur, 1994), it is not clear how individuals' HA biases are changed by certain cognitive tasks and how this change affects performance on subsequent tasks.

7.2 Experiment 6

The aim of this experiment was to clarify how changes in HA affect the efficiency of hemispheric processing and hemispheric interaction. Hemispheric interaction was assessed using the letter-matching task used in Experiments 3 and 4, which has been shown not to be lateralised (Eviatar & Zaidel, 1992, see also Chapter 2, 3, and 4). HA levels were modulated by tasks lateralised to the left or right hemispheres and performed *before* the letter task. The left hemisphere task was a rhyming task (Rayman & Zaidel, 1991) and the right hemisphere task was a mental cube folding task (Shepard & Feng, 1972). Since the successful modulation of HA relied on the presence of typical patterns of functional lateralisation, individual indexes of functional lateralisation were computed to control for the differing effects of the manipulation. These indexes reflect whether the activation procedure has been successful in activating the left hemisphere with the rhyming task and the right hemisphere with the cube task, as well as how the activation procedure has interacted with individuals' activation pattern baselines. It was expected that effects of activation would be modulated by the degree of functional lateralisation.

Another variable that needed to be taken into consideration was the strong practice effect found in this type of letter task (Liederman et al., 1985; Weissman & Compton, 2003, see also Chapter 5). Since left and right HA manipulations were performed in different sessions it was likely that differences in performance found between the two conditions might in part be due to this practice effect. Although the order of manipulation was counter-balanced, it cannot be excluded that the practice effect might interact differently for the two activation conditions since it has been shown to influence within and across visual field conditions differently (see Chapter 5). It was difficult to make precise predictions about the effects of HA on within and across hemisphere performance because artificial patterns of HA may have quite different effects compared to the latent patterns of HA reviewed above. However, in the within visual field condition it was expected that, as in a previous study (Green et al., 1992), better performance would be detected in the visual field contralateral to the active hemisphere.

It is possible, however, that the modulation of HA also modulates the allocation of visual attention. In split-brain individuals (Mangun et al., 1994) the left hemisphere allocates attention uniquely to the right visual field, but the right hemisphere allocates attention to both visual fields. In another study, Levy, Wagner, and Luh (1990) found that performance of a verbal task was more accurate in trials presented to both the left and right visual field when they had been preceded by a left visual field/right hemisphere trial. It is therefore possible that activation of the right hemisphere would improve performance in both visual fields while activation of the left hemisphere might produce an attentional bias favouring the right visual field. In this case, poorer performance would be expected in the within left visual field of the left hemisphere activation condition; this would also lower the average performance of the within hemisphere condition compared to the across hemisphere condition. Since a non-lateralised task was used (Eviatar & Zaidel, 1992) an effect of meta-control was not expected. In the across hemisphere condition, an effect of side of activation on across visual field performance would not be expected, unless the side of activation affects the allocation of attention. In this case, it would be expected that left hemisphere activation would impair within visual field performance, and the relative advantage of the across visual field condition over the within visual field condition should be increased in the left hemisphere activation condition.

7.2.1 Method

7.2.1.1 Participants

Twenty right-handed participants (10 males, 10 females) aged 18 to 30 years, were recruited on the campus of the Australian National University. Handedness was assessed with a questionnaire based on the Edinburgh Handedness Inventory (Oldfield, 1971, see Appendix B). Participants were compensated for their time and travel with A$25. The study received approval from the Human Research Ethics Committee.

7.2.1.2 Tasks and Stimuli

Cube-folding task: The mental cube-folding task (Figure 7-1a), adapted from Shepard and Feng (1972), has been shown to predominantly involve the right hemisphere. Stimuli consisted of 80 two-dimensional drawings of the six surfaces of an “unfolded” cube. In each drawing, two of the sides were indicated by arrows. Each drawing was presented once to the left or right visual field for 200 ms. Subjects indicated that the two selected sides would be touching once the cube was “folded” by pressing a button with the index finger; otherwise they pressed the second button with the middle finger. Each block consisted of 32 trials and each right hemisphere activation session consisted of 12 blocks of the cube task for a total of 384 trials. The responding hand was counter-balanced across conditions.

Rhyming task: The rhyming task (Figure 7-1b), adapted from Rayman and Zaidel (1991), was chosen because it has been shown to involve processes more lateralised to the left hemisphere. Stimuli consisted of 80 target/test words pairs, half of which were rhyming words. Target words were 3 to 6 letters long, test words always three letters long. All pairs were orthographically different. The target word was presented centrally for 400ms, followed by an inter-stimulus interval of 600ms, then the test word was presented for 200ms, pseudo-randomly to the left or right visual fields. Subjects indicated that the target word rhymed with the test word by pressing a mouse button with the index finger, or that the two words did not rhyme by pressing a second button with the middle finger. Each block consisted of 32 trials and each left hemisphere activation session consisted of 12 blocks of the rhyming task for a total of 384 trials. The responding hand was counter-balanced across conditions.

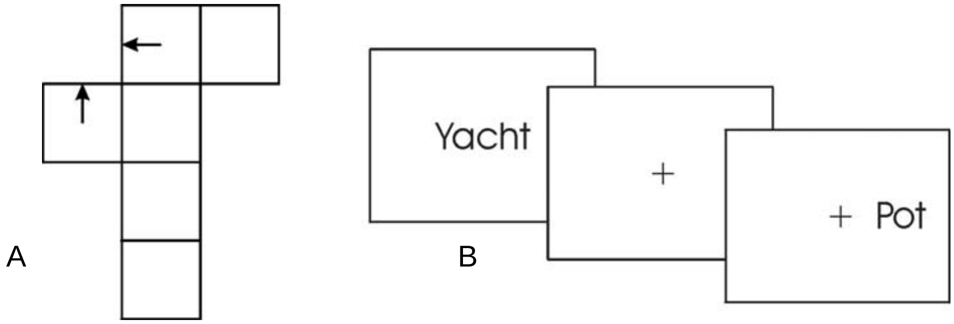

Figure 7-1. A. "Unfolded" cube stimulus with arrows pointing to touching sides. B. Rhyming word stimuli.

Letter task: This task was identical to that used in Experiment 3 except for the following modification: The responding hand was counterbalanced across blocks of trials following the pattern ABBA. Each block consisted of 40 trials and each session consisted of 8 blocks for a total of 320 trials.

7.2.1.3 Procedure

Participants were randomly allocated to one of two activation order groups and testing was spread over 2 one-hour sessions. The first group performed the right hemisphere activation condition during the first session and the left hemisphere activation condition during the second session. The second group did the reverse.

For each session participants were seated in a dimly lit room, had their chins in a chinrest, and were positioned 40 cm from a computer screen with their eyes focused on a fixation cross. Stimuli were presented on a Daewoo 17" CRT monitor controlled by a Pentium III computer. The Inquisit (Draine, 2003) software package was used for stimulus presentation and response recording.

During each session, instructions were given on-screen and one practice block was performed for the activation task as well as for the letter-matching task, after which participants' questions were answered. The practice blocks were followed by four blocks of the activation task (cube or rhyme) to activate the left or the right hemisphere. Sixteen blocks of experimental trials followed, alternating between activation and letter tasks; blocks of the activation task were interleaved with the letter task to maintain lateralised activation. Participants responded by pressing mouse buttons positioned in front of them, aligned with their body midline, and responding hands were counterbalanced across all conditions.

7.2.2 Results

7.2.2.1 Lateralised Tasks

To ascertain that the cube and rhyming tasks were lateralised in the expected direction, reaction time and accuracy measures were computed for the left visual field (LVF) and the right visual field (RVF) of the cube and rhyming tasks (Table 7-1). A 2 (VF) x 2 (Tasks) ANOVA produced a main effect of Task for the response time measure, $F(1,19) = 37.607$, $p < .001$, and for the accuracy measure, $F(1,19) = 56.646$, p

< .001, indicating that responses were faster and more accurate in the rhyming task than in the cube task. A Visual Field by Task interaction was also present for the response time measure, F(1,19) = 3.671, p < .05, but not for the accuracy measure, F(1,19) = .043, ns, demonstrating that responses were faster in the RVF/left hemisphere condition for the rhyming task, F(1,19) = 4.588, p < .05, and in the LVF/right hemisphere condition for the cube task, although not significantly so, F(1,19) = .801, ns.

Table 7-1. Response times and accuracy rates of the lateralised tasks. Standard deviations are presented in brackets.

Visual fields	Cube task		Rhyme task	
	RT	% correct	RT	% correct
LVF	1061 ms (209)	77.60 (12.26)	776 ms (159)	95.71 (2.83)
RVF	1069 ms (199)	77.08 (11.50)	761 ms (167)	95.42 (2.99)

Lateralisation indexes were computed (LVF-RVF/LVF+RVF) for each participant and for the response time measure of each task. An index of strength of typical lateralisation was computed by subtracting the cube index from the rhyme index, and dividing them by two, for each participant[5]. The average response time index was -.008 and ranged from -.028 (more typical lateralisation) to .016 (less typical lateralisation).

7.2.2.2 Letter Task

Response times and accuracy measures to matching letter pairs were computed for four visual field conditions (within left visual field, within right visual field, within-visual field average, and across-visual field for the two activation conditions and for each order in which the activation conditions were performed (rhyme first or cube first). Response times smaller than 250 ms, considered to be anticipatory responses, and larger than 1500 ms, considered to be due to attentional lapses, were excluded (approx. 6.4% of RT trials). Average response times to matching letter pairs was 1008 ms (SD = 231) with an average accuracy rate of 87.26% (SD 5.90).

7.2.2.3 Letter Task and Inter-Hemispheric Performance

Response times and accuracy rates for the within hemisphere and across hemisphere conditions and for each activation condition are presented in Table 7-2 and Table 7-3.

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[5] This index was chosen because, as each lateralised task is usually lateralised to a different hemisphere, it will indicate whether a participant is typically lateralised or not. For instance, if individuals have a typical lateralisation for the cube task their reaction time lateralisation index (LVF–RVF/LVF+RVF) will be positive whereas for the rhyming task it will be negative. Therefore, subtracting the two indexes equates to adding their absolute value. As a consequence, the more typically lateralised individuals are in the two tasks the smaller their lateralisation index will be, and vice versa.

Table 7-2. Response times for the within and across visual field conditions of the letter-matching task for the two activation conditions (right hemisphere/cube task first and left hemisphere/rhyme task second, or the reverse). Standard deviations are presented in brackets.

Order	Cube – Rhyme		Rhyme – Cube	
Activation / VF	Right	Left	Right	Left
Within	1022 ms (94)	1029 ms (104)	1024 ms (92)	1029 ms (25)
Across	1035 ms (76)	1033 ms (86)	1008 ms (81)	1006 ms (98)

Table 7-3. Accuracy rates for the within and across visual field conditions of the letter-matching task for the two activation conditions (right hemisphere/cube task first and left hemisphere/rhyme task second, or the reverse). Standard deviations are presented in brackets.

Order	Cube – Rhyme		Rhyme – Cube	
Activation/VF	Right	Left	Right	Left
Within	88.38 % (10.24)	89.38 % (6.10)	87.13 % (10.54)	79.37 % (9.08)
Across	84.38 % (9.61)	86.25 % (9.61)	88.11 % (7.30)	85.75 % (7.75)

Accuracy measure. In order to detect an effect of hemispheric activation on the letter task, a 2 Hemispheric Activation conditions x 2 Visual Field conditions (within/across) repeated measures ANOVA was conducted, with sex, and Task Order (cube or rhyme first) as between subject variables and functional lateralisation as covariate. No main effect was present, however, a Hemispheric Activation by Task Order interaction was detected, F(1,15) = 8.301, p = .011, indicating that performance in the letter-matching task was less accurate in the left hemisphere activation condition when it was conducted during the first session, t(1,9) = 6.455, p < .001, but not during the second session, t(1,9) = .677, n.s (see Figure 7-2). A three-way, Task by Visual Field by Lateralisation Index interaction was also present, F(1,14) = 15.139, p < .01. To define the influence of lateralisation, the index was recoded into two groups: participants who had a more typical lateralisation pattern (better left hemisphere performance for the rhyming task and better right hemisphere performance for the cube task, n = 10), and participants who had a less typical pattern of lateralisation (n = 10). Follow-up ANOVAs showed that in the more typically lateralised group the side of activation significantly interacted with the visual field condition (Figure 7-3A), F(1,9) = 5.437, p < .05, with the within visual field performance being more accurate in the right hemisphere activation than in the left hemisphere activation condition, t(1,9) = 3.402, p < .01. In the across hemisphere condition no difference were detected between activation conditions. In participants with a less typical pattern of lateralisation, no significant effects or interactions were detected (Figure 7-3B).

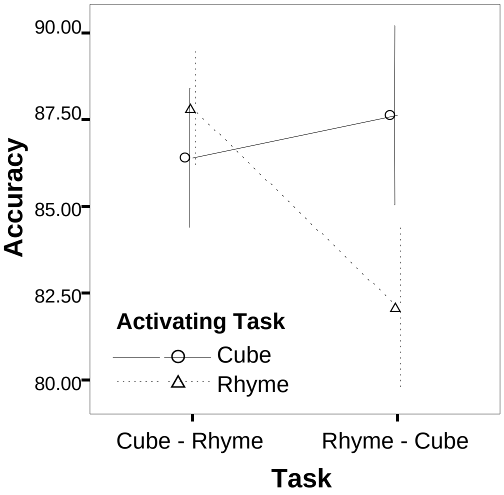

Figure 7-2. Accuracy in the letter-matching task as a function of the activating task, cube (right hemisphere activation) or rhyme (left hemisphere activation), for the two task orders (cube task performed during the first session and rhyme task during the second session or the reverse). The results indicate that performance in the letter-matching task was less accurate in the left hemisphere activation condition when it was conducted during the first session but not during the second session. Error bars represent the standard error of the mean.

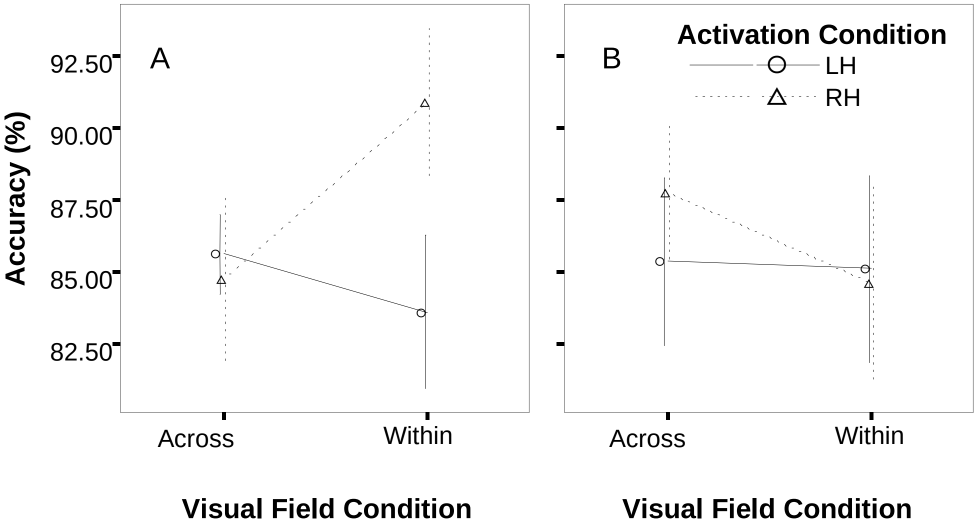

Figure 7-3. Accuracy in the letter-matching task for participants with more typical lateralisation (A) or with less typical lateralisation (B) in each visual field condition (within/across) and for the two types of hemispheric activation (left hemisphere, LH; right hemisphere, RH). Results show that in the more typically lateralised group the side of activation significantly interacted with the visual field condition, with the within visual field performance being more accurate in the right hemisphere activation than in the left hemisphere activation condition. No difference was detected between activation conditions in the across hemisphere condition. Error bars represent the standard error of the mean.

Response time measure. The analysis applied to the accuracy measure was repeated for the RT measure and did not reveal any significant effects or interactions.

7.2.2.4 Letter Task and Visual Field Performance

Response times and accuracy rates for the within left and within right hemisphere conditions and for each activation condition are presented in Table 7-4 and Table 7-5.

Table 7-4. Response times for the within left and within right visual field conditions of the letter-matching task for the two activation conditions (right hemisphere/cube task first and left hemisphere/rhyme task second, or the reverse). Standard deviations are presented in brackets.

Order	Cube – Rhyme		Rhyme – Cube Order	
Activation	Right	Left	Right	Left
LVF	983 ms (129)	974 ms (157)	1011 ms (158)	1002 ms (144)
RVF	1060 ms (111)	1083 ms (124)	1037 ms (114)	1056 ms (109)

Table 7-5. Accuracy rates for the within-left and within-right visual field conditions of the letter-matching task for the two activation conditions (right hemisphere/cube task first and left hemisphere/rhyme task second, or the reverse). Standard deviations are presented in brackets.

Order	Cube – Rhyme		Rhyme – Cube	
Activation	Right	Left	Right	Left
LVF	90.00 % (10.14)	91.50 % (7.56)	84.50 % (16.02)	77.00 % (16.24)
RVF	86.75 % (11.31)	87.25 % (6.50)	89.75 % (8.85)	81.75 % (8.98)

Accuracy measure. In order to determine whether left or right visual field performance was affected by the side of hemispheric activation a 2 visual fields (LVF/RVF) x 2 Tasks (cube/rhyme) repeated measures ANOVA with Sex, Task Order (cube or rhyme first) and Lateralisation Group (more/less typical) as between subject variables was conducted. Since no main effect or interaction involving Sex were found the analysis was rerun without this variable. A significant effect of task was found, F(1,16) = 6.538, $p < .05$, showing that the letter task was performed less accurately when performed after the rhyming task. A significant Hemispheric Activation by Task Order interaction was also detected, F(1,19) = 10.987, $p < .01$, indicating that performance in the letter-matching task was less accurate in the left hemisphere activation condition when it was conducted during the first session, although only as a trend, t(1,9) = 1.939, $p < .07$; but not during the second session, t(1,9) = .379, ns.

A Task by Visual Field by Lateralisation interaction, F(1,19) = 7.811, p = .01, was also detected; therefore, each lateralisation group was analysed separately.

For the more typically lateralised group, a 2 Tasks x 2 Visual Fields repeated measures ANOVA revealed a main effect of task, F(1,9) = 11.573, $p < .01$, showing that performance on the letter task was more accurate when conducted in the right hemisphere activation condition than in the left hemisphere condition (Figure 7-4A). A Task by Visual Field interaction was also present, F(1,9) = 6.207, $p < .05$, indicating that within right visual field/ left hemisphere performance in the letter task was less accurate in the left activation than in the right activation condition, t(1,9) = 4.114, $p < .01$, whereas there was no significant right visual field performance difference in the two activation conditions, t(1,9) = 2.029, p = .07.

For the less typically lateralised group, a 2 Tasks x 2 Visual Fields repeated measures ANOVA revealed no significant effect (Figure 7-4B).

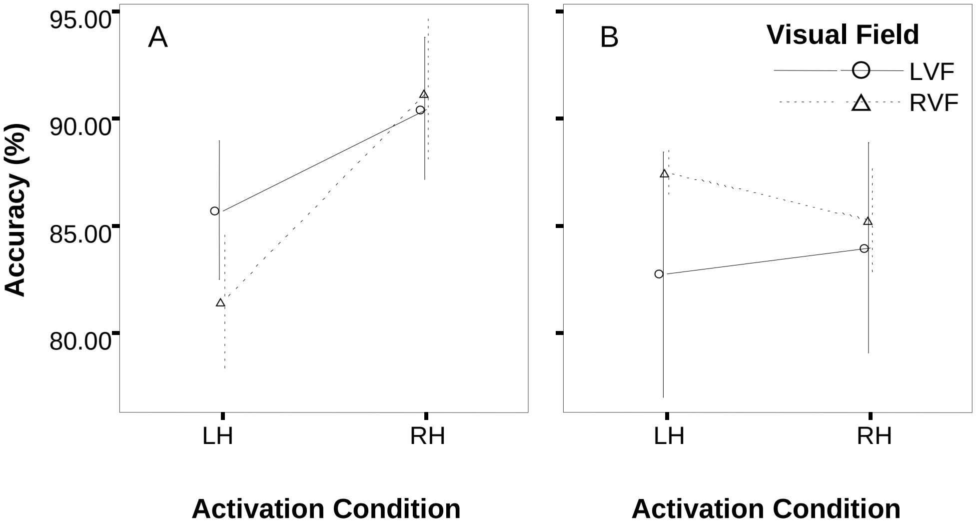

Figure 7-4. Accuracy in the letter-matching task for participants with more typical lateralisation (A) or with less typical lateralisation (B) in each visual field (LVF/RVF) and for the two types of hemispheric activation (left hemisphere, LH; right hemisphere, RH). Results showed that for the more typically lateralised group, performance on the letter task was more accurate when conducted in the right hemisphere activation condition than in the left hemisphere condition. In addition, within right visual field/left hemisphere performance in the letter task was less accurate in the left activation than in the right activation condition. No significant effect was detected for the less typically lateralised group. Error bars represent the standard error of the mean.

Response time measure. The analysis applied to the accuracy measure was repeated for the RT measure. Only an interaction of Task Order by Visual Field by Lateralisation Group was detected, F(1,12) = 6.042, $p < .05$. Since follow up analyses did not yield any significant contrast, and the cell sizes were small (n = 5), this result is interpreted as being due to low power and/or type I error.

7.2.3 Discussion

The aim of this study, in contrast with previous studies, was to assess how lateralised hemispheric activity *prior* to engaging in a non-lateralised letter-matching task would affect lateralised performance or forced interaction between hemispheres.

I predicted that when within- and across-visual field performance were compared, within-hemisphere performance would be more impaired in the left hemisphere activation condition, due to the decreased capacity of the left hemisphere to allocate attention. However, I did not expect across hemisphere performance to be affected by the side of activation, because Belger & Banich (1998) had found that across hemisphere performance was enhanced when the more active hemisphere was not the hemisphere specialised for the task being performed, and impaired when it was. Since in the present study neither hemisphere was specialised for the task, the side of activation was not expected to affect across visual field performance. I also anticipated that any effect of side of activation might be influenced by the strong practice effect found in the task (Liederman et al., 1985; Weissman & Compton, 2003, see also Chapter 5). It was also expected that individual patterns of functional lateralisation for the two activating tasks would modulate the effects of HA since in atypically lateralised individuals the left and right activation tasks would not produce the expected pattern of activation. These predictions were supported by my findings although the direction of some interactions was unexpected.

Firstly, a significant task by visual field condition (within/across) was found, but only in typically lateralised individuals. This suggests that in these individuals, left hemisphere activation impaired within-hemisphere performance but not across-hemisphere performance. These findings are consistent with the decreased ability of the left hemisphere to allocate attentional resources (Levy et al., 1990; Mangun et al., 1994).

Secondly, a significant interaction of activation condition and task order was found for the whole cohort. Performance on the letter-matching task was less accurate when the left hemisphere had been activated than when the right hemisphere had been activated, but only when the left hemisphere activation condition had been induced during the first session. These results can be explained in two ways. Since participants were included in only one order condition (left hemisphere activation first, or right hemisphere activation first) it is possible that the two groups differed in their pattern of hemispheric lateralisation or some other variable that would have interacted with HA. This is unlikely since there was no main effect of task order, and therefore the two groups performed similarly. Another explanation is that letter task performance was affected by a greater degree of left hemisphere activity but only when that task was performed the first time after such activation. This would suggest that the acquisition of the task was affected by left hemisphere activation. The rhyme task seemed to impede but the cube task seemed to enhance performance in the within visual field condition. In the across hemisphere condition, however, performance did not seem to be affected either way in any of the two activation conditions (Figure 7-3). This supports the notion that when the two hemispheres are forced to share the processing of stimuli from the start of the task, they tend to cope better under high interference and/or biased attentional conditions, than when single hemispheres were presented with all relevant stimuli and, therefore, could perform the task alone or "control" how resources in the other hemisphere are recruited. The high interference of left hemisphere activation on the letter task when performed during the first session remains to be explained. An explanation relying on competition for limited resources, as described in other studies (e.g., Davidson et al., 2000) is not appropriate, because the lateralised tasks were performed before, as well as in blocks alternating with the letter task. It is the initial activation of the left hemisphere that appears to have influenced the acquisition of the letter task while subsequent left-hemisphere activation did not affect repetition.

Since the left hemisphere is less efficient at allocating attention (Levy et al., 1990; Mangun et al., 1994), there may be a greater need for focused attention in the initial learning stages of the task. When the left hemisphere was activated first, attentional resources might not have been allocated as efficiently, and learning the letter-matching task might have been impaired. In contrast, when the left hemisphere activation condition occurred in the second session, performance of the letter task would be already sufficiently automatised and not affected by the less efficient attentional allocation.

Although the task used in this study was not lateralised as shown by a non-significant main effect of visual field (see also Eviatar & Zaidel, 1992, and experiment 3), Table 7-2 and Table 7-3 show trends suggesting a right hemisphere specialisation for this task. It is therefore important to determine whether some degree of lateralisation of the letter task could better explain the present findings. Based on Belger and Banich's findings (1998), right hemisphere lateralisation should be associated with improved performance in the across hemisphere condition when the left hemisphere is more active. My results present a completely different picture. Within hemisphere performance is impaired, not improved, when the left hemisphere is more active. Therefore, the notion that some functional lateralisation of the letter task produced these results is not supported.

When comparing performance of the left and right hemispheres, I expected that greater activation in one hemisphere would be associated with improved performance in the contralateral visual field. I also hypothesised that if attentional allocation was affected by the side of activation, left hemisphere activation would be associated with poorer performance since the left hemisphere has been shown to be less efficient in allocating attention. My findings partly supported these hypotheses but only in typically lateralised individuals. In this group, performance of the letter task was less accurate when the left hemisphere was active. A visual field difference was also detected but only when the left hemisphere was activated, and within RVF performance was less accurate compared to LVF performance. This also supports the interpretation of the pattern of my results being due to right hemisphere specialisation for attention allocation.

It is not possible to completely exclude the possibility that present results may be partly due to an effect of meta-control. An effect of meta-control was not predicted because the letter task was not expected to be lateralised. Although statistics mostly support this view, trends suggest that the right hemisphere may be more efficient at processing this task, even though this pattern may also be due to an interaction of side of activation and attentional capacities of the two hemispheres. In the case of the letter task being more lateralised to the right hemisphere I would expect that an effect of meta-control would impair left hemisphere performance, which is consistent with my results. On the other hand, the pattern of results in the within and across hemisphere conditions speak against an effect of letter task lateralisation because according to Belger and Banich (1998) it should have produced improved across hemisphere performance in the left hemisphere activation condition, which was not found. Thus, an effect of meta-control cannot be excluded but seems less plausible than an effect of allocation of attention.

Overall, I did not find an advantage for the visual field opposite the activated hemisphere. A study describing such an effect (Green et al., 1992) used a verbal task lateralised to the left hemisphere. It is possible that this effect was specific to some aspect of this task.

In conclusion, the present results show that accuracy of performance in a non-lateralised task was affected by the previous pattern of activation in the cerebral hemispheres, with left hemisphere activation producing significant impairment. Since contrary to previous studies, the activation procedure was completely separate from the experimental trials of the task from which performance was to be assessed, an explanation based on competition for limited resources in a dual task framework could be discounted. Instead, impaired left hemisphere performance in the within visual field condition appears to be due to less efficient attentional allocation when this hemisphere is more active.

As expected, division of relevant inputs in the across visual field condition decreased the impairment caused by left hemisphere activation. This is consistent with past findings showing that interference between cognitive processes is decreased when they are distributed across the two hemispheres (Merola & Liederman, 1990) and supports models suggesting that hemispheric interactions are involved in the efficient allocation of attentional resources (Banich, 1998).

These results indicate that HA is an important variable to consider in studies interested in lateralised as well as non-lateralised tasks. This is especially relevant for studies researching hemispheric interaction and comparing within and across hemisphere performance since these two conditions do not seem to be equally affected by patterns of HA. The present findings may also be of particular interest for research involving fMRI measurements since some tasks used as baseline conditions (e.g., target detection) may affect subsequent cognitive processes differently depending on whether the baseline task is more lateralised to the left or right hemisphere. The implications of the present results in the interpretation of fMRI findings need to be further researched. In these studies greater activation is usually interpreted as better cognitive functioning but as the present results demonstrate, this may not always be the case.

CHAPTER 8

8.1 Functional Tympanic Membrane Thermometry (fTMT): a new measure of hemispheric activation

In the previous chapter hemispheric activation (HA) was shown to be a factor affecting hemispheric interaction. Therefore it would be relevant to assess HA in studies investigating hemispheric interactions. Unfortunately, neither the traditional measures of hemispheric activation are readily accessible to typical psychological research due to their cost, availability, and various practical and methodological factors that will be discussed further below. The aim of the present chapter is to present a new method to assess hemispheric activation, and to assess its suitability for use in typical research. Since this new technique relies on the continuous measurement of the temperature of the ear's tympanic membrane temperature with highly sensitive infrared thermometer probes, I have called it functional tympanic membrane thermometry (fTMT).

It is well established that cerebral activity is associated with localised increases in cortical blood flow (e.g., Gur et al., 1994). It has also been shown that differences in cerebral blood flow are correlated with variations in carotid blood flow (Chu et al., 2000; Rothoerl, Schebesch, Woertgen, & Brawanski, 2003; Soustiel et al., 2003). Since the carotid arteries have two branches, one supplying blood to the cortex (including a substential contribution to the infero-parietal and occipital lobes, Jongen et al., 2002) and the other, supplying blood to the ear and facial structures it is likely that changes in cerebral activity are also associated with changes in middle ear perfusion. This hypothesis is supported by neurosurgical studies showing that cortical temperature is highly correlated with tympanic membrane temperature (TMT)(Schuman, Suhr, Gesseln, Jantzen, & Samii, 1999).

To my knowledge, Meiners and Dabbs (1977) were the first to suggest an association between ear temperature and cortical activity. Although they did not convincingly show an association between side of activity and change in temperature, they showed that as hemispheric activity increased, ear temperature decreased. It may appear paradoxical that as cerebral activity increases, which is associated with heat production, ear temperatures decrease. However, when cerebral activity increases so does cerebral blood flow. This leads to a decrease in brain temperature because carotid blood is cooler than cerebral blood. The same mechanism also produces a decrease in ear membrane temperature as carotid blood flow increases.

In another study, Swift and Perlman (1985) did not find a direct relationship between ear temperature variation and ipsilateral hemispheric activity but they demonstrated, by measuring left and right ear temperature with non-contact temperature sensors inserted in the ear canal, that participants who had a "warmer" left ear prior to testing performed better on a non-word recognition task whereas those who had a "warmer" right ear performed better on a face recognition task, suggesting that greater activation of the hemisphere specialised for a task as measured by ear temperature is associated with improved performance. These findings may appear to conflict with Meiners and Dabbs', however, they are related to very different cognitive processes. Whereas the ear temperature decrease described by Meiners and Dabbs is associated with physiological changes related to an increase in cerebral activity, the baseline ear temperature difference described by Swift and Perlman probably reflects a difference in resting hemispheric activation or bias. Such differences in hemispheric activation have been shown to affect the performance of task lateralised to the left or the right hemispheres (Levy, Heller, Banich, & Burton, 1983, see also Chapter 7).

A third study (Swift, 1991) found that participants who had a relatively larger increase in temperature in the left ear performed better in left hemisphere tasks than participants who had larger temperature increases in the right ear. These results also appear to be opposite to those of Meiners and Dabbs'. Meiners and Dabbs did not describe an association between greater change in temperature in one ear with increased performance in a task lateralised to the hemisphere on the same side, however, from their findings a decrease and not an increase in temperature would be expected on the side of the more active hemisphere. A close comparison of these two studies seems to suggest that the methodology used to measure temperature can provide a satisfactory answer. Meiners and Dabbs specifically measured ear membrane temperature using a thermocouple resting on the eardrum itself. In contrast, Swift used a thermistor inserted 5mm into the ear canal. This suggests that in Swift's study the probes did not rest on the ear membrane and therefore measured global ear temperature. This is an important point because ear temperature is influenced by three main variables: blood flow to the ear, heat radiating from the brain, and outside air temperature. In both studies the ear canal was blocked off, therefore outside air temperature would not have affected ear temperature, but the two other variables would influence the measures used in the two studies differently. The ear membrane is very thin, almost transparent, therefore it is very sensitive to small changes in blood flow. In contrast, general ear canal temperature is less likely to be affected by subtle changes in blood flow because the air in the air canal provides a buffer and is affected not only by the ear membrane temperature but also by the canal walls that have greater thermal mass. Thus ear canal temperature is likely to be more sensitive to brain temperature: since brain temperature increases with increased activity, the radiating heat in the ear canal would also increase, thus possibly increasing global ear temperature despite the cooling effect of the associated increased blood flow to the ear membrane. In this case, the findings of Meiners and Dabbs, Swift, and Swift and Perlman would be consistent.

8.2 Experiment 7

The aim of this study was to determine whether performance of lateralised cognitive tasks would affect left and right ear temperatures differently. It was hypothesised that left tympanic membrane temperature would decrease more during a left hemisphere task than during a right hemisphere task whereas the opposite was expected for the right ear. Because previous studies have shown that variations in tympanic membrane temperature are very small, infrared temperature probes specifically designed to continuously measure temperature in humans and sensitive to 0.01°C were chosen. They were integrated in a measurement apparatus designed to measure, graph, and record ear membrane temperature in the two ears while cognitive tasks are performed. This new technique has been named fTMT.

8.2.1 Method

8.2.1.1 Subjects

Seventeen volunteer subjects (9 males, 8 females) aged 20 to 37, and all but one male, right-handed, were recruited in the School of Psychology of the Australian

National University. The study received approval from Human Research Ethics Committee.

8.2.1.2 *Apparatus*

Two Exergen infrared medical temperature probes, pre-calibrated for the human physiological range and accurate to 0.01°C were used to measure TMT. The probes' analogue signals were converted into digital measures using a National Instrument signal processing system and recorded on disk. This apparatus is able to continuously record temperatures at sampling rates of at least 1kz. The probes were mounted on articulated arms fixed to a hard hat to minimise any effects of subjects' movements. Disposable, purpose-made plastic caps were positioned on the probes and changed between each participant to avoid risks of infection and to protect the probes. Subjects placed the probes into each ear and adjusted them as directed.

Inquisit software was used to present stimuli on a computer monitor, to record responses and to trigger temperature measurements.

Figure 8-1. Ear probe inserted in participant's ear (left). Helmet and flexible arms holding the ear probes (right).

8.2.1.3 *Stimuli and Procedure*

Subjects were seated in a darkened room in front of a monitor and informed about the organisation of the study. Once subjects understood the nature of the tasks, they were asked to fit the ear probes, and any adjustments were made. Subjects then placed their chin on a chinrest 40 cm from the monitor screen, and pressed the keyboard spacebar to start the experiment. All instructions were presented on screen. Subjects first performed a baseline measure, followed by two cognitive tasks involving mental processes more lateralised either to the left (verbal) or the right (visuo-spatial) hemisphere.

The baseline measure consisted of looking at a white screen for 2 minutes, and for an additional 2 minutes, looking at the white screen as well as pressing the spacebar approximately once/second with the two index fingers.

The cognitive tasks were a rhyming task and a mental cube-folding task similar to those used in Chapter 7. The rhyming task, adapted from Rayman and Zaidel (1991), was chosen because it has been shown to involve processes more lateralised to the left hemisphere. Stimuli consisted of 80 target/test word pairs, half of which were rhyming words. Target words were 3 to 6 letters long, test words always three letters long. All pairs were orthographically different. The target word was presented first for 400ms, followed by an inter-stimulus interval of 600 ms, then the test word was presented for 200 ms, pseudo-randomly to the left or right visual fields. Subjects indicated that the target word rhymed with the test word by pressing a mouse button with the index finger, or that the two words did not rhyme by pressing a second button with the middle finger.

The mental cube-folding task, adapted from Shepard & Feng (1972), has been shown to predominantly involve the right hemisphere. Stimuli consisted of 80 two-dimensional drawings of the six surfaces of an “unfolded” cube. In each drawing, two of the sides were indicated by arrows. Each drawing was presented once to the left or right visual field for 200ms. Subjects indicated that the two selected sides would be touching once the cube was “folded” by pressing a button with the index finger; otherwise they pressed the second button with the middle finger.

Each cognitive task consisted of 2 blocks of 40 trials with ten practice trials before each block. Feedback was provided after each trial to encourage accurate processing. Responses were given with the left hand in one block of trials, and with the right hand in the other. All conditions were counter-balanced. Temperature measurements in both ears were triggered 300ms after each stimulus’ presentation. This timing was chosen to ensure that at the time of measurement, the perceptual processes were completed, and that lateralised cerebral processes were in progress.

8.2.2 Results

RT and accuracy measurements were recorded to confirm that each task was lateralised to a different hemisphere. Behavioural data were first examined for task lateralisation using a 2 sex (men, women) x 2 tasks (rhyme, cube) x 2 visual fields (LVF, RVF) within-subjects ANOVA on the reaction time data. This revealed a near significant task by visual field by sex interaction, $F(1,15) = 4.2$, $p = .058$, with trends suggesting that in males, responses to LVF/right hemisphere presentations for the cube task were faster than those to RVF/left hemisphere presentations, whereas the opposite pattern was found for the rhyme task. In females, RVF reaction times were faster for both tasks but not significantly so. Analysis of the data for accuracy yielded no significant results except for a main effect of task. Average accuracy rates were 94% for the rhyme task and 60% for the cube task.

Temperature baselines were calculated for each ear and each subject by averaging the last ten temperature measurements of the baseline period. Females had higher left ear temperatures than males, $t(1,16) = 3.49$, $p = .03$, whereas right ear temperatures were not significantly different between sexes. Baseline temperatures were subtracted from temperatures measured during the rhyme and cube tasks. The average deviations from baseline for the rhyme and cube tasks (Figure 8-2) together, showed that average temperature was significantly lower during the task than during the baseline, $t(1,16) = 2.23$, $p = .04$, confirming that hemispheric activation is associated with a decrease in ear temperature. A 2 ears x 2 tasks x 2 sex within subjects ANOVA was then conducted. A significant interaction was found between ear temperature and task in the expected direction, $F(1,16) = 4.56$, $p = .048$, with the left ear temperature cooler during the rhyming task than during the cube task, and the right ear temperature showing the opposite pattern (Figure 8-2).

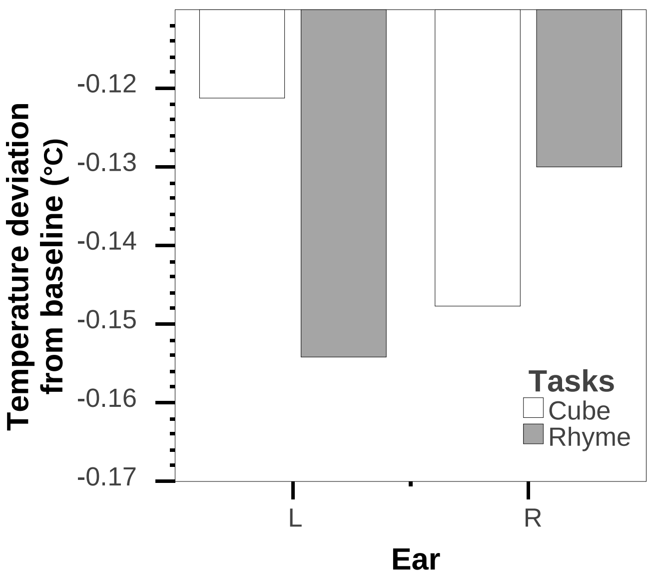

Figure 8-2. Average temperature deviations from the baseline of the left and right ear during the visuo-spatial (cube) task and the verbal (rhyme) task.

8.2.3 Discussion

The findings show that precise ear temperature measurements can reliably demonstrate patterns of hemispheric activation during lateralised cognitive task performance. Baseline temperatures were significantly higher than those during task performance. Furthermore, as activation shifted from the left hemisphere in the rhyming task to the right hemisphere in the cube task, left ear temperature increased whereas right ear temperature decreased and vice versa. Thus, ear temperature measurements can indicate not only changes in activation between resting (e.g., baseline) and active periods, but also relative changes of activation between the left and right hemispheres. This can potentially be very useful to assess not just which hemisphere is more active during performance of a specific task but also the extent to which the less active hemisphere is being recruited, reflecting hemispheric interaction.

These initial findings are encouraging, however, because the two tasks used were quite different in the type of stimuli used as well as in their level of difficulty it is difficult to gauge the sensitivity of this measure with respect to hemispheric interaction. The suitability of fTMT for such studies will be further investigated in the next experiment.

8.3 Experiment 8

In order to convincingly determine whether fTMT is sensitive enough to be used in a variety of experimental settings to assess lateralised hemispheric activation and hemispheric interactions, a task with specific characteristics would be required: it should present the same perceptual load to each visual field and should not be functionally lateralised. However, it should be possible to manipulate its cognitive load in order to vary its difficulty, and thus, the level of activity in each hemisphere.

A variation of the letter-matching task used in the previous chapters and in earlier research (Belger & Banich, 1992; Weissman & Banich, 2000) seemed to match these criteria perfectly. It presents an equal perceptual load to each visual field and has been shown not to be lateralised, or at least not very strongly (Eviatar & Zaidel, 1992). Furthermore, it is simple to vary the complexity of this task (Weissman & Banich, 2000; Weissman et al., 2000) by presenting identical matching letters (shape match) or by presenting matching letters written in upper and lower case (name match) which requires additional processing. Modulating complexity this way is especially interesting because it has been found, in a recent fMRI study (Pollman et al., 2003), that letter matching between identical letters is a relatively simple task which can be performed by each hemisphere without requiring the recruitment of resources in the other hemisphere; however, name matching is more complex, and with brief presentation times, requires the recruitment of the other hemisphere by the perceiving hemisphere. It should therefore be possible to modulate the degree of bilateral activation by using shape or name letter-matching tasks.

In summary, the aim of this experiment was to determine the suitability of infrared fTMT and to assess its sensitivity as a broad measure of hemispheric activity in typical cognitive or clinical studies. The degree of activation in each hemisphere was varied by presenting participants with a greater proportion of either left or right visual field matches. The degree of bilateral activation was also manipulated by using, for each participant, both a shape and a name letter-matching task. It was predicted that participants who were presented with more matches in their left visual field (perceived by the right hemisphere) would present with a greater decrease in temperature in the right ear than in the left ear. The reverse should be true for participants who were presented with more matches in their right visual field. Secondly, this pattern should be strongest in the simpler shape letter-matching task which seems to involve a lower level of hemispheric interaction (Pollman et al., 2003).

8.3.1 Method

8.3.1.1 Participants

Twenty-four right-handed participants (12 males, 12 females) aged 18-42, were recruited on the campus of the Australian National University. Participants were compensated for their time and travel with A$25. This study received approval from the Human Research Ethics Committee.

8.3.1.2 Apparatus

The apparatus was identical to that used in Experiment 7.

8.3.1.3 Stimuli and Procedure

Participants were tested individually in two separate sessions taking place on different days and lasting approximately one hour. Participants were randomly allocated to a left- or right-hemispheric activation group. They were given a detailed description of the procedure during the first session and encouraged to ask questions since once the temperature probes were put in place, their movements would be restricted and communication would be kept to a minimum since this could bias hemispheric activation during the experiment. Next, participants were seated, with their chin on a chinrest positioned 40 cm from a computer screen. The hard hat holding the ear probes was fitted to their head and they were asked to position the ear probes in their ear canals. Correct ear probe position and function were checked and further adjustments were made if necessary. Instructions were repeated on the computer screen and participants completed four practice blocks after which any additional questions they might have were answered. Participants were then asked to position either their left or right hand on a computer mouse, and asked to look at a black screen for three minutes to let ear probe and ear canal temperatures stabilise. Baseline temperatures were then measured in each ear over a ten second period. Participants were encouraged to concentrate on their breathing as soon as the probes were inserted and during the baseline period, to limit differences in brain activity between participants. At the end of the base line period, the experimental trials started immediately. There were 10 blocks of 48 trials. Each trial had a fixed length of three seconds and consisted of a pre-trial pause of 500 ms followed by the fixation point, presented for 500 ms, after which the stimulus was presented for 200 ms. After each block, participants were asked to change their responding hand, after which a black screen was presented for thirty seconds and participants were given the opportunity to rest. This sequence was repeated for each of the 10 experimental blocks. Thus responses were alternated between the left and right hand across blocks, with half of the participants starting with their left hand and the other half with their right hand. In the second session, the same procedure was repeated, followed by the completion of a handedness questionnaire. Half of the participants performed the shape letter-matching task during the first session and the name letter-matching task during the second, and vice versa for the other participants.

Shape letter-matching task: The stimuli were 7 capital letters (“A”, “B”, “E”, “F”, “G”, “H”, “T”) displayed in Arial 34-point bold font. Arrays of four uppercase letters were displayed in a square format. Stimuli subtended a maximum of 1.0° of visual angle and were displayed as white letters on a black background to decrease eyestrain. Each letter was presented 2.0° of visual angle to the left or right of the central fixation cross and 2.0° above or below the central fixation cross for 200 ms. In the “match” condition 2 letters were matching, whereas in the ”no match” condition none of the letters matched. The match always occurred between the two letters on the left or between the two letters on the right of the cross. The subject’s task consisted of deciding whether two letters in the display were matching while fixating on the central cross. A mouse button had to be pressed with the left or right index finger in the match condition, whereas no response was to be made in the no-match condition (go/no go). In each block, half of the trials were “match” trials and the other half “no-match” trials and were randomly presented. Feedback (average response time and % correct) was given at the end of the practice blocks, and after each trial for wrong responses (“wrong”) to encourage higher accuracy.

Name letter-matching task: This task was identical in procedure to the shape letter-matching task but the stimuli were 7 capital letters and their lower case counterparts (“Aa”, “Bb”, “Ee”, “Ff”, “Gg”, “Hh”, “Tt”). The top two letters of each display were in upper case, while the bottom two letters were in lower case. The match always occurred between the two letters on the left or between the two letters on the right of the cross and therefore always between one upper case letter and one lower case letter.

Hemispheric activation conditions: Participants were randomly allocated to a left or right-hemisphere activation group. Those in the left-hemisphere activation group had 75 % of matches presented to their right visual field in both the shape and name letter-matching tasks. The reverse pattern was used in the right-hemisphere activation group. The purpose of this activation manipulation was to increase cortical activity in the left or the right hemisphere and was based on the findings that the shape letter-matching task produces greater unilateral activation in the hemisphere detecting the match whereas the name letter-matching task produces bilateral activation even when the match occurs in the left or the right visual field (Pollman et al., 2003). Half of the trials were match trials and the other half non-match trials.

8.3.2 Results

8.3.2.1 Temperature Measures

Average temperature measures at the beginning of the experiment were 37.04 (SD = .91) °C in the left ear and 36.99 °C (SD = .92) in the right ear. The temperature difference between the two ears was not significant, t(1,23) = .352, ns.

Baseline temperatures in each ear were computed by averaging temperature measures over a ten second period immediately before the start of each task. This was done to let the probes and ear canal temperature stabilise after insertion of the probes. No difference was found between average baseline temperatures in the left ear 36.80 °C (SD = .74) and that in the right ear 36.83 °C (SD = .74), t(1,23) = .202, ns.

A 2 Ear x 2 Probe Position ANOVA was conducted to determine whether a difference in temperature measurements in the two ears differed as a function of ear probes but none was detected, F(1,47) = .636, ns.

In order to determine how ear temperatures varied from baseline temperatures during the experimental period, each participant's left and right ear baseline temperature for the left- and right-hemisphere activation groups (Activation) were subtracted from left and right ear temperature measures, respectively, taken during the shape and name letter-matching tasks. Average temperature measurements at the beginning of the experiment, during the baseline period, and during the experimental trials are presented in Table 8-1.

Table 8-1. Baseline temperatures (BL) and temperature deviations from baseline in the left (WL) and in the right (WR) visual field conditions for the shape and for the name letter-matching tasks with left- or right-hemisphere activation.

		Shape letter-matching task			Name letter-matching task		
		BL	WL	WR	BL	WL	WR
Left-hemisphere activation	Left Ear	36.64°C	-.089°C	-.113°C	36.73°C	-.029°C	-.042°C
	Right Ear	36.82°C	-.002°C	-.032°C	36.77°C	-.044°C	-.042°C
Right-hemisphere activation	Left Ear	37.1°C	.009°C	.001°C	36.74°C	-.030°C	-.039°C
	Right Ear	36.79°C	-.035°C	-.042°C	36.93°C	-.049°C	-.022°C

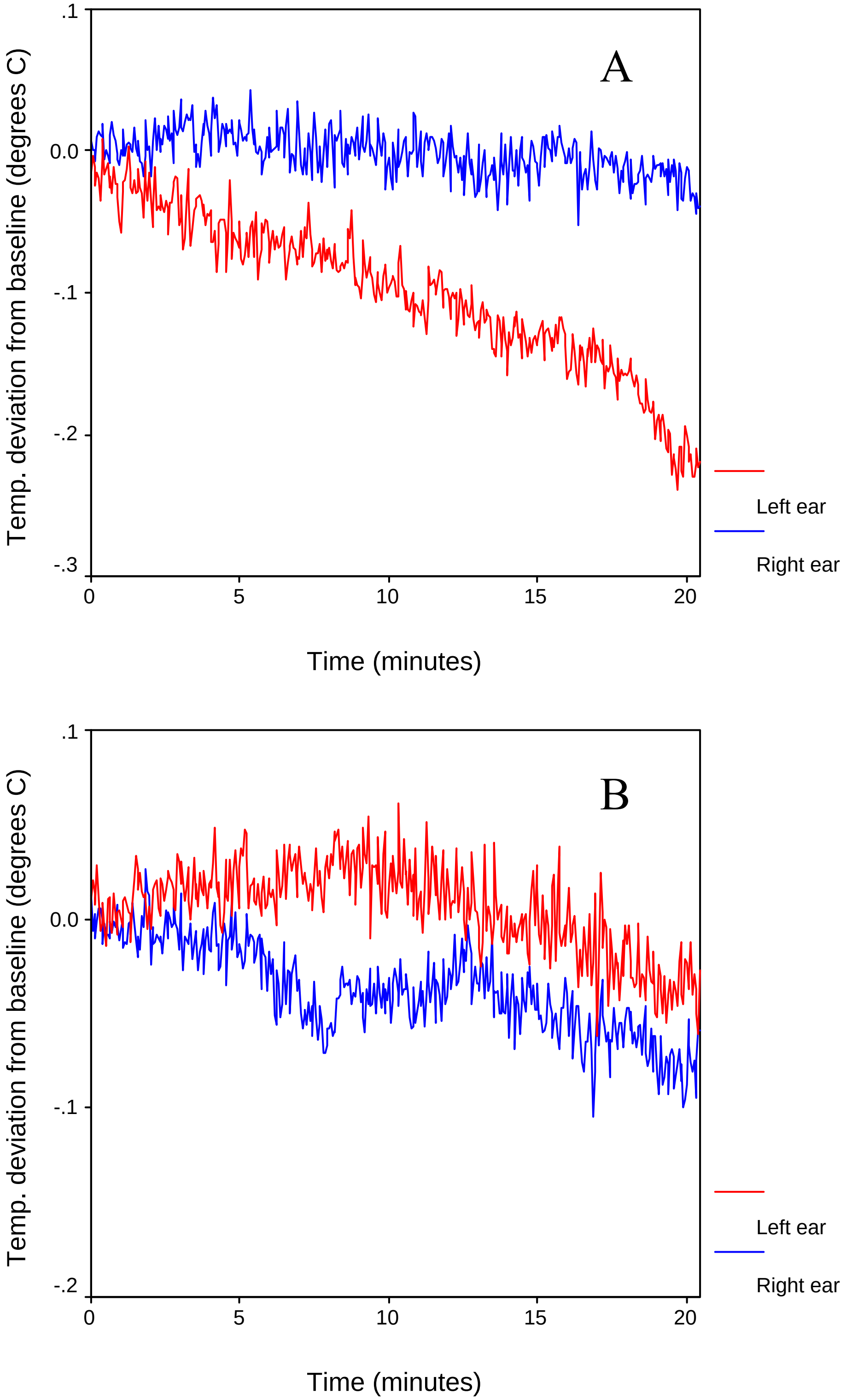

Figure 8-3. Temperature deviation from the baseline for the left-hemisphere activation (A), and for the right-hemisphere activation (B) conditions for the shape letter-matching task over time.

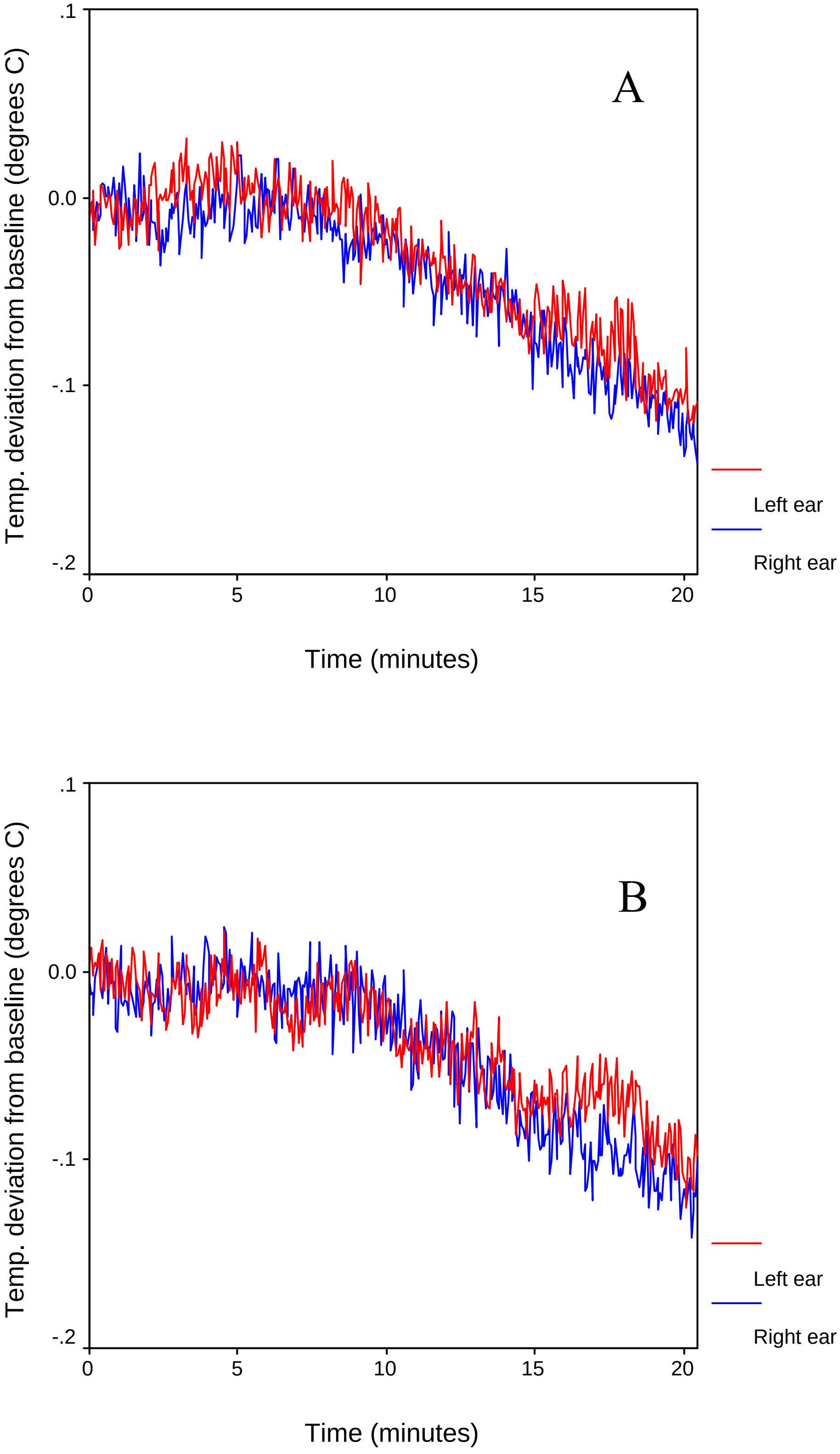

Figure 8-4. Temperature deviation from the baseline for the left-hemisphere activation (A), and for the right-hemisphere activation (B) conditions for the name letter-matching task over time.

Average temperature deviations from baseline over time for each activation condition and in each ear are shown in Figure 8-3 and Figure 8-4. A 2 Task x 2 Ear x 2 VF within subject ANOVA with Activation and Sex as between subject variables was conducted to determine whether ear temperatures were influenced by the task being processed, the side of activation, the visual field to which the match was presented, and the sex of participant. No main effects were found but a significant Task by Activation by Ear was detected, $F(1,20) = 5.473$, $p < .05$, as well as a four-way interaction between Task, Activation, Ear, and visual field, $F(1,20) = 10.748$, $p < .01$. In order to further define this interaction, each task was analysed separately.

Shape letter-matching task. A 2 Ear x 2 VF within subject ANOVA with Activation as between subject variable revealed a significant Activation by Ear interaction (Figure 8-3), $F(1,22) = 5.422$, $p < .05$, indicating that in the left-hemisphere activation condition, the left ear temperature decreased more than the right ear temperature, $t(1,11) = 2.317$, $p < .05$. An Activation by Ear by VF interaction was also present, $F(1,22) = 4.427$, $p < .05$. Follow up analyses were conducted for each activation condition. For the left-hemisphere activation condition, a significant VF by Ear interaction was detected, $F(1,11) = 9.597$, $p < .01$, indicating that the temperature in the left ear, $t(1,11) = 3.075$, $p < .05$, but not in the right ear, $t(1,11) = .914$, ns, decreased more during right than left visual field trials (see For the right-hemisphere activation condition, no main effects or interactions reached significance.

In order to better define the time course of the decrease in ear temperature during the shape letter-matching task the data were split into five epochs (approximately 4 minutes in length) and a 2 Ear x 5 Epoch within subject ANOVA, with Activation as a between subject variable was conducted. A main effect of Epoch was found, $F(4,19) = 4.273$, $p < .05$, indicating that ear temperatures were significantly lower in the last than in the first epochs, $t(1,23) = 2.201$, $p < .05$, with the largest differences taking place between the third and fourth epochs, $t(1,23) = 2.228$, $p < .05$, and between the fourth and the fifth epochs, $t(1,23) = 2.793$, $p = .01$. An Ear by Activation interaction already described above was also present, $F(1,22) = 6.720$, $p = .017$ (see also Figure 8-3).

Name letter-matching task. A 2 Ear x 2 VF within subject ANOVA with Activation as a between subject variable only revealed a near significant Activation by Ear by VF interaction (Figure 8-4), $F(1,11) = 3.661$, $p = .069$.

A 2 Ear x 5 Epoch within subject ANOVA with Activation as a between subject variable was also conducted to define the decrease in temperature over time. A main effect of epochs was detected, $F(1,20) = 4.284$, $p < .01$, indicating that ear temperatures were significantly lower in the fifth than the second epochs, $t(1,23) = 2.467$, $p < .05$, with the largest decrease in temperature occurring between the third and fourth epochs, $t(1,23) = 2.986$, $p < .01$ (see also Figure 8-4).

8.3.2.2 Behavioural Measures

Response times and accuracy measures to matching letter pairs were measured for two visual field conditions (within left visual field (wl), and within right visual field (wr)) for the left and right hemispheric activation groups (Table 8-2). Response times smaller than 250 ms, considered to be anticipatory responses, and larger than 1300 ms, considered to be due to attentional lapses, were excluded (2.3%).

Table 8-2. Response times and accuracy rate in the left (WL) and in the right (WR) visual field conditions for the shape and for the name letter-matching tasks with left- or right-hemisphere activation.

		Shape letter-matching task		Name letter-matching task	
		WL	WR	WL	WR
Left-hemisphere activation	RT	648 ms	609 ms	856 ms	845 ms
	Accuracy	97.6 %	97.8 %	87.3 %	89.9 %
Right-hemisphere activation	RT	549 ms	688 ms	697 ms	938 ms
	Accuracy	98.7 %	97.9 %	93.8 %	80.6 %

Average response times to matching letter pairs were 709 ms (SD = 64 ms) for the left-hemisphere activation group and 738 ms (SD = 51 ms) for the right-hemisphere activation group and were not significantly different from each other, t(1,22) = 1.219, ns. Response accuracy was 92.75% (SD = 3.281) for the left-hemisphere activation group and 92.72% (SD = 3.819) for the right-hemisphere activation group and were not significantly different from each other, t(1, 22) = .19, ns.

Paired samples t-tests were conducted to determine whether the tasks were more lateralised to one hemisphere. These tests were conducted on the practice trials data because the degree of hemisphere activation was not manipulated on these trials. No differences were found between the left and right hemisphere for the response time measure, t(1,23) = .355, ns, or for the accuracy measure, t(1,23) = 1.226, ns, of the shape-matching task, nor for the response time measure, t(1,23) = 1.714, ns, or for the accuracy measure, t(1,23) = 1.772, ns, of the name-matching task.

A 2 VF x 2 Tasks within subject ANOVA with Activation and Sex as between subject variables was computed to determine whether the hemispheric activation manipulation had an effect on performance of the left and right visual field for the two tasks. A main effect of task, F(1,22) = 203.343, p < .001, and of visual field, F(1,22) = 12.809, p = .01, was found for the response time measure, showing that responses were faster for the shape-matching task compared to the name-matching task and faster in the left compared to the right visual field. A visual field by side of activation interaction was also present, F(1,22) = 18.450, p < .001, indicating that responses by the activated hemisphere were faster than those of the other hemisphere in the name-matching task, F(1,22) = 16.079, p = .001, and in the shape-matching task, F(1,22) = 18.086, p < .001.

For the accuracy measure, a 2 VF x 2 Tasks within subject ANOVA with Activation and Sex as between subject variables revealed a main effect of task, F(1,22) = 87.721, p < .001, and of visual field, F(1,22) = 5.223, p < .05, showing that responses were more accurate for the shape-matching task compared to the name-matching task and more accurate in the right compared to the left visual field. A task by visual field by side of activation interaction was also present, F(1,22) = 9.463, p < .01, indicating that responses by the activated hemisphere were more accurate than those of the other hemisphere in the name-matching task, F(1,22) = 13.023, p < .01, but no difference in accuracy was detected between hemispheres in the shape-matching task, F(1,22) = .195, ns.

8.3.2.3 Relationships between Temperature and Behavioural Measures

In order to determine whether a relationship between resting hemispheric activation bias (left or right hemisphere more active/warmer) and behavioural performance existed (Levy et al., 1983; Swift, 1991), the differences between the left and right ear temperatures baselines at the beginning of the shape and name letter-matching task were computed and were shown to significantly correlate with each other, r = .503, p < .05. A correlation analysis between these measures and response time and accuracy performance in each task was conducted. Table 8-3 shows that higher right ear temperatures were associated with more accurate performance in both the shape and name letter-matching task.

Table 8-3. Correlation between hemispheric bias indexes (left ear – right baseline ear temperature) of the shape and name letter-matching task and average response time and accuracy performance during these tasks (significance levels are shown in brackets).

	Shape letter-matching task		Name letter-matching task	
	RT	Accuracy	RT	Accuracy
Correlation between Hemispheric bias and behavioural performance	-.245 (n.s)	-.550 (p < .01)	-.093 (n.s)	-.516 (p < .01)

8.3.3 Discussion

The present study was designed to assess the sensitivity of fTMT measurements as broad indexes of hemispheric activation and to confirm the suitability of this measure in typical cognitive and clinical studies. It was expected that patterns of change in ear temperature should be detected following modulation of hemispheric activity produced by a letter-matching task which has been shown to produce different hemispheric activation patterns under different experimental conditions (Pollman et al., 2003). Such a modulation was produced in two ways. First, by manipulating the proportion of matching trials in the left or the right visual field. Second, by using two versions of a letter-matching task, where matches took place either between identical letters (A – A, shape letter-matching) or between letters of same identity (a – A, name letter-matching). It was expected that a greater proportion of matches occurring in one visual field would produce a greater degree of activation in the contralateral hemisphere in the simpler shape letter-matching task, because Pollman et al. (2003b) have shown, in an fMRI study, that in this type of task the hemisphere perceiving the match is more active than the other hemisphere. In contrast, the two hemispheres were expected to be more similarly activated in the name letter-matching task because this task is more complex, requires the perceiving hemisphere to recruit resources in the other hemisphere, and has been shown to produce bilateral activation (Pollman et al., 2003).

Greater activity in one hemisphere was expected to be associated with a greater decrease in ear temperature on the same side because as hemispheric activity increases so does carotid blood flow on the same side. The carotid supplies a major part of the blood requirement to the cortex and the ear. Since carotid blood is cooler than both cerebral temperature and ear temperature an increase in carotid blood flow produces a decrease in cerebral and ear temperature.

As predicted, an interaction between side of activation and type of match was detected in the temperature data. In the perceptual match task, participants whose left hemisphere was activated by presentation of a larger proportion (75%) of matching letter pairs to the right visual field showed a greater decrease in temperature in their left ear than in their right ear over time whereas the reverse pattern was found in participants whose right hemisphere was activated. In the identity match task, no interaction was detected. However, temperatures in both ears decreased over time. This is consistent with fMRI findings (Pollman et al., 2003) indicating that in the simpler perceptual match task less recruitment/activation of the non-perceiving hemisphere was observed, while in the identity match task similar degrees of activation were found in the hemisphere perceiving the match and the non-perceiving hemisphere.

It could be argued that the activation measured by fTMT has not been produced by the greater number of matches detected by the left or the right hemisphere, but instead, that it is the attentional bias directed towards the side presenting a greater number of matches that has produced this increased lateralised activation. Although possible, this explanation seems unlikely since, if it were the case, the attentional bias should have produced similar patterns of results in the shape and name letter-matching tasks, but it has not. The influence of attentional bias on hemispheric activation, however, cannot be clearly ruled out in the present experiment and should be further researched in future studies.

A strong practice effect was also found. The difference in temperature deviation from baseline in the two ears increased over time, although not in a monotonic fashion, with the largest deviation occurring after approximately twenty minutes in the left-hemisphere condition, and after ten minutes in the right-hemisphere condition. This point is important because it illustrates the need for testing periods to be long enough in order to maximise the power of this measurement technique. The optimal length will depend on the degree of lateralisation of the task used and its difficulty but it appears that tasks lasting twenty minutes or more will provide the best results.

To further test the limit of this measurement method, the difference between each ear temperature deviation from baseline was computed and compared for different types of trials, those where matches predominantly occurred in the left (wl) or right (wr) visual fields. This test is particularly informative because wl and wr trials were randomly mixed throughout the experiment. Hence, differences in temperature between these trials would suggest that TMT is highly sensitive to slight differences in hemispheric activation taking place only a few hundreds of milliseconds apart. Not only were ear temperatures affected differently in the left- and right-hemisphere activation group throughout the experiment but temperature deviations specifically associated with one type of trial (wl) or the other (wr) could also be detected. In the perceptual matching task, an interaction between visual field and difference in ear temperature deviation was detected indicating right ear temperature decreased more during wr than during wl matches. This is consistent with our hypothesis that the hemisphere detecting the match becomes more active and suggests that fTMT is sensitive enough to detect subtle activation changes between different types of trials presented in a random order.

Analysis of the behavioural data demonstrated that the more active hemisphere is faster and more accurate at the letter-matching task. This is in agreement with a study by Davidson, Cave, and Sellner (2000) showing that if the left hemisphere is activated by performing a task lateralised to the left hemisphere (letter-memory task) the detection of a briefly presented stimulus is faster if it is presented to the visual field contralateral to the activated hemisphere.

It was also found that neither the perceptual match nor the identity match tasks were functionally lateralised to one hemisphere for response time or accuracy, prior to the experimental manipulation. However, once the proportion of matches taking place in each visual field was manipulated, a left visual field/right-hemisphere advantage appeared. It is not clear how this lateralised effect should be interpreted as past studies have found very similar tasks not to be lateralised. Studies in split-brain (Mangun et al., 1994) and intact individuals (Levy et al., 1990) have shown that the right hemisphere is specialised for attention allocation. Since the task used in this study required a high level of sustained attention it is likely that the left visual field advantage found in this study is due to the specialisation of the right hemisphere for attentional allocation.

A more speculative explanation of these findings is based on a hypothesis relating to the evolution of human functional lateralisation. An important difference between the task used in the present study and those used in previous studies, the unequal proportion of matches in the two visual fields (25%/75%), points to a possible explanation related to hypothesis formation by each hemisphere. In probability guessing experiments, animals tend to use a maximising strategy (Hinson & Staddon, 1983). That is, if food is present in one branch of a maze 75% of the time, they will always choose this branch in order to guarantee a reward 75% of the time. Humans, however, tend to use a frequency matching strategy where if a stimulus is presented 75% of the time on the left they will guess left 75% of the time and right 25% of the time (see M. S. Gazzaniga, 2000). Because this is a non-optimal strategy that leads to correct answers only 58% of the time, Wolford, Miller, & Gazzaniga (Wolford, Miller, & Gazzaniga, 2000) tested split-brain individuals to better understand how each hemisphere was dealing with such a task. They found that the left hemisphere tended to use a frequency-matching strategy while the right hemisphere tended to adopt a maximising strategy which produced greater accuracy rates. The present results are consistent with Wolford, Miller, & Gazzaniga's findings. The small difference between left- and right-hemisphere performance in the present study could be explained by the constant hemispheric interaction in individuals who have not had their cerebral commissures severed. It is interesting to note that in this experiment, participants were not told about the uneven proportion of matches in the two visual fields, and that, at the end of testing, only two out of 24 participants were able to report this manipulation. This might indicate that probability guessing might be conducted largely subconsciously in the type of task used in this study.

An interaction between visual field and side of activation was also present indicating that the activated hemisphere was more accurate than the other hemisphere in the name-matching task and faster in both the shape-matching and name-matching tasks.

A previous study (Swift, 1991) had shown that ear temperature difference was a factor predictive of behavioural performance. To assess whether this was also the case in the present study, hemispheric biases at the beginning of the each task were computed by subtracting right from left baseline temperature. A significant association was found between hemispheric bias and accuracy performance in both the shape letter-matching task ($r = -.550$) and the name letter-matching task ($r = -.516$), suggesting that individuals who had a more active right hemisphere at the beginning of each task were more accurate than individuals who had a more active left hemisphere. These results support previous findings suggesting that greater right-hemisphere activation may improve attentional allocation.

The present findings confirm that fTMT is a measurement method well suited for use in cognitive and clinical studies. It was shown that temperature measurements can be taken continuously during experimental trials in a typical cognitive study, and variations in temperature were associated with manipulations taking place not only across testing sessions but also between experimental groups, and types of trials within testing sessions. fTMT's effective temporal resolution has not been fully explored, however, our ability to detect temperature differences between different conditions which are made up of randomly intermixed trials suggests a temporal resolution smaller than the trial length. The validity of the present results is further demonstrated by the ability to predict measurement patterns which are in accord with fMRI findings of a study using a similar task (Pollmann et al., 2003b). fTMT may be especially useful in indirectly assessing hemispheric interactions, since behavioural measures can tell us about the effectiveness of hemispheric interaction but not about the *degree* of hemispheric interaction. Other possible measurement techniques such as fMRI or evoked potentials are less practical, more difficult to analyse, and significantly more expensive.

In conclusion, fTMT is a new measurement technique which permits the continuous assessment of broad hemispheric activity in the context of typical cognitive and clinical studies while being non-invasive, easy to analyse, compact, fast to set up and relatively cheap. It seems to be particularly suited to experimental research that intends to assess lateralised hemispheric activation over prolonged periods (e.g., to study sustained attention or practice effects in lateralised tasks), while certain motor tasks are being performed (e.g., exercise), or in various postural conditions (e.g., sitting, standing, lying down). It might be a useful tool to determine the lateralisation of speech production centres and as such might be used as a screening instrument by neurosurgeons to assess certain surgical risks in their rooms before other more specialised and invasive tests are conducted in hospital. It is also likely to be valuable in conducting research in young children, the elderly, and in certain clinical groups where typical scanning techniques may be impractical, or inadequate. Finally, it might be the only non-behavioural technique available to assess lateralised cerebral activity where testing needs to occur outside typical testing facilities (e.g., schools, nursing homes, in the field). Furthermore, fTMT is relatively simple to use, require no special training, and can be operated by a single experimenter.

CHAPTER 9

9.1 General Discussion

The study of hemispheric interactions has been neglected compared to research into functional laterality during most of the past century, but the last two decades have seen a growing interest in this field with the realisation that, except in split-brain individuals, independent, single hemisphere processing is unlikely to exist.

Hemispheric interaction research has now accumulated a substantial body of data describing when and how hemispheric interactions contribute to behavioural performance. This research, however, has so far mostly focused on the properties of the cognitive tasks being performed, or on the type of stimuli used and their modality (e.g., Banich & Belger, 1990; Belger & Banich, 1998; Hellige et al., 1988; Liederman & Meehan, 1986). Surprisingly, since hemispheric interaction by definition involves the corpus callosum (CC), very little attention has been paid to properties of the CC and variables that may affect its efficiency in interhemispheric transfer. Furthermore, little is known of the effects of variables that vary between individuals (such as sex, age, handedness, functional lateralisation, attention), or within individuals across time (e.g., practice, hemispheric activation), on hemispheric interactions. Based on the literature, the following predictions could be made of the effect of these variables on interactions between the cerebral hemispheres:

- More efficient callosal transfer may be expected to be associated with more efficient hemispheric interactions since it would decrease the transfer costs of recruiting resources in the other hemisphere when one hemisphere is overloaded. However, excessively fast callosal transmission, such as that described in individuals with dyslexia (Davidson et al., 1990; Fabbro et al., 2001), may be expected to disrupt processes relying on hemispheric interaction because it may interfere with the synchronisation of neural processes across the two hemispheres.
- Age differences may be expected to affect hemispheric interactions since the pattern of functional lateralisation has been shown to change over the lifespan (Reuter-Lorenz, 2002), and because the CC is known to change with ageing (Barnea-Goraly et al., 2005; Giedd et al., 1996; M. Keshavan et al., 2002; Rajapakse et al., 1996).
- Handedness and functional lateralisation may be expected to modulate hemispheric interaction. More left-handed and less functionally lateralised individuals may be expected to benefit most from hemispheric interactions since left-handed individuals tend to have less lateralised brains (see Beaton, 1997 for a review), and since decreased functional lateralisation has been shown to be associated with greater callosal connectivity (Rosen et al., 1989).
- An effect of sex may be anticipated due to numerous, if small, differences in anatomical and functional lateralisation demonstrated between the sexes (Aboitiz, Scheibel, Fisher et al., 1992; Aboitiz, Scheibel, & Zaidel, 1992; Kovalev et al., 2003; Luders et al., 2005; Shaywitz et al., 1995), suggesting that females, who tend to be less functionally lateralised, might demonstrate more efficient hemispheric interactions.
- A potential role of attention in hemispheric interaction is more difficult to define but may be expected given the increasing number of reports showing an association between the efficiency of allocation of attention and the efficiency of callosal

transfer (Mikels & Reuter-Lorenz, 2004), as well as an association between attentional deficits and certain neurological syndromes (e.g., Mather, 2001; Riley & McGee, 2005). Higher attentional performance would be expected to be associated with more efficient hemispheric interactions.

- Practice may be expected to influence hemispheric interaction because it has been shown to have a greater effect on within- than an across-hemisphere performance (Liederman et al., 1985; Weissman & Compton, 2003). Therefore extended practice may be associated with proportionally less efficient hemispheric interactions compared to single hemisphere processing.
- Hemispheric activation prior to performance of hemispheric-interaction tasks may be predicted to have an effect on hemispheric interactions either by modulating the allocation of attentional resources within and across the hemispheres, and/or by influencing which hemisphere and which strategy is in control of a task (Belger & Banich, 1998).

Therefore, the aim of the present thesis was to assess how the above variables such as callosal transfer efficiency, sex, age, handedness, functional lateralisation, practice, attention and hemispheric activation affect the efficiency of hemispheric interactions.

9.1.1 Methodology

Methodological issues related to the measurement of hemispheric interaction and interhemispheric transfer time were discussed in Chapter 2. A review of past research showed that a letter-matching task similar to that used by Banich and colleagues (e.g., Weissman et al., 2000) would be a suitable measure of hemispheric interaction because it has been extensively studied, has been shown to require callosal transfer, is likely to use callosal channels that can be assessed by the selected measure of interhemispheric transfer time, and is not lateralised.

Experiments 1 and 2 were conducted to determine whether modification in response (go/no go vs. forced-choice response) and display shape (square vs. v-shaped) of the letter-matching task would produce comparable results to those of previous studies in this field. Neither the type of response nor the shape of the display were found to affect the measure of hemispheric interaction. However, interestingly, results of these two studies revealed effects of, or interactions between age, sex, handedness, and hemispheric interactions despite the fact that these experiments were not specifically designed to study the effects of these variables. These results confirmed the adequacy of this task for the proposed study.

The suitability and validity of the Poffenberger paradigm as a measure of interhemispheric transfer time were also assessed. Based on previous research, it was concluded that despite the variability of this measure, the benefit of using a behavioural measure that can index small group differences taking place at different stages of cognitive processing involved in hemispheric interactions was substantial.

Since both the measure of hemispheric interaction and of IHTT would rely on precise timing measurements, an audit of the experimental apparatus was conducted (Appendix A). It revealed that the apparatus planned for this research was highly accurate in its timing capacity and well suited to answering the questions posed.

9.1.2 Callosal Efficiency

Experiments 3 and 4 were specifically designed to probe the relationship between interhemispheric transfer time and hemispheric interactions in a large group of right- or left-handed participants (Exp. 3 & 4, respectively) and to define how other individual variables of interest affected this relationship. A significant association between IHTT and hemispheric interaction, demonstrating that more efficient callosal transfer was associated with greater hemispheric interaction efficiency, was found in both right- and left-handed participants. Since the samples were large, eighty and twenty participants respectively, it is unlikely that these findings were due to chance. Moreover, the possibility that other variables could potentially underlie this relationship was excluded by showing that, with the exception of handedness (Experiment 4), they were not significant predictors in the regression analysis used.

This latter finding is surprising since Chapter 1 outlined strong theoretical reasons for an influence of sex, age, functional lateralisation, or attention in hemispheric interactions. This does not necessarily mean, however, that these variables do not contribute to hemispheric interactions. Instead, it is more likely that these variables partly affect hemispheric interactions by influencing callosal transfer. Thus, the individual effects of sex, age, functional lateralisation, and attention might not have reached significance in the analysis because they substantially overlap with the effect of callosal transfer. This view is supported by evidence presented in Chapter 1 showing that callosal morphology and neurophysiology vary with sex, age, handedness, and attentional differences. The results of Experiment 1 which revealed interactions between within- and across-hemisphere performance and sex, age, and handedness using the same task as that used in Experiments 3 and 4 also confirm a significant effect of these variables on hemispheric interactions.

9.1.3 Handedness and Functional Lateralisation

A handedness effect was found in Experiment 4 (left-handed group) but not in Experiment 3 (right-handed group). This suggests that this effect was either small and required a greater spread in the measure to be detected, or mostly overlaped with the effect of IHTT possibly due to an association between handedness differences and callosal neurophysiology (e.g., Moffat et al., 1998). This might indicate that the effect found in Experiment 4 reveals an influence of handedness on hemispheric interactions unrelated to callosal properties. Although handedness differences have been shown to be associated with differences in callosal efficiency (Driesen & Raz, 1995), it is possible that at least, in part, handedness directly affects hemispheric interactions through an independent effect. A possible explanation would be that the handedness effects found in Experiment 4 are related to differences in anatomical lateralisation (Aboitiz et al., 2002; Aboitiz, Scheibel, Fisher et al., 1992; Aboitiz, Scheibel, & Zaidel, 1992) rather than differences in callosal transfer. This would be consistent with the finding, in Experiment 4, that greater efficiency of hemispheric interaction based on the RT measure was associated with greater left-handedness, but that this measure of hemispheric interaction was not correlated with IHTT. In contrast, IHTT was a predictor of the accuracy measure of hemispheric interaction which was only weakly associated with the handedness measure, and in the opposite direction. It should also be noted that the response time and accuracy measures of hemispheric interaction were significantly correlated in Experiments 3, 4, and 5 (below). This suggests that some variability in hemispheric interaction, assessed by the accuracy measure, might be explained by the same underlying neural architecture as that producing the latency measure and that this may be related to differences in functional lateralisation.

The results of Experiment 4 also confirm that, on average, left-handed individuals are less functionally lateralised. This is consistent with evidence showing that left-handed individuals are less anatomically lateralised (Knecht et al., 2000; Tzourio et al., 1998). Since it has been shown that more symmetrical brains have more callosal connections (Rosen et al., 1989), left-handed individuals are likely to have more callosal connections. Provided that a greater number of callosal connections is associated with more efficient callosal transfer, this would be in agreement with left-handed individuals showing more efficient hemispheric interactions. These findings also underline the need for precise multi item handedness assessments in psychological studies. It is clearly relevant to hemispheric interaction research but is likely to be important for most research involving higher-order processes.

9.1.4 Age

Neuroanatomical changes related to aging predict an effect of age on hemispheric interaction, however, no effect of age was found in Experiments 3 and 4. This is not surprising as the samples used probably had an age spread narrower than optimally required to demonstrate an age effect, and were skewed towards younger participants. On the other hand, the results of Experiment 1 showed an interaction between age and within/across-hemisphere performance despite a smaller sample size (n = 24) and a narrower age spread (18 – 47). It has been shown that older individuals benefit more from hemispheric interactions than younger individuals (Reuter-Lorenz, 2002; Reuter-Lorenz & Stanczak, 2000). However, these studies have compared younger adults (18-25 years) to older adults (65-75 years) but have not described how hemispheric interactions change between these age groups. Therefore, future research should study the effect of ageing on hemispheric interaction using age groups spread over each decade, up to the eighth or ninth decade.

9.1.5 Attention

An effect of attention was not found in Experiments 3 and 4. It could be argued that the attentional measure used in these experiments (average simple RT) was too specific and was probably a better index of sustained attention than focused attention. However, in Experiment 6 (below), in which factors affecting hemispheric interactions were assessed in individuals with dyslexia, out of nine measures of attention (focused as well as sustained) it was the measure of sustained attention that was more highly correlated with the measure of hemispheric interaction, although the other measures also tended to be significantly correlated with hemispheric interactions. This might suggest that in neurologically normal individuals, attention might not be a major factor of influence on hemispheric interactions, or that this influence is mediated by callosal properties. When attention is disrupted, such as in dyslexia, it may either play a greater role or have an effect independent of callosal properties. The correlational nature of Experiment 6 (see below) means that these results should be interpreted with caution. It is not possible to know from the findings whether attention affects hemispheric interactions in dyslexia or whether other factors affect both hemispheric interactions and attention, or, conversely whether hemispheric interactions affect attention.

9.1.6 Hemispheric Interaction in a Clinical Sample: Dyslexia

The study of clinical populations can provide important information about normal brain processes and their determinants.

Individuals with dyslexia are ideally suited to investigate the relationship between properties of callosal transfer, hemispheric interactions, attention and handedness since these individuals have been shown to differ from normal controls in interhemispheric transfer time (Davidson et al., 1990), interhemispheric interactions (Fabbro et al., 2002), attentional processes (Wijers et al., 2005), and functional lateralisation (Boles & Turan, 2003; Heim et al., 2004; Walker et al., 2001).

Therefore, the same experiment conducted with neurologically intact individuals in Chapters 3 and 4 was repeated in individuals with dyslexia and matched controls, in order to confirm that abnormal interhemispheric transfer would disrupt hemispheric interaction (Experiment 5). Individuals with dyslexia performed overall less well than controls, but their measure of hemispheric interaction did not significantly differ from controls despite demonstrating an uncharacteristically fast IHTT.

It is clear, however, that in dyslexia, an abnormally fast IHTT, attentional deficits, hemispheric interactions and language performance seem to be intimately related. The findings of Experiment 5 showed that all these measures are significantly intercorrelated and appear to indicate that an abnormally fast IHTT is associated with impaired language skills and attentional deficits while decreased hemispheric interactions seem to be associated with poorer attentional and language skills. While it is not possible to determine a causal relationship based on the present results they highlight the need for models of dyslexia that can incorporate such findings.

9.1.7 Practice

One particularly interesting finding was that hemispheric interactions were strongly affected by practice: within-hemisphere performance becoming more efficient over time compared to across-hemisphere performance, although a practice effect was also found in the across-hemisphere condition. Such practice effects have been described elsewhere (Liederman et al., 1985; Weissman & Compton, 2003) but were based on comparatively low numbers of trials, and suggested that these practice effects only affected within-hemisphere processing. As the present results demonstrate, this practice effect is not restricted to within-hemisphere processing but is in fact more beneficial in this condition, presumably because increased efficiency with practice is limited in the across-hemisphere condition due to callosal transfer costs.

It was hypothesised by Weissman and Compton (2003) that their practice effects were due to a change of strategy, from algorithmic to memory retrieval. The analyses conducted in Chapter 5 show that this is not the case in the letter task used in Experiment 3, and that the practice effect is not due to strategy changes but is due mostly, if not entirely, to a general practice effect. The origin of this practice effect is not entirely clear but is probably due to neuronal tuning, or better allocation of cognitive resources. This leads to fewer processing resources being needed, which can be more efficiently recruited in a single hemisphere and, therefore, do not attract the cost of interhemispheric transfer.

These results are important because they show a need for testing participants over more and longer testing sessions if a true picture of hemispheric interaction and functional lateralisation is to be obtained. It may be that some complex tasks, which appear to be less lateralised than a simpler task, could nevertheless be more lateralised. However, because initially, more resources would need to be recruited bilaterally in more complex tasks, results might suggest that these tasks are not lateralised. With practice, fewer resources would need to be recruited across the two hemispheres, thus revealing a stronger functional lateralisation. Little is known about hemispheric interaction and practice effects when lateralised tasks are used. It has been suggested that they produce a decreased level of hemispheric interaction but this has only been shown in a small number of studies, which, furthermore, did not compare different levels of task complexity in the same task (e.g., Belger & Banich, 1998, see also Chapter 1 for a discussion). Therefore the interaction of functional lateralisation, hemispheric interaction, and practice is speculative at this stage and should be tested in future research.

The consequences of practice effects in real life situations should also be researched as they may vary from those detected in the laboratory. Differences in hemispheric interactions in different populations should also be scrutinised. Young children seem to benefit less from hemispheric interactions than adults, due to an incompletely developed corpus callosum (Banich, Passarotti, & Janes, 2000; Chicoine et al., 2000; Hagelthorn et al., 2000), when a typical short (one session) task is used to assess hemispheric interactions. Older adults (> 70 years of age), on the other hand, appear to benefit most from hemispheric interactions in these tasks (Reuter-Lorenz, 2002; Reuter-Lorenz & Stanczak, 2000), probably because hemispheric interactions allow the recruitment of more resources in a system where the availability of intrahemispheric resources may have decreased as a consequence of the aging process. This suggests that practice effects should affect these age groups differently and may affect both the speed of learning and ceiling effects. Young individuals might initially be slowed down in tasks requiring high levels of hemispheric interaction but once fewer interhemispheric resources are required as an effect of practice, their learning capacity might be improved. In contrast, older adults may demonstrate normal or faster initial learning in tasks that require high levels of hemispheric interaction but might not demonstrate the typical practice effects since these require the better harnessing of intrahemispheric resources, which seem to be diminished in this age group. It should be noted that in very young children, intrahemispheric resources are also limited and therefore their performance may resemble that of older adults better than that of older children (Banich, Passarotti, & Janes, 2000).

9.1.8 Hemispheric Activation

The relative levels of activation of the left and right hemispheres appear to vary both across individuals, and within individuals over time. However, very little is known about the influence hemispheric activation patterns might have on behaviour and on hemispheric interactions. A previous study found that the benefits of hemispheric interactions were maximised if the active hemisphere was not the hemisphere specialised for the task being conducted (Belger & Banich, 1998). In Experiment 6, I investigated the effect of hemispheric activation on hemispheric interactions when the target task was not lateralised, by selectively activating the left or the right hemisphere prior to task performance. The results were consistent with an effect of allocation of attention, with better within-hemisphere performance produced by right-hemisphere activation. This was thought to reflect the specialisation of the right-hemisphere for allocation of attention. In contrast, left-hemisphere activation produced a decrease in performance but only if it was induced in the first session, suggesting an influence on the learning of the task. These findings are interesting because they reveal new effects of hemispheric activation on hemispheric interaction. First, they show that even when the target task is not lateralised, hemispheric activation has an effect on hemispheric interactions. Secondly, they show that the effects of hemispheric activation can be modulated by learning or practice and interact with individual patterns of functional lateralisation. Thirdly, these findings demonstrate that greater activation is not necessarily beneficial, since left-hemisphere activation produced decreased performance in the within-hemisphere condition. Furthermore, across-hemisphere processing seems to be more resilient to interference, since performance was not affected by changing hemispheric activation patterns in this condition. Finally, the results also show that hemispheric interactions are not only affected by latent hemispheric activation patterns, as demonstrated by Belger and Banich (1998), but also by patterns of hemispheric activation artificially induced in participants.

These findings have important implications. Since it cannot be assumed that hemispheric activation is similar across different individuals, processes studied in different individuals may be differentially affected by individual patterns of hemispheric activation. Therefore hemispheric activation should be measured where possible, particularly when a task's functional lateralisation is believed to vary between individuals or when strong practice effects are expected. When multiple tasks are tested consecutively, the effect a cerebral activation pattern (induced by a previous task) has on a subsequent task should be carefully considered and controlled for. Furthermore, in the context of fMRI studies, the activation effects of baseline tasks should also be analysed since they may affect measurements in the experimental task. The present findings also provide another note of caution: Greater activity is not necessarily associated with better performance and this should be kept in mind when interpreting fMRI results.

9.1.9 Measure of Hemispheric Activation

The need for greater scrutiny of the role of hemispheric activation in typical cognitive research was discussed in the previous section. It should be recognised, however, that monitoring cerebral activation in typical psychological experiments is not trivial. It requires expensive equipment, and specialised skills; as well, it can be impractical and may interfere with the phenomena being studied. With this in mind I sought to develop a simple, cost-effective, practical device and technique to assess lateralised hemispheric activation. In Chapter 8, I have demonstrated that functional tympanic membrane thermometry (fTMT) is well suited to assessing cerebral activation when high spatial resolution is not required.

Functional tympanic membrane thermometry relies on the fact that local increases in brain activity are associated with a reflex increase in blood flow to the activated areas (e.g., Gur et al., 1994). Since most of the blood flow to the cortex, including a substantial part of the blood supply to the infero-parietal and occipital lobes (Jongen et al., 2002), is provided by the left and right internal carotid arteries, increases in activity lateralised to the left or right hemisphere are associated with increases in blood flow to the left or right carotid arteries respectively (Chu et al., 2000; Rothoerl et al., 2003; Soustiel et al., 2003). While the internal carotids supply blood to the brain, the external carotids supply blood to the face, scalp, and ear. The internal and external carotids share the same blood supply (common carotid), and an increase in blood flow to the left or right hemisphere is associated with an increase in blood flow to the ear (and ear membrane) on the same side. Paradoxically, because carotid blood is cooler than the brain and the middle ear, an increase in carotid blood flow cools the brain and the ear. Since the ear membrane is a very thin membrane, even slight changes in blood flow can change its temperature. These changes can be measured by the very sensitive infrared temperature probes (0.01°C) used in the apparatus described in Chapter 8.

All of the parameters and applications of this technique have not been fully tested but it was shown in Experiments 7 and 8 that fTMT can accurately measure lateralised activation at the group level (when performance is averaged over all individuals). Moreover, because the letter-matching task used in Experiment 8 presented identical perceptual loads to the left and right visual field, results suggest that this measure is very sensitive. In this experiment, only the proportion of matches in the left and right visual fields varied between conditions, yet this produced, as predicted, a greater decrease in temperature in the ear ipsilateral to the more active hemisphere. The fact that it was possible to show differences in average temperature between LVF and RVF matches within an activation condition (i.e. greater proportion of matches in the LVF or in the RVF) also points to this measure being more sensitive than perhaps might be expected.

The availability of this new technique for routinely measuring hemispheric activation could assist research in a number of domains. Since fTMT is inexpensive and easy to apply, it could be used as a covariate measure in many laterality studies. It could confirm that psychological tasks performed in such studies are lateralised in the expected direction and it could give an indication of the level of hemispheric interaction required to perform these tasks.

As discussed above, since the benefit of hemispheric interactions seems to decrease with practice, fTMT could be used as a measure of learning/practice. This could be done in two ways. First, recruitment of fewer cerebral resources over time due to practice should be associated with smaller decreases in ear temperature when compared with baseline measures. Secondly, because more complex tasks tend to require higher levels of hemispheric interaction and given that the degree of interaction decreases with practice (as shown in Chapter 5), practice effects of lateralised tasks are likely to be associated with a progressive shift from bilateral decreases in ear temperature to a greater unilateral decreases in ear temperature, on the side of the specialised hemisphere.

Functional tympanic membrane temperature might also be used as a measure of cognitive effort. More complex tasks would be expected to be associated not only with greater bilateral (as opposed to unilateral) decreases in ear temperature but also with larger decreases in temperature from baseline in one or both ears depending on the lateralisation of the task.

Lateral bias is a term used to define the prevalent mode of processing used by different individuals and is different from the pattern of activation found after performance of a lateralised task. Thus, at rest, an individual might have a more active left or right hemisphere. This type of bias has been shown to affect behaviour but has usually been assessed using behavioural measures which, as demonstrated in Chapter 7, can affect performance on subsequent tasks. In contrast, fTMT is a passive measure which is unlikely to affect future tasks, and is, therefore, suited to assessing such biases. This measure can subsequently be used as a predictor of performance. It might also give an indication of an individual's degree of functional lateralisation. However, this latter point has not been investigated and is therefore speculative, and should be studied in future research.

The reliability of fTMT as a measure of lateralised activity has not been confirmed at the individual level in the present research. Future studies should address this issue. If fTMT is reliable at the individual level, a number of other possible applications might be envisaged particularly in clinical studies. Ideally, the reliability of fTMT measures should be assessed by comparing them to other recognised measures of cerebral activation such as fMRI (or EEG) in within-subject design studies.

9.1.10 Scanning Biases

Finally, since research for this thesis was completed, Fecteau and Enns (2005) suggested that some of the measure of hemispheric interaction assessed with letter-matching tasks might be attributable to scanning biases and not to hemispheric interaction.

The present research was not specifically designed to investigate the influence of scanning biases in the measure of hemispheric interactions. However, in Experiment 1, the potential enhancement of scanning biases produced by a square compared to a V-display was investigated to confirm that results of studies using a square display would be comparable to those of previous studies that have used v-displays. No effect of display shape was detected and, therefore, it was concluded that a square display does not enhance scanning bias effects, and based on previous studies it was thought that any effects of such biases would be small.

Fecteau and Enns (2005) have found that such biases may be greater than originally expected, at least in some versions of the letter-matching task used in this field of research. They argued that when the attentional focus is on one stimulus, selective attention is most efficient when another stimulus is either presented in the same position or in the position farthest away from the first stimulus. Since letter-matching tasks use displays in which the distance between letters is slightly larger in the across condition than in the within condition, they argued that such tasks might be assessing scanning biases rather than hemispheric interaction. They showed that it was possible to modulate the bilateral distribution advantage by instructing participants to scan letter displays in specific sequences and concluded that at least part of the BDA could be accounted for by scanning biases. The implications of these findings for the present research are unclear. Although the results of Fecteau and Enns are consistent with scanning bias effects, they have not excluded the possibility that other effects might be produced by instructing participants to scan a display with a specific strategy. It is likely that such instructions divert some attentional resources from the main task of detecting a match and that such an effect might differentially influence the within- and the across-hemisphere condition. Such differential effects have been demonstrated in relation to practice in Chapter 5. Furthermore, the methodology used by Fecteau and Enns differs significantly from that used in other studies in this field. They presented letters at greater eccentricities and used greater horizontal (5 degrees of visual angle) than vertical eccentricities (2.5 degrees of visual angle). These changes have the effect of proportionally lengthening the distance between matching letters in the across condition compared to that in the within condition, and therefore enhancing or creating the scanning effects found in their study. It is also unclear whether a four-letter display like the one used in this research would be affected in the same way as the three-letter display used by Fecteau and Enns. It would appear that since the scanning bias could occur on a greater number of comparisons in a four-letter display (four, compared to two in a three-letter display), the difference between across-visual field and within-visual field performance should be enhanced, because it is argued by Fecteau and Enns that the scanning bias advantages the across-hemisphere condition. However, in four-letter displays, the BDA is decreased, not increased (Weissman et al., 2000) and therefore inconsistent with a scanning bias explanation. Furthermore, Fecteau and Enns have not convincingly explained hemispheric interaction effects found in other modalities (auditory and haptic) which cannot be explained by scanning biases. Therefore, it seems unlikely that the letter-matching task used in the hemispheric interaction literature does not assess hemispheric interaction. On the other hand, Fecteau and Enns have shown that, at least in certain circumstances, for instance, when the distance in the across condition is substantially larger than in the within condition, results appear to be affected by scanning biases. Future studies should pay special attention to the potential effect of scanning biases on measures of hemispheric interaction.

9.2 Future Research

The present research could be productively extended in a number of directions. It would be particularly interesting to show that the relationship between hemispheric interaction and IHTT found in letter matching holds for other tasks. This would allow for a generalisation of the present findings. In such studies, particular emphasis should be put on handedness, functional lateralisation, and attention. A handedness questionnaire as well as a behavioural measure of handedness would be useful since these assessments might better explain how handedness relates to functional lateralisation, and how these variables interact with hemispheric interactions. Measures of functional lateralisation could also be expanded. In the present study, measures of functional lateralisation were based on the performance of the letter-matching task and are therefore limited in its scope. The use of measures independent of the measure of hemispheric interaction would ensure that findings could be more generalised. Measures of attention similar to those used in Experiment 6 should also be used if possible. Given the results of this experiment, it is clear that much could be learned about the role of sustained and focused attention in hemispheric interactions in such a design. As explained in Chapter 3, I do not think that IQ would have played a major role in the present findings, had it been measured, since the population of tertiary students sampled was likely to be homogenous with regard to IQ. There are indications, however, that when the population sampled is heterogeneous with respect to IQ, this variable might have a greater influence on hemispheric interactions (Singh & O'Boyle, 2004). Therefore, the inclusion of a measure of cognitive performance might help clarify its role in the variability of hemispheric interactions.

As discussed earlier in this chapter, although few age effects were found in the present research, there is strong evidence showing that hemispheric interactions change over the lifetime. Since most research in this area has focused on childhood and old age and because methodologies have varied between studies, it would be informative to conduct identical experiments in different age groups, spanning each decade of life. This would enable better comparisons between age groups and clarify which variables affect hemispheric interactions most at different stages of the lifespan.

This would also provide normative data for comparisons with clinical populations. There is evidence of hemispheric interaction deficits in a number of clinical populations (dyslexia, schizophrenia, multiple sclerosis, bipolar disorder, alcoholism). A better picture of hemispheric interactions in healthy individuals would make it possible to make better predictions about the performance of clinical groups, which should also be assessed using the same neuropsychological instruments.

Another focus of research could be the strong practice effects demonstrated in Chapter 5. It would be interesting to study how other types of hemispheric interactions vary with practice; it might be even more useful to compare practice effects in different populations. Of particular interest is how practice effects might vary with age since precise predictions can be made based on our knowledge of brain development and the ageing process.

The role of latent or induced hemispheric activation is not well understood in relation to hemispheric interactions, and in relation to cognition in general, but it is expected to influence many if not most cognitive processes. As discussed in Chapter 7, hemispheric activation patterns are likely to interact with attentional allocation and meta-control. Future research should systematically study latent hemispheric activation patterns and experimentally modulate lateralised activation, and assess the effect of these variables on behaviour. Knowledge of normal patterns of hemispheric activation at rest, and during specific tasks, might also be useful as a predictive and diagnostic tool in healthy and clinical populations.

Since activation of the left hemisphere has been found to impede learning (at least in the letter-matching task), future studies should also investigate under which parameters this effect takes place, and its relationship to lateralisation of attention and functional lateralisation.

Finally, a new technique, fTMT, to measure lateralised activation shows great potential. However, much work needs to be conducted to confirm the validity and reliability of this measure in different experimental paradigms, and in different populations. Future research should first concentrate on testing this technique with tasks of known functional lateralisation, thus replicating previous findings. Because functional lateralisation varies widely across individuals, special care should be taken to include in the design of such studies variables such as sex, age, handedness, and functional lateralisation. Also, testing fTMT against typical measures of hemispheric activation, such as fMRI and EEG, is essential to provide strong proof of validity but also to convince the scientific community that this measure is a useful tool in experimental and clinical research. Studies should also be conducted to demonstrate that fTMT is particularly suited to assess hemispheric activation in young children, older adults, and clinical patients, since the use of other techniques can be particularly problematic in these populations.

9.3 Concluding Remarks

Since its discovery at the end of the 19th century, functional cerebral lateralisation has attracted a lot of interest. Its study has led to a better understanding of the brain's modular structure but it has also overshadowed the importance of the interactions taking place between the brain's hemispheres during normal cognition. More recently, the importance of studying the joint contribution of the two cerebral hemispheres to behaviour has been recognised, and has produced results of great relevance to researchers interested in both hemispheric specialisation and hemispheric interaction.

Research into hemispheric interaction has focused mainly on the influence of factors external to the participants tested, such as the type of task and stimuli used, the length of trials, and the modality in which stimuli were presented. Past studies have shown that hemispheric interactions are particularly beneficial when complex and demanding tasks are being performed. Such benefits of hemispheric interactions have been shown to be present in the visual, but also in the auditory and in the tactile modalities, and can be generalised to a variety of tasks, and of stimuli such as words, objects, shapes, sounds and faces. The effect of variables that differ between individuals, or within individuals across time, have been largely disregarded. A better understanding of such effects is important because variables such as sex, age, handedness, functional lateralisation, practice, attention, and hemispheric activation have been shown to interact with each other, and with interhemispheric transfer and brain structure, and therefore are likely to influence hemispheric interactions. Moreover, hemispheric interaction deficits have been shown to be associated with attentional deficits and some neurological syndromes such as dyslexia, schizophrenia, and bipolar disorder, all clearly associated with substantial inter-individual variability.

The current research was aimed at assessing some of the influences of interhemispheric transfer, sex, age, handedness, functional lateralisation, practice, attention, and hemispheric activation on hemispheric interactions and to determine whether this influence was merely detectable or whether it might play a significant role in influencing behaviour. The present findings indicate that these variables do interact in significant and meaningful ways with hemispheric interaction and consequently, inter-individual variability in these factors should affect hemispheric interactions. Therefore, hemispheric interaction is likely to influence differently the performance of many complex cognitive tasks in different individuals, in different populations, in different environments, and across time. Furthermore, unless the effect of varying levels of hemispheric interaction in different individuals is taken into account, seemingly inconsistent results between experimental studies investigating hemispheric interactions may be produced.

The present findings are not only relevant to researchers interested in hemispheric interactions. Using designs that allow for the assessment of hemispheric interactions in typical experiments might also better explain inter-individual variability in other areas of cognition and provide information on task parameters such as complexity, rate of learning, and functional lateralisation. A better understanding of the dynamics of hemispheric interactions is also likely to shed light on the pathological mechanisms involved in disorders such as dyslexia and also on the normal mechanisms underpinning brain development and the ageing process.

Finally, the new measurement technique (fTMT) developed as part of this research relies on precise measurements of ear membrane temperatures as an index of lateralised hemispheric activation. This measure was shown to be more sensitive than originally expected and is likely to have a wide range of applications once its operating parameters have been further defined, and the measure has been validated against other physiological measures of brain activation such as fMRI and EEG.

These results are important because they show a need for testing participants over a greater number of sessions of potentially longer duration if a true picture of hemispheric interaction and functional lateralisation is to be painted. It may be that a complex task which appears to be less lateralised than a simpler task is in fact more lateralised. However, because initially more resources need to be recruited bilaterally in the complex task, results might suggest that it is not lateralised. With practice, less interhemispheric resources will be recruited which might reveal a stronger functional lateralisation. Since little is known about the effect of task lateralisation on hemispheric interaction and the effect of practice in this context, these suggestions are speculative and should be tested in future research.

These results are important because they show a need for testing participants over more and longer testing sessions if a true picture of hemispheric interaction and functional lateralisation is to be painted. It may be that a complex task which appears to be less lateralised than a simpler task is in fact more lateralised. However, because initially more resources need to be recruited bilaterally in the complex task, results might suggest that it is not lateralised. With practice less interhemispheric resources will be recruited and might reveal a stronger functional lateralisation. Since little is known about the effect of task lateralisation on hemispheric interaction and the effect of practice in this context, these suggestions are speculative and should be tested in future research.

APPENDIX A

A.1 Audit of the Timing Accuracy of the Experimental Apparatus

The aim of this audit was to determine whether the timing accuracy of the software and hardware selected for the present research were sufficiently accurate.

When auditing an apparatus for timing accuracy the auditing software and hardware must be kept completely separate from the experimental apparatus if the risk of creating interactions between these elements is to be avoided. Therefore, a separate computer controlling a dedicated data acquisition box and a specialised, highly accurate timing software package (customised for this application) have been used to monitor the timing of the visual stimuli, the manual response, and overall behavioural performance. A second computer was used to run an experimental program with specifications similar to those used in the present research.

A.1.1 General Method

A.1.1.1 Experimental Apparatus and Stimuli

The experimental apparatus consisted of a standard 666 MHz Pentium III computer with 256 Meg of RAM, running the MS Windows 2000 operating system, using standard input devices (serial mouse and ps2 keyboard), and a 17” Hyundai cathode ray tube monitor with a refreshment rate of 80 Hz. The contact of the right mouse button was fitted with two additional wires so that a mouse press could be simulated by the auditing computer.

A custom program was scripted in Inquisit software (Draine, 2003). This software package was selected because it has been designed to have high timing accuracy. It accesses the peripherals using Microsoft directX drivers. This means that, at critical times, when stimuli are being displayed and response times are being measured, the program takes full control of the input and output devices (mouse and monitor) which are then no longer accessible by any other program that may be running in the background. The program also increases the number of times the mouse is polled for responses to the maximum frequency, can trigger external devices (i.e. the computer auditing the timing accuracy) via the parallel port, and only allows activity of processes necessary to the stability of the operating system.

Stimuli consisted of a white square with sides of 2 cm presented in the top left corner of the screen on a black background. Since the stimuli were used to trigger the auditing computer, and since the screen refresh starts in the top left corner and finishes in the bottom right corner of a cathode ray screen, it was important that the stimuli be presented in the top left corner of the screen so as to indicate the beginning of the screen refresh.

During each trial, a stimulus was presented for 50 ms, and a mouse response was expected from the auditing computer to indicate detection of the stimulus. The trial terminated either when the mouse response was received or after a time-out period of 400ms. Each trial was followed by an intertrial interval of 500 ms.

A.1.1.2 Auditing Apparatus

The auditing apparatus consisted of a 1.6 Mhz Pentium IV computer with 512 Meg of RAM, and fitted with a National Instrument analog/digital data acquisition card and connection box. Two inputs were connected to this system. One came from a solenoid probe sensitive to light signals, which was attached to the screen of the experimental computer and served to detect the presentation of stimuli. The other came from the parallel port of the experimental computer and was used to read signals indicating significant events (stimulus presentation and end of trial) of this system. The connection box also provided one output used to simulate a mouse response and trigger the experimental computer. A customised program was developed to control this hardware using National Instruments' LabView software. This program was designed to detect the stimulus onset and presentation time, trigger a mouse response after a fixed period of time, detect the data sent from the mouse to the computer, and measure the total trial length by detecting parallel port signals from the experimental computer sent at the beginning and end of each trial.

A.1.1.3 Design and Procedure

In all experiments, a stimulus was generated by the experimental computer while at the same time, a parallel port signal was send to the auditing computer. This was done to measure the length of the delay between stimulus initiation and its appearance on screen. Unlike the parallel port signal, which is transmitted almost instantaneously, the screen stimulus needs to be buffered and synchronised with the screen refresh. If one of these events was not adequately controlled by the software, the difference between parallel port signal and appearance of the stimulus on the screen would be substantial. If this were the case, this would translate in a significantly shortened stimulus presentation time.

Each stimulus was presented for 15 refresh frames lasting 11.76 ms each for a total duration of 176.47 ms. The appearance of the stimulus on screen was detected by a solenoid detector attached to the screen and connected to a signal processing box, itself connected to the data acquisition box of the auditing computer. This signal started two timers in the customised software of the auditing computer. One timer measured the length of different events produced by the experimental computer (e.g. total trial length, stimulus-to-mouse response length, stimulus presentation length). The other timer was used as a response delay, and simulated a mouse response by triggering the right mouse-button switch of the experimental computer after 300 ms.

The experimental computer's mouse was also wired to provide information about the data it sent to the computer. These wires could be connected either to the data acquisition box to determine the internal delay of the mouse, or to an oscilloscope to measure the shape of the data signal.

Once the mouse was triggered, the signal received by the experimental computer terminated the current trial, which in turn triggered a second parallel port signal to indicate to the auditing computer that the trial was terminating. This signal stopped all the active counters in the auditing computer.

A new trial was then started after a 500 ms inter-stimulus interval. The Inquisit software recorded stimulus lengths and trial lengths to file.

The auditing computer was fitted with three counters and therefore, had the capacity to record a maximum of three durations. As more than three measures needed to be recorded to audit the experimental apparatus, a number of experiments were run to measure different variables of interest. All these experiments shared the procedure described above. Additional manipulations, specific to each experiment, will be described in the next sections.

A.1.2 Experiment 1

This experiment was designed to assess the delay between the start of a trial and the appearance of the stimulus on-screen, and to measure the delay between mouse button trigger and the mouse digital data transfer to the computer (mouse buffer).

This second variable is particularly important because input devices, such as computer mice, do not forward a response directly to the computer. Instead the button press is stored in a memory buffer in the mouse and transferred only when the computer polls the mouse for responses. The computer polling frequency is controlled by the operating system under normal circumstances and can be adjusted. However, the software, when MS directX is used, can adjust this parameter to allow for the fastest possible scanning of the mouse buffer, thus improving the timing accuracy of the mouse response.

A.1.1.4 Procedure

One timer measured the duration between detection of the first parallel signal (start of trial) and detection of the visual stimulus on-screen. The second timer measured the duration between visual stimulus detection and the mouse button trigger. This was done to ensure that the length of the delay of the auditing computer before initiating a mouse response was accurate. The third timer measured the duration between closure of the mouse switch (mouse press simulation) and detection of the data transfer from the mouse to the computer. Simultaneously, an oscilloscope also connected to the mouse data cable recorded the length and the shape of the data sent to the computer and provided a graphical snapshot that could be viewed on a computer. This was done because the experimental computer would not be able to pass the mouse response to the software before the complete data packet was read. Therefore, the length of the data packet would add a fixed delay to the response time recorded by Inquisit which would need to be included in the timing audit. One thousand trials were recorded in one testing session.

A.1.3 Results and Discussion

The measurements of the three timers, parallel port signal – stimulus onset, stimulus onset – response simulation, and response simulation – mouse data to computer, and for the response time recorded by Inquisit were averaged over the one thousand trials. Two outliers, one in each of the first two measures were excluded. This was done because they clearly indicated an aberration in the auditing computer measure and not in the experimental computer signal. These measures are reported in Table A1. They show that there was an almost fixed delay between the parallel port signal and the appearance of the stimulus on-screen. Furthermore, the trigger delay from the auditing computer was highly accurate. The greatest variation was found in the delay between mouse-press simulation and the mouse data being sent to the computer.

Table A1. Average measured durations of parallel port signal to stimulus onset, stimulus onset to response simulation, and response simulation to mouse data transfer to computer, as well as the response time recorded by Inquisit for one thousand trials.

Measures	Milliseconds	SD
PP signal → Stimulus onset	1.37	0.01
Stimulus onset → Response simulation	300.00	< 0.01
Response simulation → Data transfer	41.56	7.55
Inquisit RT measure	345.89	7.56

If the auditing and experimental computers were perfectly accurate we would expect that the following equation would hold.

RT = (PP sig.→stim. onset)+(stim. onset→resp. simul.)+(resp. simul. →mouse data)

And therefore:

RT - (PP sig.→stim. onset)-(stim. onset→resp. simul.)-(resp. simul.→mouse data) = 0

Instead it was found that:

345.89 ms (7.56) – 1.37 ms (.01) – 300 (< .0001) – 41.56 ms (7.55) = 2.94 ms

This shows that less than 3 ms of the response time recorded by Inquisit have not been accounted for. It also shows that most of the variation in the Inquisit RT measure is due to the variability in the mouse buffering. To further assess the characteristics of the mouse response, the oscilloscope data were analysed next.

Figure A1 shows the oscilloscope trace of the mouse data transfer (bottom line). The length of time of the data packet was 3.12 ms. Because its length is dictated by the mouse clock it did not vary over an number of readings. The time between the end of the data packet and Inquisit issuing a parallel port signal (top line), indicating the end of the trial, was 530 μs.

When all these measures are considered, the difference between the trial length/response time recorded by Inquisit and that computed based on the auditing apparatus is 710 μs which is most likely due to measurement error when visually reading the oscilloscope display.

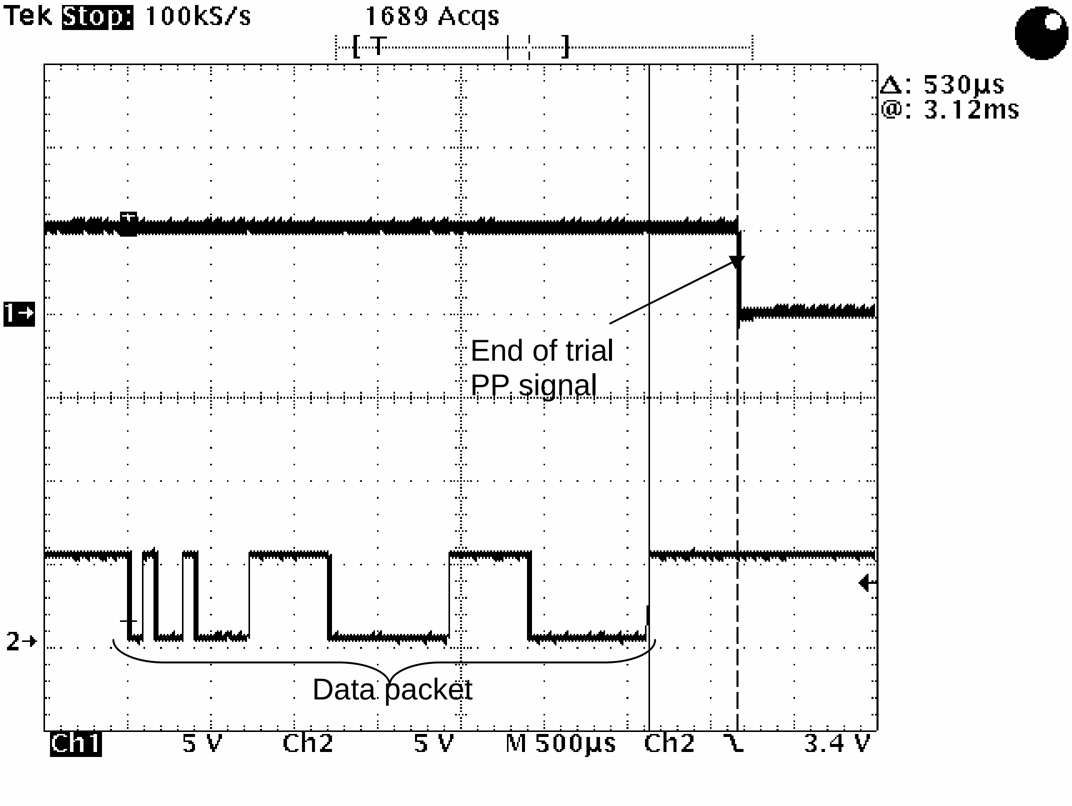

Figure A1. Oscilloscope measurements of the mouse data packet (bottom line) and parallel port signal (from Inquisit) indicating the end of the trial (top line).

A.1.4 Experiment 2

This experiment was designed to assess the accuracy of the visual stimulus presentation time and to demonstrate further that the difference in Inquisit timing and the timing done by the auditing apparatus was due to the mouse data transfer.

A.1.1.5 Procedure

One timer measured the duration between detection of the first parallel port signal (start of trial) and detection of the visual stimulus on-screen. The second timer measured the duration between the stimulus onset and the stimulus offset. The third timer measured the duration between the first parallel port signal and the start of the data transfer from the mouse. Oscilloscope measurements were also made on the solenoid signal to detect the number and length of the screen refreshes. One thousand trials were recorded in one testing session.

A.1.5 Results and Discussion

The measurements for the three timers, parallel port signal – stimulus onset, stimulus onset – stimulus offset, and stimulus onset – mouse data to computer, and for the response time recorded by Inquisit were averaged over the one thousand trials. These measures are reported in Table A2. They indicate that the response time reported by Inquisit is very similar to that recorded in the previous experiment, 345.81 ms in this experiment compared to 345.89 ms in experiment 1. They also reveal that the delay between the start of the trial (PP signal) and the stimulus onset remained the same (1.37 ms) across the two experiments. The duration between the stimulus onset and the start of the data transfer from the mouse is also almost identical in the two experiments, 341.52 ms in this experiment and 341.56 ms in experiment 1.

Based on the previous experiment we can build the following equation:

RT- (PP sig.→stim. onset)-(stim. onset→mouse data)-packet length-software delay = 0

After substituting these variables with the measured values we find:

345.81 ms – 1.37 ms – 341.52 ms – 3.12 ms -.71 = 0.9 ms or 900 μs

A measurement error of 900 μs indicates that Inquisit's timing is millisecond accurate and that these findings can be replicated across experimental sessions.

Table A2. Average measured durations of parallel port signal to stimulus onset, stimulus onset to stimulus offset, and stimulus onset to mouse data transfer to computer, as well as the response time recorded by Inquisit for one thousand trials.

Measures	Milliseconds	SD
PP signal → Stimulus onset	1.37	0.01
Stimulus onset → Stimulus offset	178.46	0.01
Stimulus Onset → Data transfer	314.52	7.65
Inquisit RT measure	345.81	7.67

The third timer was used to measure the duration of the stimulus presentation. The stimulus was presented for 15 refresh frames. Since the monitor scanning rate was set on 85 Hz we would expect each frame to last for 11.76 ms and the whole stimulus to be presented for 176.47 ms. The experimental data showed that the stimulus was effectively presented for 178.46 ms (SD .01) indicating a 2.01 ms discrepancy with the predicted value.

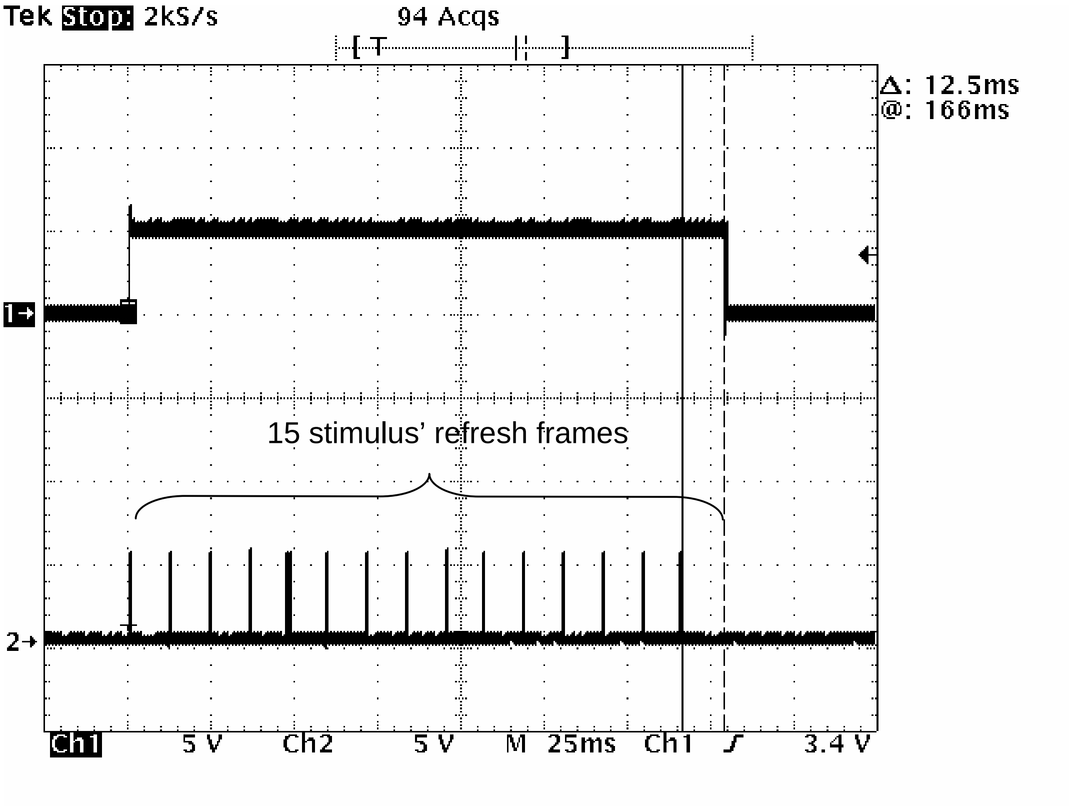

Figure A2. Oscilloscope measurement of the solenoid light detection probe signal during a 15 frame stimulus presentation (bottom line) and the electronic signal transferred from the signal conditioning box to the data acquisition box.

In order to determine the origin of this discrepancy the oscilloscope data were studied further. This revealed that the stimuli were presented for 15 frames (Figure A2) but that the last frame lasted longer (13.25 ms, Figure A3) than the expected 11.76 ms. Further analysis of the auditing circuitry showed that after each frame refresh, the light detecting circuit kept a high signal for approximately 13.3 ms. This had no effect for the first 14 frames, since they were consecutive, but lengthened the last frame by 1.5 ms. Therefore, the discrepancy between predicted and measured stimulus presentation length is mostly accounted for by measuring circuit characteristics and probably some measurement error, in the order of 600 μs.

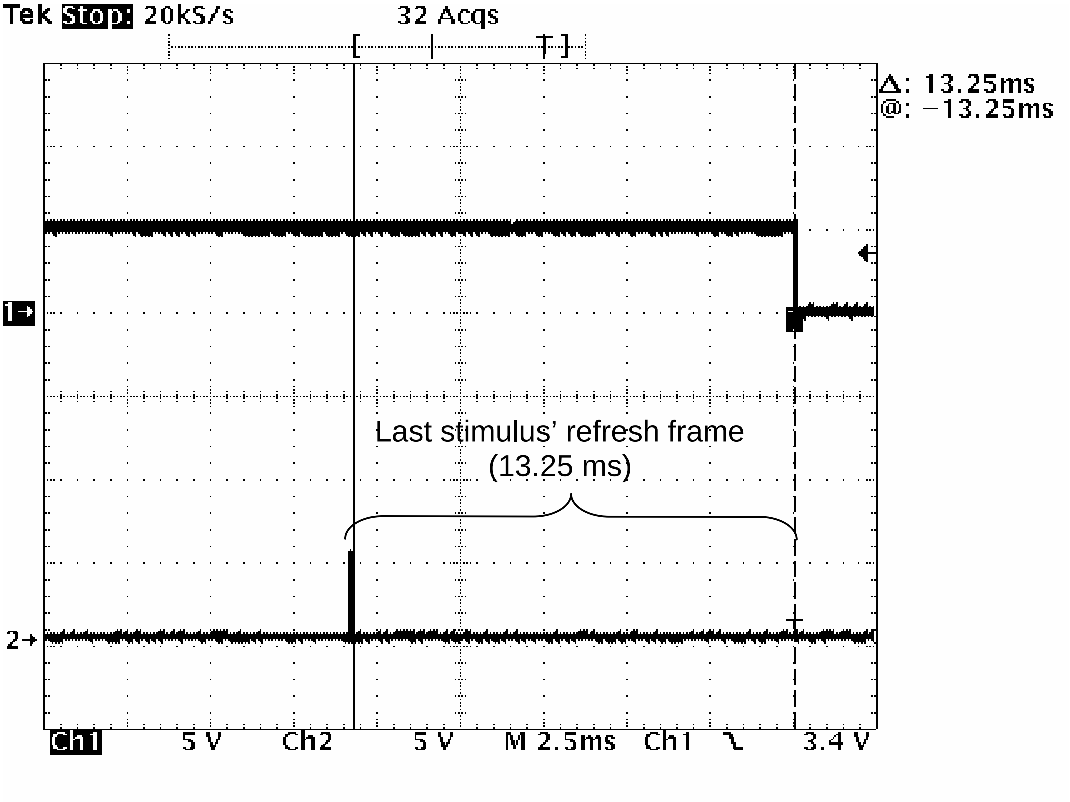

Figure A3. Oscilloscope measurement of the solenoid light detection probe's signal during the last frame of the stimulus presentation.

A.1.6 General Discussion

The aim of this audit was to determine whether Inquisit software (in conjunction with the selected hardware) was sufficiently accurate, that is, close to millisecond, in its stimulus presentation and response timing, to be deemed an appropriate tool to use in the types of experiment used in this thesis.

It was found that the software itself was highly accurate with measures differing from predictions by only a few hundreds of µs. The results also showed that the response times recorded by Inquisit were systematically overestimated (approx. 46ms). This was due to one major factor, the dynamics of the mouse internal buffer (41.56 ms). Although this factor increased the variability of the RT measure, it is unlikely to have a major impact on the type of studies conducted, since these studies involved large numbers of trials, and each trial condition would be similarly affected by this variability as they were presented in random order. Other variables affecting the RT measure were a fixed delay between the start of the trial and the appearance of the stimulus on-screen (1.37 ms), the fixed length of the data packet sent from the mouse to the computer (3.12 ms), and the delay in processing the mouse data in the experimental computer (0.71 ms), which were also very minor and would not influence the outcome of the studies conducted.

In conclusion, the combination of hardware and software chosen is adequate for the type of experiments that has bee conducted in this thesis.

APPENDIX B

B.1 Handedness Questionaire

The handedness questionnaire was computer-based and adapted from Provins and Cunliffe’s handedness questionnaire (1972) and The Edinburgh Inventory (Oldfield, 1971). The answers to questions printed in bold print were extracted to match those of Oldfield’s questionnaire from which a handedness index was computed.

1. **"With which hand do you write?"**
2. **"In which hand do you prefer to use a spoon when eating?"**
3. **"With which hand do you throw a ball?"**
4. **"In which hand do you prefer to hold the toothbrush when you are cleaning your teeth?"**
5. "In which hand do you prefer to hold a tennis, squash racquet?"
6. "If both hands were free, which hand would you use to put a key in a key hole?"
7. **"In which hand do you hold the box when striking a match?"**
8. **"When cutting paper, in which hand do you hold the scissors?"**
9. **"With which hand would you prefer to use a knife to sharpen a pencil?"**
10. "In which hand do you prefer to hold the pack when dealing cards?"
11. "In which hand do you prefer to hold the eraser to rub out a pencil mark?"
12. "Which hand do you use to 'pilot' a computer mouse"
13. "When pinning a notice on a notice board, which hand presses in the drawing pin?"
14. "With which hand do you prefer to turn on a tap?"
15. "When washing dishes, in which hand do you prefer to hold the dish?"
16. **"When pouring tea, in which hand do you prefer to hold the pot?"**
17. "With which hand do you use a comb?"
18. "With which hand do you adjust a window blind?"
19. "When buttering bread, which hand holds the bread?"
20. "With which hand do you hold the thread when threading a needle?"
21. "In which hand do you prefer to carry a suitcase?"
22. **"In which hand do you prefer to hold a jar when unscrewing the lid?"**
23. "With which hand do you put a plug into a power point?"
24. "With which hand do you hold a hammer?"
25. "In which hand would you carry a full glass of water?"
26. "In which hand would you hold an apple while peeling it?"
27. "Which hand do you prefer to remove an object from a high shelf?"

28."Which hand do you use to draw?"

29."If catching a ball with one hand, which hand would you use?"

30."With which hand do you hold the bowl\plank steady when using a hand rotary mixer or drill?"

31."When feeling material to determine the texture or thickness which hand would you use?"

APPENDIX C

C.1 Meta-Analytic Technique Applied to Single Subject Data

Meta-analytic techniques are usually used to compare the results of a number of studies which have researched a similar question but which might have differed in significant ways, particularly with regard to sample size, number of trials used, the age and sex of participants, and other variables that are deemed relevant to the question being answered.

The rationale behind meta-analysis is that like participants in a single experiment, means from different studies belong to a population of means that are assumed to be normally distributed. Based on this assumption, it is possible to test whether different studies come from a single population that shares the same mean or whether these studies are so different that they cannot belong to the same population. In other words it is possible to ask the question "are these studies homogenous?" and show one consistent result or "do they differ?" in important ways. If they are not homogenous it is also possible to test whether this heterogeneity can be accounted for by specific variables membership (e.g. sex, handedness, etc.).

When multiple trials have been collected for a number of participants, it is usual practice in psychological research to average all trial measures for each condition and each participant and to analyse these measures with t-tests or analyses of variance. When considering the meta-analytic example above, this is similar to comparing the means of differing studies without considering the fact that variability in their results might be due to significant differences in the population or the methodology used (e.g. number of trials, sample size, sex, age, etc.).

In individual studies, it is known that each participant has been tested on an identical number of trials because this is controlled by the design of the study. However, the variability in each participant's results may be due to either the sampling of a normally distributed population or to other factors that systematically vary between two or more populations or categories (e.g. control compared to clinical group). When there is no reason to believe that individual variability is due to factors other than random sampling, averaging measures over each condition is more efficient and practical. However, when there are reasons to believe that within participant variability is associated with specific variables, for instance when one control group is compared to a clinical group, taking within subject variability into account will lead to a more sensitive and statistically powerful test.

Meta-analysis, when applied to a sample of single participants, allows for the significance of differences in variability between subjects to be tested and to ask whether category differences exist beyond differences between means.

In Chapter 6, a measure of hemispheric transfer of a group of individuals with dyslexia was compared with controls matched for age, sex, and handedness. Because this measure required each participant to perform a large number of trials and because there are theoretical reasons to believe that response variability between the two groups should vary over and beyond normal variability due to sampling, the use of meta-analysis was appropriate.

C.1.1 Statistics

Measures on a number of trials (n) have been collected for K participants. The mean of the i^{th} participant is μ_i, for i =1, … , k. It may be assumed that the distribution of these measures is normally distributed for each participant with a mean μ_i and a standard error $\nu_i = \sigma_i/\sqrt{n_i}$.

When participants belong to the same group it is assumed that they share the same estimate of effect size which is a weighted average of m_i, the sample estimate of μ_i.

Where according to Hedges and Olkin (1985), the weight is:

$$w_i = 1/\nu_i^2$$

and the weighted average of m_i:

$$\overline{m} = \frac{\sum_{i=1}^{K} w_i m_i}{\sum_{i=1}^{K} w_i}$$

producing the statistic:

$$Q = \sum w_i (m_i - \overline{m})^2$$

where Q follows approximately a chi-square distribution with df = K-1. Consequently the null hypothesis of homogeneity may be rejected if Q is large enough.

Furthermore if the participants are divided into P categories (e.g. controls and dyslexic groups) with the subscript j, a similar test can be conducted to determine whether these categories differ significantly.

$$Q_B = \Sigma_i \Sigma_j w_{ij} (m_{+j} - m_{++})^2$$

With df = P-1

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