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Hemispheric interaction in simple reaction time as a function of handedness

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Abstract

Efficiency of hemispheric interactions in simple reaction time as a function of hand preference was investigated. Research suggests that left-handed individuals have more efficient hemispheric interactions. This is possibly due to their need to transfer information between hemispheres more frequently than right-handed individuals, a result of differing patterns of cerebral dominance explained by Annett's (1998) right shift theory.

Forty-eight right-handers and 48 non-right-handers, assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) completed the study. Mean reaction times for the Poffenberger paradigm (Poffenberger, 1912) were used to calculate the crossed-uncrossed-difference (CUD); a measure of inter-hemispheric transfer time. Analyses revealed a non-significant CUD, and no effect of hand preference. Possible methodological limitations and alternative explanations accounting for these findings are discussed.

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Compliance with ethical guidelines

This study was designed and conducted with adherence to the British Psychological Society's code of conduct, ethical principles and guidelines. It was granted ethical clearance by the School of Psychology's ethics committee within the University of Plymouth.

Informed consent was obtained from participants prior to the study. Each participant was provided with an information sheet outlining procedures of the study, their right to withdraw, and their anonymity. Written consent was obtained, which was witnessed by means of a countersignature by the investigator. No deception was necessary in this study. Participants were informed about the aims and objectives of the study and how their participation informed these aims in their debriefing.

No physical or psychological harm was involved in the study. Participants were not put at any greater risk from harm than they would normally be at in their everyday lives. Participants were able to withdraw if they felt uncomfortable with the procedures involved in the study. Participants had the right to withdraw from the study at any point, without having to give reason. They were informed that should they wish to do so, they would incur no penalty, receive full credit for their participation and any responses or data relating to them would be removed.

Participants were debriefed verbally and provided with a debrief sheet on completion of the study. Their experience of the study was discussed in order to identify any unforeseen negative effects. This outlined the nature and aims of the study, and rights regarding confidentiality. The information provided by participants was held confidentially, and anonymously, so that it was impossible to trace the information back to an individual participant.

The data reported in this study was collected by three researchers and pooled for analysis and use in three separate reports. Data for subjects 1-30 were collected by Helena Smith, data for subjects 31-66 were collected by Sarah Blunden, and data for subjects 67-96 were collected by the author.

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Introduction

The lateralisation of function of the brain means that interhemispheric interaction is required to transfer information between the two cerebral hemispheres and co-ordinate their activities. This transfer occurs primarily through the corpus collosum, the largest neural pathway in the brain. (Innocenti & Bressoud, 2003).

Poffenberger (1912) was the first to put forward a neuropsychological model of interhemispheric transfer (IT) (Marzi, 1999). The so-called Poffenberger paradigm was based on the findings of a series of Simple Reaction Time (SRT) experiments which involved subjects responding to lateralised light flashes with a unimanual key press by either the right or left hand (Marzi, 1999). Poffenberger (1912, as cited in Zaidel & Iacoboni, 2003) found that stimuli presented to the visual field on the side ipsilateral to the responding hand ('uncrossed' conditions) yielded shorter reaction times (RTs) than stimuli presented to the visual field on the side contralateral to the responding hand ('crossed' conditions). Poffenberger (1912, as cited in Zaidel & Iacoboni, 2003) offered a parsimonious anatomical explanation for these findings. He reasoned that faster reaction times observed in uncrossed conditions occurred because there was no need to transfer information from one hemisphere to the other. This is because the same hemisphere that initiates the motor response receives the visual stimulus (Marzi, 1999). It follows that reaction times in crossed conditions are slower because interhemispheric transfer *is* required, as the hemisphere that controls the motor response is contralateral to the one that received the visual stimulus (Zaidel and Iacoboni, 2003). The longer RT in the crossed condition can be accounted for by the interhemispheric transfer via the corpus collosum involving more synapses than the intrahemispheric pathway (Savazzi, Fabri, Rubboli, Paggi, Tassinari & Marzi, 2007).

The need for interhemispheric transfer can be explained by the representation of visual and motor information in the brain. At the juncture of the optic chiasm in the visual pathway from the eye to the brain, the axons of the ganglion cells completely cross forming 2 optic tracts (Hellige, 1993). The result of which is that all fibres from the left half of each retina run towards the right side of the brain, and the fibres from the right half of each retina run towards the left side of the brain. The result of this is that the left hemisphere looks at the right visual world, and the right hemisphere looks at the left visual world (Hellige, 1993). The primary motor cortex of each hemisphere controls voluntary movement primarily in the contralateral side of the body, with the extent of contralateral motor control increasing for movement of body parts further away from the centre of the trunk (Hellige, 1993). Therefore, in an uncrossed condition, the visual input is received by the same side that controls the motor response. In a crossed condition, transfer is required as opposite sides receive the visual input and control the motor response.

An estimated measure of interhemispheric transfer time (IHTT); namely, the crossed-uncrossed difference (CUD), is derived by subtracting reaction times for uncrossed conditions from crossed conditions and dividing this figure by two (Zaidel & Iacoboni, 2003). The CUD represents a behavioural estimate of callosal conduction time, which is still prominent today in its use as a tool in neuropsychological research (Marzi, 1999). The average

CUD in normal subjects ranges from 2-6ms across studies (Fendrich, Hutsler & Gazzaniga, 2004). A frequently cited meta-analysis by Marzi, Bissiachi and Nicoletti (1991, as cited in Marzi, 1999) found a range of 1-10ms. The CUD is thought to be relatively reliable across reaction times, in that it does not vary as a function of speed of reaction time (Iacoboni & Zaidel, 2000, as cited in Tettamanti, Paulesu, Scifo, Maravita, Fazio, Perani & Marzi, 2002). The CUD is, as a rule, a positive value, as the interhemispheric transfer required in crossed conditions is time-consuming (Derakhshan, 2006). Nonetheless, negative CUDs have been observed.

The reason for the negative CUD is poorly understood. However, Derakshan (2006) proposed that the negative CUD results from cases in which a subject's neural handedness (the side opposite to the major hemisphere) does not correspond with their behavioural handedness (professed preference). This is assumed to occur in a considerable proportion of people (Derakhshan, 2006). In most individuals, behavioural and neural handedness are congruent, in that their dominant hemisphere is contralateral to the preferred hand (Hellige, 1993, Annett, 2002). In neural right-handers, the direction of motor signals is from the left hemisphere to the right. In contrast, this direction is reversed in neural left-handers (Derakhshan, 2006). Twenty percent of people exhibit behavioural handedness that is opposite to their neural handedness (Derakhshan, 2006). In terms of the CUD, this means that individuals with a negative CUD are those whose neural and behavioural handedness are incongruent.

Support for the role of the corpus collosum in IT, and the CUD as a measure of IT, is evidenced by studies of split-brain patients. Interhemispheric transfer is still possible in such patients, and assumed to be effected by sub-cortical pathways (Savazzi et al., 2007). However, CUDs are markedly longer in split-brain patients. For example, CUDs of patients with callosal agenesis range from 13 - 52 ms and from 20 - 96 ms for patients with total collosotomy (Lassonde, Sauerwein, & Lepore, 2003, as cited in Savazzi et al., 2007). The conclusion that can be drawn from this evidence is two-fold; firstly transfer is much slower in the absence of the corpus collosum, highlighting its role in effective IT. Secondly, the duration of CUDs correspond with the extent of damage to the corpus collosum, demonstrating its validity as a measure of IT. Further corroborating evidence that IT occurs through the corpus collosum comes from the use of functional magnetic resonance imaging (fMRI) techniques. Iacoboni and Zaidel (2004) Event-related fMRI was employed to investigate the relationship between the CUD and brain activity (signal intensity changes). It was found that crossed responses generated more activation than uncrossed responses in prefrontal, dorsal premotor, and the right superior parietal cortex. Furthermore, the CUD was strongly correlated with activation in the right parietal area (Iacoboni & Zaidel, 2004). The results implicated the superior parietal cortex in visuo-motor integration required by the Poffenberger paradigm. Manipulations of motor parameters have been shown to affect the CUD (Iacoboni and Zaidel, 2004). This suggests that the type of information transferred through the corpus collosum is best described as a 'motor intention' (Iacoboni & Zaidel, 2004, p424).

In view of the primarily contralateral control of voluntary movements, especially in distal extremities such as fingers, hand preference denotes that that one hemisphere's hand control is either better than or preferred to the

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other (Hellige, 1993). Handedness can be defined through either preference or performance measures (Brown, Roy, Rohr, Snider & Bryden, 2004). Hand preference can be determined according to the hand preferred for a salient action, the most common of which being writing hand (Annett, 1992). Writing hand is the preferred method laypersons use to classify handedness. However, preference is predominantly measured in empirical research through questionnaires such as the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971) that comprise closed questions about hand preference for a *number* of unimanual tasks (Cavill, 2003). Preference measures are more readily applied than performance measures due to the ease of assessment by administration of questionnaires, but are subject to biases (Annett, 2002). Performance measures on the other hand provide a more objective measure of handedness, as hand skill can be directly observed (Brown et al., 2004).

A number of tests are used in research to assess hand skill, or performance such as the peg moving task (Annett, 1970 as cited in Annett, 2002) and finger tapping (Brown et al., 2004). Hand preference and performance measures are not necessarily linearly related (Brown et al., 2004), although some studies have demonstrated this (Peters & Durding, 1978, as cited in Annett, 2002). The disparity between preference and performance is exemplified by the distributions the two measures generate when plotted (Annett, 2002). Preference measures uniformly produce a 'J' shaped bimodal distribution, with a large peak at strong right hand preference (Annett, 1972, as cited in Annett, 2002). In contrast, performance measures yield a unimodal normal distribution curve, displaced slightly to the right of zero (Annett, 1985, as cited in Annett, 2002). The principal issue in the assessment of handedness is which type of measure- preference, performance, or a combination of the two- best defines handedness for the purposes of classifying samples into meaningful handedness groups (Annett, 2002). Clear definitions of handedness are important as they better facilitate the neuropsychological study of its correlates (Brown et al., 2004). Intuitively, when handedness is assessed in terms of preference, estimates of right and left handedness should be fairly consistent across studies. However, this is not the case. Indeed, the frequency of left-handedness ranged from 1 to 40% in a review by Hecaen and Ajuriaguerra (1964, as cited in Annett, 2002). This considerable variation is likely to hinder the creation of meaningful divisions of right and left-handers. Annett (2002) suggests that this may be because the concept of 'mixed' handedness is often overlooked. Mixed handed individuals prefer one hand for particular skilled actions, but the preferred hand differs between tasks (Annett, 2002). This implies that the lack of agreement between reported frequencies of left-handedness is due to the arbitrary classification of mixed handed subjects as left handed (Annett, 2002). Handedness is thus best thought of as a continuum ranging from strong left to strong right, inclusive of mixed handedness (Annett, 1998).

It is a general assumption in the literature that cerebral dominance (CD) and handedness are linked. Laterality of speech is the most widely referred to example of CD (Annett, 2002). It is broadly established that speech is lateralised to the left-cerebral hemisphere in right-handers (Shimodo, Takeda, Imai, Kaneko, & Kato, 2008). The left cerebral hemisphere was deemed dominant by neurologists based on the observation that in the majority of individuals it is the side that controls both speech and the preferred hand, the right (Annett, 2002). This advocates a theory that speech should be represented in the hemisphere opposite to the preferred hand. What follows from this 'opposite' hypothesis is that speech should be represented in the right hemisphere for left-handers, contralateral to the preferred hand. However, it has been found by Goodglass and Quadfasel (1954, as cited in Annett, 2002) that left and right CD are observed equally in left-handers; thus ruling out this hypothesis. If the hemisphere dominant for speech is independent of handedness, left CD should be as prevalent in left-handers as right-handers, but this is not the case (Annett, 2002). Another possibility is bilateral representation of speech, which has also been revealed in studies of left-handers. Rasmussen and Milner (1975, as cited in Annett, 2002) conducted a canonical study of speech laterality related to handedness. They found that 96% of right-handers had left CD, and the remainder had right CD. Left dominance was observed in 70% of left-handers, bi-laterality in 15% and right-dominance in 15%. This demonstrated that speech laterality cannot be reliably defined in either right or left-handers; there can be variation in both groups (Annett, 2002). Nonetheless, it does suggest that speech lateralisation is inconsistent in left-handers.

It seems an obvious progression from the observation of differences between right and left-handers in CD to the conclusion that CD and handedness are related, though the relationship between the two seems complex. Why are left-handers more likely to have right-sided or bilateral cerebral dominance than right-handers?

The right shift theory proposed by Annett (1972, as cited in Annett, 1998) accounts for the differences between patterns of cerebral dominance among right and left-handers whilst maintaining that the causes of the two asymmetries are *not* in fact, directly related. The right shift theory provides an account of the strong human tendency to develop speech in the left hemisphere. As described earlier, it is possible that mixed handed individuals are often classified arbitrarily as right or left handed. This may have led to difficulty in interpreting the variation in cerebral dominance among handedness groups (Annett, 1998). The right shift theory was founded on Annett's (1998) research into hand preference. As noted earlier, preference distributions usually take the form of a 'J' shaped curve, and performance distributions a normal 'bell shaped' curve. This difference could be accounted for when considering the thresholds used to divide mixed and consistent handedness groups. Annett (1998) discovered that the distribution of right, left and mixed handedness in animals produced a normal distribution centred around zero. He found an identical distribution in humans that differed in only one respect: it displayed a mean shift to the right of zero (Annett, 1998). The fact that the only difference between humans and animals is a shift to the right suggests that some additive factor is that is relevant to humans may be the cause of the right shift of hand preference. Annett (1998) proposed this was advantage for left hemisphere speech dominance; which was produced by the presence or absence of the right shift (RS) gene.

The RS gene could be present or absent. In individuals where it is absent, CD is likely to be determined by congenital chance factors (Annett, 1998). The premise that RS is 'for' typical CD was upheld by a number of important observations. Firstly, no other primate has speech. Secondly, the right shift (RS) gene is more effective in females than males in that females are more biased to dextrality than males, and less prone to speech disorders or dyslexia. The right sided or bilateral localisation of speech may result from the same accidental variation in the absence of the RS gene that induces left hemisphere dominance that affects handedness (Annett, 1998). The implication of the cause of the right shift for handedness being for left hemisphere advantage is that there is no direct relationship between hand and brain asymmetries. The causes of typical CD (RS) could be independent of the causes of handedness but could influence handedness by weighting the probabilities in favour of the right hand (Annett, 1998).

For left and mixed handed individuals, cerebral dominance, and thus handedness is likely to be determined by chance factors, due to the absence of the RS gene establishing normal CD (Annett, 1998). The reduced chance of normal CD may result in bi-hemispheric lateralisation (as discussed earlier), which necessitates increased hemispheric transfer. Cherbuin and Brinkman (2006) assessed hemispheric interaction in left-handed individuals using letter matching tasks within the Poffenberger paradigm. They showed that left-handers had faster and more efficient hemispheric interactions, compared to right-handers assessed in a previous study using identical measures (Cherbuin & Brinkman, 2006). This may be due to the increased practice of interhemispheric transfer in left-handed brains. Cherbuin and Brinkman (2006) point out that previous research in this area has been limited by their classification of handedness, in that some studies failed to consider the strength of hand preference but simply distinguished between direction of professed handedness; left or right. This may have obscured the extent of effects of handedness on efficiency of hemispheric interaction. The present study will overcome this problem by using the Edinburgh Handedness Inventory (Oldfield, 1971), a measure that allows degree of handedness to be measured along a continuum from strong left to strong right preference. Research has shown different patterns of hemispheric interaction in left and right handed samples (Cherbuin & Brinkman, 2006). It would be of value to assess these differences with a division that allows mixed handedness, Due to the limit of a small sample size however, left handed and mixed handed individuals were classified as 'non-right-handed', in accordance with Annett's (2002) suggestion that mixed handedness should only be classified in larger samples.

This study aimed to assess the efficiency of hemispheric interactions in non-right handed individuals compared with right handed individuals. Hand preference was classified using the EHI and groups were divided according to a criterion of 75. The CUD as generated by the Poffenberger paradigm was calculated as a measure of interhemispheric transfer time.

It was predicted that both right-handed and non-right-handed groups should perform better on uncrossed trials, (a field x hand interaction). In addition, the non-right-handed group were expected to perform better than the right-handed group on crossed conditions compared to uncrossed conditions (a field x hand x group interaction).

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Method

Participants

Thirty subjects completed this study. The sample comprised 13 males and 83 females between the ages of 18 and 44, with a mean age of 21 ± 5.56 years. Forty-eight were classified as right-handed and 48 were classified as non-right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971).[1] Subjects were drawn from the undergraduate psychology student population at the University of Plymouth, who participated to fulfil a course requirement. They were recruited using the University's online experiment management system.

Design

A mixed factorial design was used. The first independent variable was the visual field in which the stimulus was presented; which consisted of 2 levels; left (LVF) and right (RVF). The second independent variable was hand used to respond to stimuli by pressing the spacebar with the index finger. This consisted of two levels; right (RH) and left (LH).

The respective combinations of visual field and response hand produced 4 conditions, 2 crossed (visual stimulus and response hand on opposite sides) and 2 uncrossed (visual stimulus and response hand on the same side). The 2 crossed conditions were left response hand and right visual field (LH/LVF), and right response hand and left visual field (RH/LVF). The 2 uncrossed conditions were left response hand and left visual field (LH/LVF), and right response hand and right visual field (RH/RVF).

The third independent variable was hand preference, which consisted of two levels; right-handed or non-right-handed. Subjects were classified according to the Laterality Quotient (LQ), derived from scores on the 12-item version of the Oldfield (1971) Edinburgh Handedness Inventory (see appendix 2). The Laterality Quotient (LQ) was derived according to the formula [(100 x (R – L)/(R – L)], where R refers to the number of crosses placed in the right-hand preference column, and L refers to the number of crosses placed in the left hand preference column (see 'materials and apparatus' section for more details). Laterality Quotients had a possible range of -100 to +100.

The dependent variable was reaction time (RT) for each condition. Reaction time was operationally defined as the time elapsed in milliseconds (ms) from the end of the 500ms duration presentation of the stimulus to the spacebar being depressed on the keyboard. To discourage anticipatory responses, there was a delay of 500, 1000, 1500, or 2000ms, which followed the spacebar press that initiated each trial. This was determined randomly on each trial.

Materials and Apparatus

RT task.

E-Prime software (version 1.2) was used for stimulus presentation and response recording. Stimuli were presented on a monitor controlled by a Pentium IIII PC mounted 57cm from the participant's eyes. The RT task was

[1] Groups were divided according to a criterion of LQ= +75 for right handedness. See 'design' and 'materials and apparatus' sections for more detail.

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based on the Poffenberger paradigm (Poffenberger, 1912). The fixation screen comprised a black cross centrally aligned on a grey background. Instructions appeared at the bottom of the screen that instructed participants which index finger they should respond with, and to use this finger to both start the trial and respond to the stimulus. The target stimulus consisted of a white opaque square that subtended 2.4° of visual angle presented on a grey opaque background with inner edge at 5.15° eccentric to the fixation point. A total of 100 trials comprised a block. There were 2 blocks, one for each hand. The response hand was counterbalanced across participants. Reaction times were logged up to 2000ms. After this period the reaction time was reported as zero. There was a delay of 500, 1000, 1500, or 2000ms, which followed the spacebar press that initiated each trial. This was determined randomly on each trial. There were 50 trials per condition. An adjustable chin rest (Richmond Products, adjustable table model) was used.

The Edinburgh Handedness Inventory (EHI).

The 12 item version of the Edinburgh Handedness Inventory (Oldfield, 1971) (see appendix 2) was administered in word processed format. Ten items assessed hand preference for everyday tasks such as writing and using a spoon (see appendix 2). The remaining 2 items assessed eye and foot preference. Instructions describing how to fill in the questionnaire were printed at the top of the page. Responses took the following format: '++' indicated a strong preference, '+' indicated a mild preference, and one '+' in each column indicated an indifference to using either hand for the task. There were 2 columns to the right of the question items in which these responses could be entered, labelled 'LEFT' and 'RIGHT'.

Procedure

Informed consent was obtained prior to participation. Subjects carried out the experiment individually. They were seated in a comfortable position at a desk in front of a computer monitor mounted 57cm away from them. They were informed that they would fill out a written questionnaire assessing hand preference. The EHI (Oldfield, 1971) (see appendix 2) was then administered. Subjects were asked to read the instructions that appeared at the top of the questionnaire. They were then asked if they had any questions about the instructions. Any questions were answered. Participants then proceeded to provide written responses to the questionnaire in their own time.

Once participants had completed the questionnaire, they were informed that they would now complete a computer based reaction time task. Participants were asked to read the instructions that appeared on the computer screen (see 'general instruction screen', appendix 3). Subjects were asked to centre the keyboard as requested by the instructions, and told that they would need to use the spacebar to move between instruction screens. The key points of the experimental procedure were reiterated. Any remaining questions participants had were answered.

The experimental session began once it was clear that the participant understood what they had to do, and had no further questions. Subjects placed their head on the chin rest with their forehead touching the top metal bar. The height of the chin rest was adjusted to suit the participant if required. Subjects were told press the spacebar to begin the experiment when they were ready, and to focus their eyes on the central fixation cross on the screen

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when it appeared. There was no further verbal contact with the subject throughout the duration of the experiment until the task had ended, unless participants encountered problems during the experiment. A screen appeared following the first instruction screen (see general instruction screen, appendix 3) advising subjects of which response hand they would be using for the first block of trials. The fixation screen followed. The target stimulus appeared after a pseudorandom interval of either 500, 1000, 1500, or 2000ms from the spacebar press that initiated each trial. The stimulus was presented for 500ms randomly to the left or right of the fixation point. Subsequently, a feedback screen appeared indicating participants' response time. This sequence of screens was repeated for each trial. Following the first block of trials, another instruction screen (see example instruction screen, appendix 3) appeared advising subjects to respond to the next block of trials using the opposite response hand. Subjects were notified that the experiment was complete by a screen that appeared after the last (200th) trial.

Subjects were debriefed verbally and given a debrief sheet. The subject's identification number was written on their debrief sheet should they wish to have their data withdrawn at a later date. Participants were advised of this right and dismissed.

Results

Errors

A discrepancy was observed in one subject's responses to the EHI, whereby crosses were not placed exclusively in the right-hand or left-hand column. It is assumed that this subject did not understand the instructions for the EHI. It is expected that they may have interpreted the 2 columns as a scale between strong right hand and strong left hand preference, and made their responses according to estimates of how strong their preference was along this continuum. This data was included, as it was easy to decipher which hand the subject preferred.

In addition, 3 subjects' RT data were identified as anomalous due to long RTs. These data were excluded from all analyses. The total sample size after outliers had been removed was 93; 46 right-handed and 47 non-right-handed.

Reaction times

Mean RTs were calculated for each subject and for each of the 4 response hand – visual field conditions. Means and standard deviations for RTs for hand-visual field conditions for right-handed and non-right-handed groups are shown overleaf in Table 1.

The mean of the 2 crossed conditions (RH/LVF, LH/RVF) were subtracted from the mean of the two uncrossed conditions (RH/RVF, LH/LVF). This difference was then divided by 2 to obtain the CUD.

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Criterion for defining handedness groups
The sample was divided into two preference groups: right handed (LQ range of +76 - +100, N= 46) and non-right handed (LQ range –100-+75, N=47).[2] The criterion for this division was set at 75 according to consistency of right hand preference; in that left-handed individuals are often inconsistent in their hand preference for different tasks due to constraints of the so called right-handed world (Humphreys, 1951, as cited in Annett, 2002). Thus, a lower criterion was decided against as it may have artificially inflated the proportion of right-handers as a result of natural left-handers who have adapted to use their right hand, for tasks such as using scissors (item 4 on the EHI, see appendix 2).

Table 1.
Means and standard deviations for reaction times in milliseconds for hand-visual field conditions for right-handed and non-right-handed groups (right-handed: N=46, non-right-handed: N=47).

	Right handed			**Non-right handed**		
	Right hand	Left hand	Collapsed mean	Right hand	Left hand	Collapsed mean
Right visual hemifield	320.29 (35)	329.20 (49.68)	324.76 (42.34)	318.19 (42.95)	318.43 (40.15)	318.31 (41.55)
Left visual hemifield	314.97 (31.50)	334 (43.48)	324.49 (37.49)	315.39 (35.17)	323.73 (42.98)	319.56 (39.08)
Collapsed mean	317.63 (33.25)	331.60 (46.58)		316.79 (39.06)	321.08 (41.57)	

Note. Standard deviations are presented in parentheses

Table 1 shows that the non-right-handed group responded faster than the right-handed group across all conditions. Both groups responded faster in right hand response conditions. Contrary to predictions, both right-handed and non-right-handed groups reacted faster in crossed conditions (RH/LVF and LH/RVF) compared to uncrossed conditions. Variance in both groups is similar across all conditions.

[2] It has been noted that sample sizes of the 2 handedness groups are unequal. It was considered unnecessary to take steps to correct this marginal difference. However, tests for homogeneity of variance and normality are reported later, and any violations accounted for.

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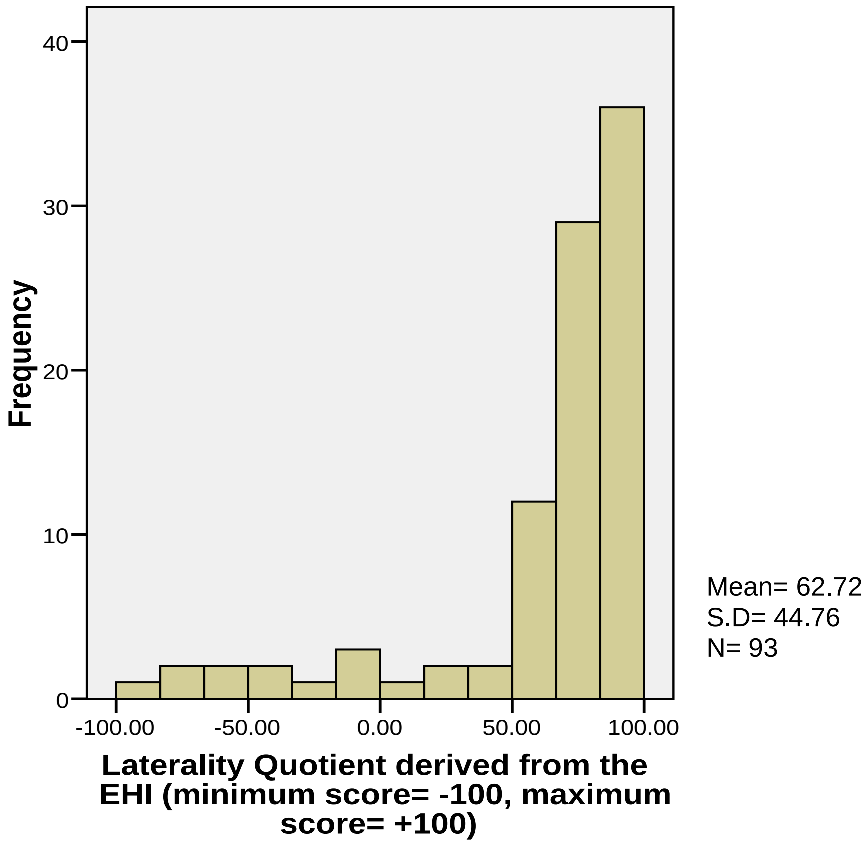

Figure 1. Frequency distribution of EHI Laterality Quotients for all subjects.

Note. Criterion to divide right handed and non-right handed groups set at LQ=75.

Figure 1 demonstrates the expected "J" shaped distribution of hand preference, shown by a high proportion of positive scores, peaking at an LQ of +100. However, the expected bimodal distribution usually evidenced by a peak at –100 is absent. The data therefore assumes a unimodal distribution.

Crossed-uncrossed difference

CUDs ranged from –25 to 17. There were a high proportion of negative CUDs. The mean CUD was –2.23 (S.D= 8.06). The mean CUD for the right-handed group was –2.13 (S.D= 8.53). The mean for the non-right-handed group was –2.34 (S.D= 7.66). These values are not within the range of CUDs reported in Marzi, Bissiacchi and Nicoletti's (1991, as cited in Marzi, 1999) meta-analysis, which was 1 to 10ms.

Main effects and interactions

Shapiro-Wilk's test of normality and Levene's test of homogeneity of variance were applied to reaction time data to test whether the respective assumptions for analysis of variance were met. Tests revealed that homogeneity of variance could be assumed in all four visual-field – response hand conditions. Normality could not be assumed. The violation of the normality assumption

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was accounted for by adopting a lower significance level (p<0.01) than would normally be used.

A three-way mixed factorial ANOVA was carried out on mean reaction times to test the significance of the CUD, and explore possible field x hand x group interactions. The within subjects factors were response hand (left and right) and visual field (left and right), and the between subjects factor was handedness group (non-right handed and right handed). Analysis revealed a main effect of response hand [$F(1,91)= 10.177$, $p<0.01$], and an interaction between response hand and visual field [$F(1,91)= 8.783$, $p<0.01$). There were no main effects of visual field or handedness group, nor any interactions between visual field and handedness group or response hand and handedness group (Fs<4). There were no reasons to analyse these relationships further.

It is necessary to note that the interaction between response hand and visual field was not in the direction expected by the CUD. This relationship is shown in figure 2, below.

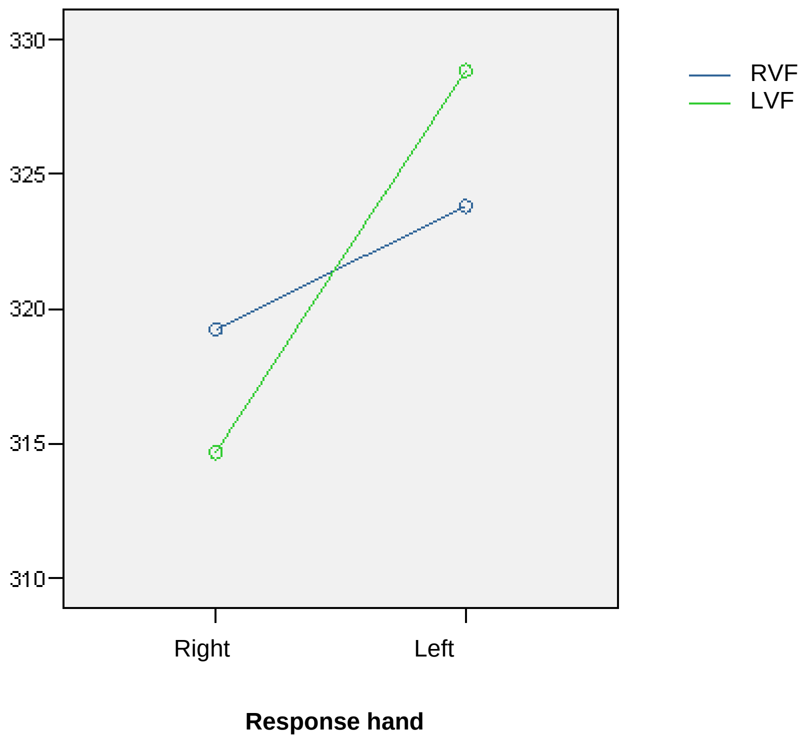

Figure 2.
Mean reaction times in milliseconds for the Poffenberger paradigm for all subjects as a function of response hand and visual field.

Note. A PP plot was used for data presentation as this better represented the nature of the response hand x visual field interaction than a bar graph.

Figure 2 shows that the fastest reaction times were in the RH/LVF and RH/RVF conditions. This indicates that right hand responses were faster overall, regardless of visual field stimulated. This was supported by the main

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effect of response hand reported earlier. However, the fastest RT for right hand responses was yielded by the crossed (RH/LVF) rather than uncrossed (RH/RVF) condition, contrary to hypotheses. This effect can also be seen for left hand responses; in that the crossed (LH/RVF) condition yielded faster RT than the uncrossed condition (LH/LVF). It should be noted that crossed conditions (RH/LVF, LH/RVF) were not faster overall compared to uncrossed conditions (RH/RVF, LH/LVF).

In summary, it can be seen that the significant response hand x visual field interaction reported earlier was not in the direction expected; and was therefore not analysed further. Please refer to appendix 4 for all data and analyses output files.

Discussion

Crossed uncrossed difference

Contrary to hypotheses, results revealed an unusual reversed CUD evidenced by faster reaction times in crossed conditions. In addition, a high proportion of CUDs (62%) were negative. There were no differences in the CUD as a function of handedness group. Hypotheses were therefore not supported. Considering the CUD as generated by the Poffenberger paradigm has been well replicated (Marzi, 1999) the finding of a non-significant CUD is likely to be due to methodological limitations.

The observed CUD was not within the normal range reported by Marzi, Bissiachi and Nicolletti's (1991, as cited in Marzi, 1991) meta-analyses: 1-10ms, nor the range of 2-6ms, reported by Fendrich, Hutsler & Gazzaniga (2004). The largest CUD observed (25) is more indicative of CUD values from patients with colossal agenesis or total callostomy (Lassonde, Sauerwein, & Lepore, 2003, as cited in Savazzi et al, 2007). Normal subjects were used in this study, and this is therefore not a viable explanation of the large range of the CUD. The mean CUD (-2.23), however, is closer to the ranges reported above. The wide range of CUDs may therefore possibly be attributed to random variation.

The surprising reversal effect observed in the CUD could be a result of anticipatory responses, to some extent. This was partly controlled by the pseudo random intervals of 500, 1000, 1500, or 2000ms between the initiation of the trial via a spacebar press and the presentation of the target stimulus. However, it is possible that subjects may have tried to decipher some kind of pattern in the side the stimulus was presented on, causing them to anticipate the side the stimulus were to appear on next, meaning their fixation is focused away from the cross. However, this effect is only conjectured. The incorporation of catch trials where no stimulus appears, may further control against anticipatory responses, and enable errors to be monitored more closely.

Negative CUD

A prominent finding is the high proportion of negative CUDs observed in the sample (how much percent). The mean CUD across groups was –2.23. This is not in line with previous research that suggests the CUD is generally positive (Derakhshan, 2006). The reason for the positive value of the CUD is that RTs generated by the crossed conditions are longer, as they necessitate

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interhemispheric transfer via the corpus collosum involving more synapses than the intrahemispheric pathway (Savazzi, 2007). The CUD is derived by subtracting reaction times for longer uncrossed RTs from shorter crossed RTs, which produces a positive value.

Research addressing the existence of the negative CUD is lacking, and the concept remains obscure. Derakhshan (2006) has conducted the only research to the experimenter's knowledge into neurological foundations of the negative CUD. Derakshan (2006) proposed that the negative CUD results from cases in which a subject's neural handedness (the side opposite to the major hemisphere) does not correspond with their behavioural handedness (professed preference). This is assumed to occur in a considerable proportion of people (Derakhshan, 2006). In most individuals, behavioural and neural handedness are congruent in that the dominant hemisphere is contralateral to the preferred hand (Hellige, 1993, Annett, 2002). The reaction time of the neurally dominant side of the body is shorter than that of the opposite side by an interval equal to the interhemispheric transfer time. Thus, 1 in 5 people exhibit behavioural handedness that is opposite to their neural handedness-cerebral dominance (Derakhshan, 2006). This figure of 20% is much lower, however, than that observed in this sample (62%). This therefore suggests that Derakhshan's (2006) explanation regarding incongruent neural and behavioural handedness cannot provide a complete account for the high proportion of subjects with negative CUD.

More research is needed as to the nature of the negative CUD to uncover its implications in terms of interhemispheric connectivity. Despite the well-established validity of measures such as the Poffenberger paradigm, such measures would benefit from the use of fMRI and evoked potential (EP) techniques concurrent with behavioural measures, to provide supporting evidence of the neurological underpinnings of the CUD. This would be especially advantageous in the case of the negative CUD.

Criterion for defining handedness groups

The EHI produced a 'J' shaped preference distribution as expected. This was in line with previous research, and facilitated division of groups. However, the distribution did not demonstrate bimodality. The lack of strong left-handers in the sample meant that the expected mode at strong left-handedness was not observed. This may be overcome by increasing sample size.

A main effect of hand was observed in RTs; right hand responses were faster in all subjects. This may have been a result of the chosen criterion for division of hand preference. The criterion was set at 75 for right-handedness. It is possible that the small sample size meant natural right-handers with some tendency to mixed handedness were classified as non-right-handed. In addition, as can be seen in the lack of bimodality in figure 1, there was only one strong left-hander (LQ= –100) in the sample. It is possible that hemispheric interactions are only markedly different in strong left-handers, which were only marginally represented in the study. The high criterion for right-handedness coupled with the few consistent left-handers in the sample may account for the absent effect of group on the CUD. The obvious solution is to run the experiment on a larger sample, with the aim of sampling more left-handers. However, this would not overcome the limitations associated with preference measures. A co-ordination of measures of preference and

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performance would better facilitate accurate and meaningful classification of hand preference groups (Corey, Hurley & Foundas, 2001).

Conclusions

The findings for the present study did not support any of the hypotheses originally set out. An unexpected reversal of the CUD was observed, whereby subjects responded faster to crossed conditions as opposed to uncrossed conditions. It is doubtful that this constitutes evidence to counter the validity of robustness of the CUD as a measure of interhemispheric transfer. Methodological limitations are considered. However, these must be taken as speculation, as the effect may also be closely related to the finding of a mean negative CUD. Derakhshan's (2006) explanation of the CUD is palpable, yet this may not account for the high proportion of subjects in the present study producing negative CUD, as the incongruity of neural and professed handedness only occurs in a minority of individuals (Derakhshan, 2006).

Uncovering the mystery surrounding the negative CUD is an important avenue for future research. An improved understanding of the neurological underpinnings of the phenomenon is fundamental to establishing why it occurs, and how these findings can inform understanding of interhemispheric transfer in general.

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Appendices

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