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Handedness: Does it affect interhemispheric transfer time?

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Abstract

Left- handed people have different patterns of cerebral dominance to the rest of the population, as explained by Annett's (1996) right shift theory. Left handers are considered to have bilateral functionality unlike right handers who have left cerebral dominance, which is believed to lead to faster interhemispheric transmission time in left- handers. The current research examined the effect of handedness on interhemispheric transfer time. The study was conducted online using fifty-one left and fifty-one right handers classified by laterality quotients obtained from Oldfield's (1971) 12 item Edinburgh Handedness Inventory. The crossed uncrossed difference was calculated using mean reaction times yielded from the task based on Poffenberger's (1912) paradigm. The laterality quotients produced a "J" shaped distribution curve. Results demonstrated that mean reaction times for left handers were faster than right handers in both the uncrossed and crossed state of the four visual field x hand conditions. The crossed uncrossed difference was 1 millisecond faster for right handers suggesting faster right hemisphere to left hemisphere transfer. A mixed ANOVA confirmed interaction between visual field and responding hand and handedness and responding hand, affirming the validity of the study. This was however, not observed with handedness and visual field. An explanation for this may be due to the handedness measure used and this is discussed in detail in this paper.

Keywords: Interhemispheric Transfer Time, Edinburgh Handedness Inventory, Right Shift theory, handedness, left handers, right handers, cerebral asymmetry, Crossed Uncrossed difference, reaction times

Introduction

Interhemispheric transfer

Interhemispheric transfer (IHT) refers to the communication between the two brain hemispheres mediated by the corpus callosum (CC) (Van der Knaap & Van der Ham, 2011). The fibres in the CC appear to have variable thickness and thicker myelinated fibres communicate faster than smaller fibres (Cherbuin, 2005). Those with larger CC have a better right hand (RH) / right visual field (RVF) performance possibly due to suppression of right hemisphere by the left and those with smaller CC have better left hand (LH) and left visual field (LVF) performance due to lack of inhibition of the right hemisphere by the left (Clarke, 1994).

Interhemispheric Transfer Time (IHTT) and methods of estimation

Crossed Uncrossed Difference

Poffenberger (1912, as cited in (Marzi,1999) created a behavioural paradigm called the Poffenberger's paradigm (PP) with the intent of gauging interhemispheric transmission time (IHTT) and proposed that the crossed uncrossed difference (CUD) is an indicator of IHTT. Stimuli were presented to the left or right visual field for a few milliseconds (ms) and participants were required to respond with either their left or the right hand when the stimulus appeared; this was measured as reaction time (RT). The RT difference between the crossed / contralateral and uncrossed/ ipsilateral conditions (crossed condition RT minus uncrossed condition RT) (termed CUD) was used as a surrogate marker for IHTT. RT is quicker when the stimulated visual field and motor response are controlled by the same hemisphere (uncrossed condition). The delay in the crossed condition due to motor control and visual fields being controlled by opposite hemispheres, is attributed to time required to transfer information to the other hemisphere (Zaidel & Iacaboni, 2003) via the CC, involving more synapses than the intra-hemispheric passage (Savazzi et al., 2007). Given that IHTT in the crossed condition takes longer, the CUD is expectedly positive, but this is not always true due to disparity between neural (actual) and behavioural (self-professed) handedness in 20% (Derakhshan, 2006).

Event Related Potentials

Event related potentials (ERPs) are electrical potentials that are time locked to specific processes, such as sensory or cognitive functions allowing brain wave patterns to be tracked and recorded in response to an event (Banich & Compton 2018). ERP can also be used to measure IHTT by estimating latency differences between ERPs from homologous sites (Brown, Bjerke & Galbraith, 1998); (Saron & Davidson, 1989) In order to do this, homologous sites over both brain hemispheres are recorded concurrently when a stimulus triggers brain activity in one hemisphere.

CUD vs ERP

The two means of measuring IHTT appear to be different. IHTT ranged between 8 – 19 ms using ERP (Saron & Davidson, 1989; Whitford et al., 2011) but when using the CUD method this ranged from 1-10 ms (Marzi, Bisiacchi & Nicoletti 1991; Fendrich, Hutsler & Gazzaniga, 2004) and even 1 – 28.5 ms (Bashore, 1981). ERP has been suggested as the more valid measure of IHTT (Saron & Davidson, 1989), yielding consistent results in the anatomically expected direction compared to CUD measures. It appears that the two methods may measure two different processes leading to the different estimates. ERPs are shorter for recordings made centrally where motor cortex activations occur (Rugg, Lines & Milner, 1984) and yet when recordings are made over the occipital cortex using PP, ERPs are longer suggesting that CUD measures motor IHTT (Saron et al., 2003). Hence, IHTT according to Milner & Lines's hypothesis (Milner & Lines, 1982 as cited in Rugg, Lines & Milner, 1984) occurs at varying rates in different regions of the corpus callosum. In fact, (Saron et al., 2003) concluded that for crossed conditions there are 2 pathways: a faster central callosal pathway responsible for visuomotor routes and a slower posterior sensory visual route. This may have resulted in the disparity seen between ERP & CUD. However, both methods show that IHTT is faster with information flowing from right hemisphere to left hemisphere compared to left flowing to right (Brown et al., 1994; Marzi, Bisiacchi & Nicoletti, 1991; Barnett & Corballis, 2005).

Interhemispheric transfer and handedness

Neuroanatomical organisation in the CC appears to be different between left handers (LHs) and right handers (RHs) with diffusion tensor imaging showing more connectivity in LHs than RHs and larger callosal area (Westerhausen et al., 2004). Morphological studies have confirmed a larger CC in LHs than RHs hence, IHTT is expected to vary between RHs & LHs (Witelson, 1985; Witelson, 1989). Marzi, Bisiacchi & Nicoletti's (1991) meta-analysis of 16 studies confirmed the difference in CUD between RHs and LHs; the mean RT of the combinations showed the longest RT for RVF / LH. Averaging across the 16 studies they showed that the CUD was the largest suggesting faster right to left transfer than left to right. Yet, there was no mention of the use of a handedness measure- either preference or performance, to account for this independent variable and its effect on IHTT.

Faster CUD in LHs compared to RHs have been reported (Bernard & Seidler, 2008) but in this study the details of the Edinburgh Handedness Inventory (EHI) are not available and only had a small number of participants (n = 21 with 17 RHs). It was reported that when the absolute value of laterality quotient (LQ) and CUD are taken into consideration, there is no significant correlation. Two studies showed no difference between RHs & LHs (Banich & Belger, 1990; Hatta & Yoshizaki, 1996) and another showed advantage for RHs in letter matching task both within and across visual fields (VF) (Eviatar, Hellige & Zaidel 1997). Cherbuin & Brinkman, 2006a; 2006b) studied the effect of handedness using EHI, PP and a letter matching task. However, the proportion of LHs to RHs were small (RHs 4: LHs 1) with LH and RH data combined from two separate experiments. They reported greater efficacy in LHs compared to RHs when RT was considered but reduced efficacy when accuracy measures were considered, suggesting two different neural pathways. This disparity could also be due to direction of handedness which is less related to IHTT than the degree or magnitude of handedness (Cherbuin & Brinkman, 2006b).

Handedness

Definition and Incidence

Handedness refers to the way that individuals use one hand preferentially over the other during tasks that require agility and fine motor control (Christman, 2012, as cited in Ramachandran, 2012). Cross cultural studies estimate the incidence of right handedness to be around 90 per cent (Springer & Deutsch, 1998) - particularly when writing. In western cultures, such as in North Americans and Europeans this varies between 8 – 15%, whilst for non-western cultures this is estimated between 2- 8% for writing and eating control (Ramachandran, 2012). The relation between handedness and the distribution of function between the two hemispheres is complex. Right-handedness reflects left cerebral hemisphere control of language but

LHs are not mirror images of RHs, displaying more variable brain asymmetry of control (Ramachandran, 2012). Annett (1998; 2002) refers to individuals where the preferred hand for specific action changes for different tasks as mixed handed and suggests that these people are classified as LHs, leading to the differences in reported frequencies of LHs.

Right Shift theory of handedness
Whilst monogenic models for handedness have been proposed, this cannot account for the fact that there is a 0.09 chance of LH offspring from two RH parents, 0.19 from one LH, one RH parent and 0.26 for two left- handed parents (McManus & Bryden, 1992). Another model of handedness termed the "Right shift theory" (RS theory) suggests not a single gene for handedness but rather that a dominant gene (RS^{+}), for language lateralisation to the left hemisphere (Annett & Alexander 1996). The recessive form (RS^{-}) in LHs lacks a system bias to one side for language and handedness, with chance and the environment operating at random to determine the degree of lateralisation. The homozygous allele (RS^{++}) shifts it by two standard deviations (SD) to the right of neutrality, augmenting the chances of RH. The heterozygote (RS^{+-}) shifts it one SD from neutrality and the homozygous recessive allele (RS^{--}) is fixed round neutrality. This means RS+ can be inherited but it may not be expressed, as in LHs (Annett, 1998). Recently, this was proposed as a cerebral rather than manual bias so right handedness refers to left cerebral dominance (CD). LHs show more asymmetry in brain processing so some processes may be bi-hemispheric in LHs. Speech laterality is the best portrayal of CD with lateralisation to the left hemisphere as dominant for RHs (Annett, 2002). This implies the hemisphere contralateral to dominant hand should be responsible i.e., the right should control speech in LHs. Yet, Rasmussen & Milner's (1977) study of speech laterality and handedness showed while 96% of RHs had left CD, speech was lateralised to the left hemisphere for 70% of LHs, the right for 15% or 15% either hemisphere (bi-laterality), indicating the inconsistent nature of CD in LHs. Bi- hemispheric processes like speech are thought to lead to more frequent and stronger IHT (Annett, 1998). Thus, cerebral dominance and laterality appear to be different between RHs & LHs. Recent genetic linkage analyses indicate not a specific gene but rather an independent polygenic complex trait to account for handedness (Somers et al., 2015). Therefore, RS theory as well as more frequent bi-hemispheric processing in LHs with more frequent and stronger IHT, are a rationale for faster IHTT in LHs.

Measuring Handedness
Handedness can be assessed by using performance or preference measures (Brown et al., 2004) and occasionally, both.

Performance measures of handedness
Performance measures include the Annett pegboard and finger tapping (Brown et al., 2004) tasks. Performance measures produce unimodal distribution on a bell curve with slight right shift (Corey, Hurley & Foundas 2001), meaning there is no clear distinction between hand groups. They are more reliable as they are objective and do not rely on self – report. However, factors like confidence, gender, age and culture may affect the results (Oldfield, 1971). Secondly it is hard to choose a task that will predict performance scores properly as some do not accurately reflect handedness (Brown et al., 2004). Individual performance variables cannot distinguish between handedness groups with an overlap present (Corey, Hurley &

Foundas, 2001). Finally, different performance instruments tap on various areas of manual proficiency in the brain (Fleishman, 1972) in that finger tapping and pegboard tasks use different areas than grip strength (Corey, Hurley & Foundas, 2001).

Preference measures of handedness

Preference measures such as the EHI (Oldfield, 1971) list a series of tasks and subjects indicate the hand they would use to complete each task. They generate a 'J' shaped bimodal distribution curve (two separate groups) (Raczkowski, Kalat & Nebes, 1974). The disadvantage of preference measures is that they have reduced reliability as a person may not necessarily use the hand for a task that they claim to (Annett M, 1998). Raczkowski, Kalat & Nebes (1974) credit this to inaccurate memories or a 'halo effect'- a cognitive bias where an orthodox way of answering questions sways a subject's response to unknown items. It is also likely that people use different hands to meet diverse skills that various tasks demand (Annett, 1998). An advantage of preference over performance measures is that they form the basis upon which handedness groups can be allocated (Corey, Hurley & Foundas, 2001). They are also quick and easy to administer.

Summary of existing evidence

In summary the research evidence about the effect of handedness on IHTT remains contentious with two studies (Banich et.al., 1990; Hatta & Yooshizaki,1996) showing no difference and one showing advantage for RHs (Eviatar et al., 1997) and another showing an advantage for LH's (Cherbuin &. Brinkman, 2006a & 2000b). In some studies handedness has not been included, others have small sample size or unequal RHs and LHs. Therefore, this requires further exploration.

Aim of current research

This research aimed to overcome shortcomings of previous research by using a similar number of RHs & LHs. It examined the effect of handedness on IHTT, connecting Poffenberger's (1912) and Annett's (1998) RS theory. It was predicted that the CUD will demonstrate faster right to left hemisphere transmission i.e., RH/ LVF – RH / RVF is smaller than LH / RVF – LH / LVF and LHs will have more efficient IHTT than RHs due to bi-hemispheric processing.

Methodology

Apparatus and materials

Edinburgh Handedness Inventory

The choice of measuring handedness lay between use of a performance or preference measure. It is uncertain which measures (performance or preference) best determines handedness (Corey, Hurley & Foundas, 2001). Due to higher research efficiency of preference measures, being more practical and easier to administer (Annett, 1998), a preference measurement was chosen for this research. Secondly, preference measures can be applied efficiently and universally to participants of all backgrounds and abilities for comparison (Oldfield, 1971). The EHI with 12 items (see Appendix D) was used in this study to classify participants as left or right handers. This was chosen over the 22- item version due to the ambiguity of some items on the 22- item scale, for example use of a comb and rake. These tasks can be completed using either hand generally. The 12- item EHI appeared on the online software prior to the reaction time task along with instructions to fill it in (see

Appendix E**)**. Hand preference for ordinary day to day tasks, for example writing and using a toothbrush were assessed by ten of the twelve items, one of the other two items assessed foot preference while the last item assessed eye preference.

Reaction Time task

Although there are two methods of IHTT measurement and according to (Saron et al., 2003) “ERPs provide anatomically predicted IHTT estimates in keeping with predictions based on transcallosal fibre conduction times than behavioural estimates”, CUD was the preferred approach in this study due to the logistics of conducting an online study where conducting ERPs was virtually impossible. The RT task used to record participants’ responses to stimuli was a bespoke online software that was prewritten by the University of Plymouth tech office. The same principle for measuring RT as used in Poffenberger’s (1912) paradigm was used, although unlike other studies of CUD and IHTT, the timing accuracy could not be established due to the software being pre coded. However, between subjects’ differences of interconnectivity in the hemispheres was not a factor for this study. Throughout each trial, participants focused on a fixation mark that appeared centre screen. Following a brief delay of either 500, 750, 1000, 1250 or 1500ms, a dot appeared shortly to the right or the left of the fixation mark (see Appendix F**)**. The delay was randomised on each trial to avert anticipatory responses from participants from predicting trial patterns. Participants pressed the space bar using the index finger of the hand indicated in the instructions, as fast as possible when the dot appeared. Reaction times longer than 800ms were logged as a ‘time out’. Non-appearance of a dot was included as control trials where subjects were not meant to press the spacebar. There were two blocks consisting of 88 trials each, one for each hand and the order in which these blocks were presented was counterbalanced between participants, thus eliminating potential order effects.

Design

This is an experimental quantitative study of mixed factorial design, consisting of three independent variables. The first independent variable was hand preference determined by using the 12- item version of Oldfield’s (1971) EHI. The EHI was used to calculate a LQ, by means of the formula $[(100 \times (\sum R - \sum L) / (\sum R + \sum L)]$, where R and L represent the number placed in the right or left hand preference columns. The possible range for LQ spans from -100 to +100, representing pure left hander and pure right hander respectively. The second variable was visual field- either left (LVF) or right (RVF) to which the stimuli was presented. The third independent variable was the responding hand (either LH or RH) used by participants to respond to the stimuli. Responses were recorded by pressing the spacebar with the index finger. The four response patterns produced were as follows: two crossed (VF and responding hand controlled by contralateral hemispheres); LH / RVF as well as RH/ LVF and two uncrossed conditions: LH/ LVF and RH / RVF (stimulus and hand controlled by ipsilateral hemispheres). This study design incorporates both between – subjects (handedness) and within- subjects (VF and responding hand) variables which enable the differences between two or more groups of participants and individual subject’s differences to be studied (APA Dictionary of Psychology, 2020). The dependent variable was the RT, which was measured in milliseconds.

Participants
One hundred and eight participants consented to participate, although six were later removed from the sample (see results, data cleansing). Hence, 102 participants (14 male and 88 female), between the ages of 18 and 47, with mean age of 22.3 and median age of 20 made up the final sample. All subjects were drawn from a pool of first, second and final year Psychology undergraduates from the University of Plymouth, who participated for course credit. They were recruited via the university online study system. Participants were classified by handedness, indicated by LQ (51 LHs and 51 RHs), using a preference measure of handedness- the EHI (Oldfield, 1971).

Procedure
This study was conducted online due to the coronavirus pandemic. Subjects signed up via the Plymouth University psychology online pool and gained access to the link which was live from November 2020- February 2021 and they completed the study on a laptop using the link. They were informed of the study objectives, guaranteed anonymity and their right to withdraw from the research at any point throughout, or after the study- in this case, data would be destroyed. They were also informed that the study did not lead to mental and physical harm with safety / risks assessed by appropriate authorities under COSSH regulations. Subjects were encouraged to contact researchers at any time - both during and after the study, with any questions they had about the research. Informed consent was obtained after this.

All participants were asked to disclose their gender and age, to collect demographic data. They were then presented the EHI to fill in using the on screen instructions as a guide (see Appendix E). The RT task followed on from the EHI and a second screen displayed another set of instructions (see Appendix G). Once they understood these, they pressed the spacebar to begin the experiment, which began with a screen informing participants of which hand would be used for the first set of trials. For every trial, the stimulus appeared either to the left or right of the fixation cross, for 500ms, following a delay (see apparatus and materials- RT task). Once the first block of trials was completed, another instruction screen informed subjects that they could take a break if desired before proceeding to the second block of trials, using the other hand for responses. Following the final trial, subjects were told that the experiment was complete and a debrief was displayed on screen. Contact details were provided and subjects were reminded to contact researchers with any queries.

Results

Data Cleansing

Prior to data cleansing, 108 participants took part. Data for six participants were excluded before the final analysis for the following reasons: two were excluded as there was only data for the EHI and no RT task; one participant's EHI data was all 0 and another filled it in incorrectly, RT data of two subjects were inconclusive as most of their trials timed out. The final sample size for analysis was n= 102. RTs less than 100ms (33/ 9064 trials = 0.36% of full sample), as they were considered anticipatory responses. Incorrect and trials exceeding 800ms were also excluded, in keeping with previous research. Twelve participants completed the EHI twice but only had one data set for the RT data. This is explained by the browser being closed and restarting the study again or misinterpretation of the EHI instructions. Only one set of EHI data was included for each subject, where both the time of completion of RT and

EHI matched; if the attempt was incomplete there was no time of completion. Analysis was conducted on R studio.

Laterality Quotients

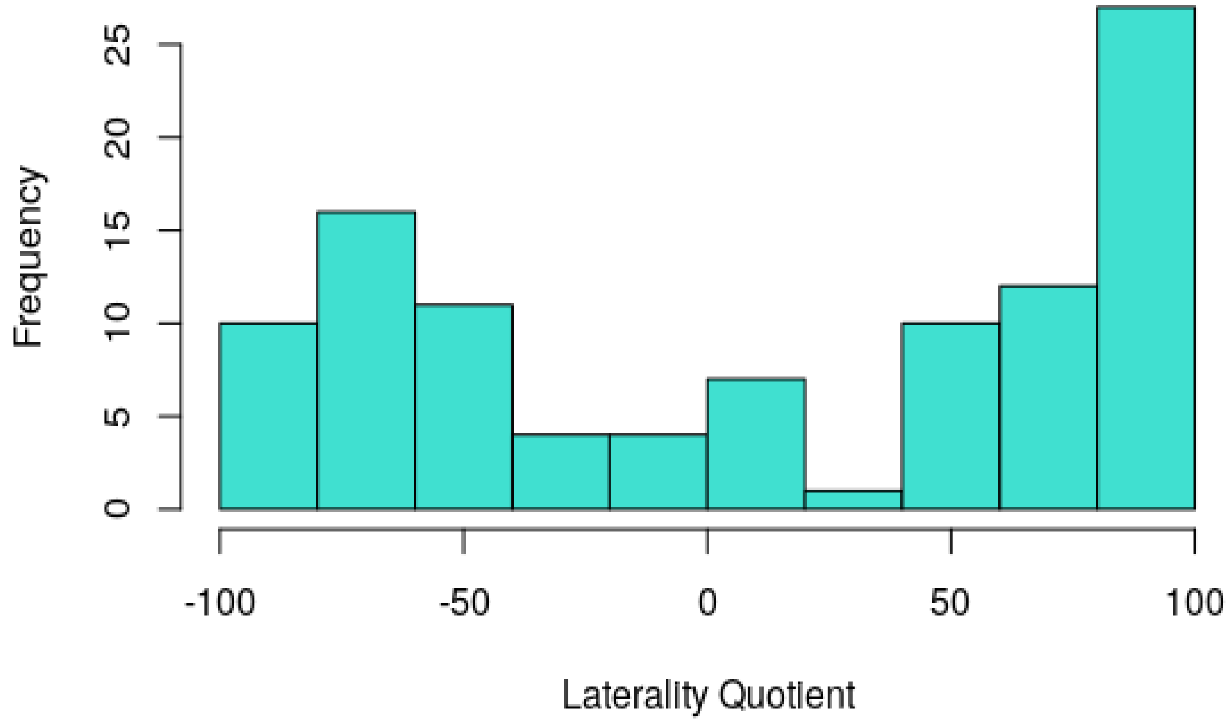

Figure 1: Histogram of Frequency distribution of all participants' laterality quotients from EHI measure of handedness, ranging from strong left handers at -100, to strong right handers at +100. (Ambidexterity set at +17 for this study).

There were 50LHs and 52RHs, based on the self- reported answers to the EHI however, when LQs were calculated, two participants: one LH and one RH both produced the same LQ score of +16.66. Therefore, as guided by the data, +17 was considered as the point of ambidexterity and this was the point of division for the handedness groups. Following this, two preference groups were formed based on this division and for both groups (n = 51). Being to the right of zero, it prevented false inflation of the proportion of right handers resulting from left handers who sometimes use their right hand. Left handers are often variable in hand preference for diverse tasks, a result of adaptation to using their right hand due to social conformity (Banich & Compton, 2018; Humphreys, 1951, as cited in (Annett, 2002). Similar to previous research, the distribution was bimodal (see Figure 1) with a 'J' curve, as expected with a preference measure. The peak for the RH group is at +100 and the peak for the LH group fell at -75.

Reaction times

The overall mean RT was faster in the LH (493ms) compared to RH (497 ms) without taking into consideration the visual field and handedness. A mean RT was calculated for each of the four conditions (hand x visual field), as has been reported previously (Table 1). A second set of mean RTs were calculated for each condition, grouped by handedness (Table 2).

Table 1: Mean RT in ms for each hand x visual field condition (Conditions are indicated in parentheses UC (Uncrossed) and C (Crossed)).

	Responding Hand	
	Left Hand	Right Hand
Left Visual Field	490.00 (UC)	500.00 (C)
Right visual Field	497.00 (C)	494.00 (UC)
Overall Mean	493.50	497.00

Table 2: Mean RT in ms for all hand x visual field conditions, grouped by handedness (Conditions are indicated in parentheses UC (Uncrossed) and C (Crossed)).

	Left Handers		Right Handers	
	Left Hand	Right Hand	Left Hand	Right Hand
Left Visual Field	488.00 (UC)	520.00 (C)	494.00 (UC)	488.00 (C)
Right Visual Field	496.00 (C)	514.00 (UC)	500.00 (C)	481.00 (UC)
Overall Mean	492.00	517.00	497.00	484.50

To summarise, the RTs in Table 2 show the following:
For both LHs (488 ms) & RHs (481 ms) the dominant hands were faster in the uncrossed condition than the crossed condition. For the non-dominant hand also in both LHs (514 ms) and RHs (494 ms) the RT was faster in the uncrossed condition. Overall, the RHs are faster than LHs when handedness is taken into account.
In the crossed condition, RHs participants using the dominant responding RH had faster RTs (RHs / RH / LVF = 488 ms) compared to LHs using their dominant LH (LHs / LH / RVF 496ms). The same is also true in the crossed condition for RHs using non dominant LH (RHs / LH / RVF 500 ms) compared to LHs with non-dominant RH (LHs / RH / LVF 520 ms). Table 1 suggests that LHs had a faster RT than RHs, when handedness was excluded but when handedness was also considered, (Table 2) LHs were slower than RHs. The faster RT data is for uncrossed conditions without handedness i.e., LH / LVF or RH / RVF or when considering handedness LHs / LH / LVF or RHs / RH / RVF.

Crossed Uncrossed difference
The mean RTs were used to calculate CUDs which ranged between -73.91 and 56.75ms (mean = 6.5ms) but 36% of individual CUD's were negative. The mean CUDs for responding LH and RH were 7 and 6 (decimal places rounded) respectively, falling within the previously reported CUD range (1- 10ms).

Observed effects
A three way mixed factorial ANOVA was used to analyse the RTs, confirming that the uncrossed route had faster RT than the crossed route and explore possible hand x VF x handedness interactions. This is interpreted as a test of validity of the CUD method (Cherbuin, 2005) and was reported in studies of CUD using PP (Marzi, Bisiacchi & Nicoletti, 1991; Cherbuin, 2005). The within - subjects' factors were VF (left and right) and response hand (left and right), while the between - subjects factor was handedness (left or right). Assumptions of variance were met using Levene's test where homogeneity of variance could be assumed in all four combinations (2 hand x 2 VF conditions). Normality assumptions ware also met, as tested using the Shapiro – Wilk test ($p > 0.05$). The ANOVA highlighted main interactions of handedness and response hand [$F(1, 88) = 20.23$, $p < 0.001$] (see figure 2.) as well as between responding hand and visual field [$F(1,89) = 18.42$, $p < 0.001$] (see figure 3). Post hoc analysis using a multiple comparisons Tukey HSD test indicated that the responding hand group differed significantly $p < 0.05$. The interaction plots confirm the validity of this data. Although differences were marginal, faster RTs occurred where dominant hand was the responding hand (see figure 2).

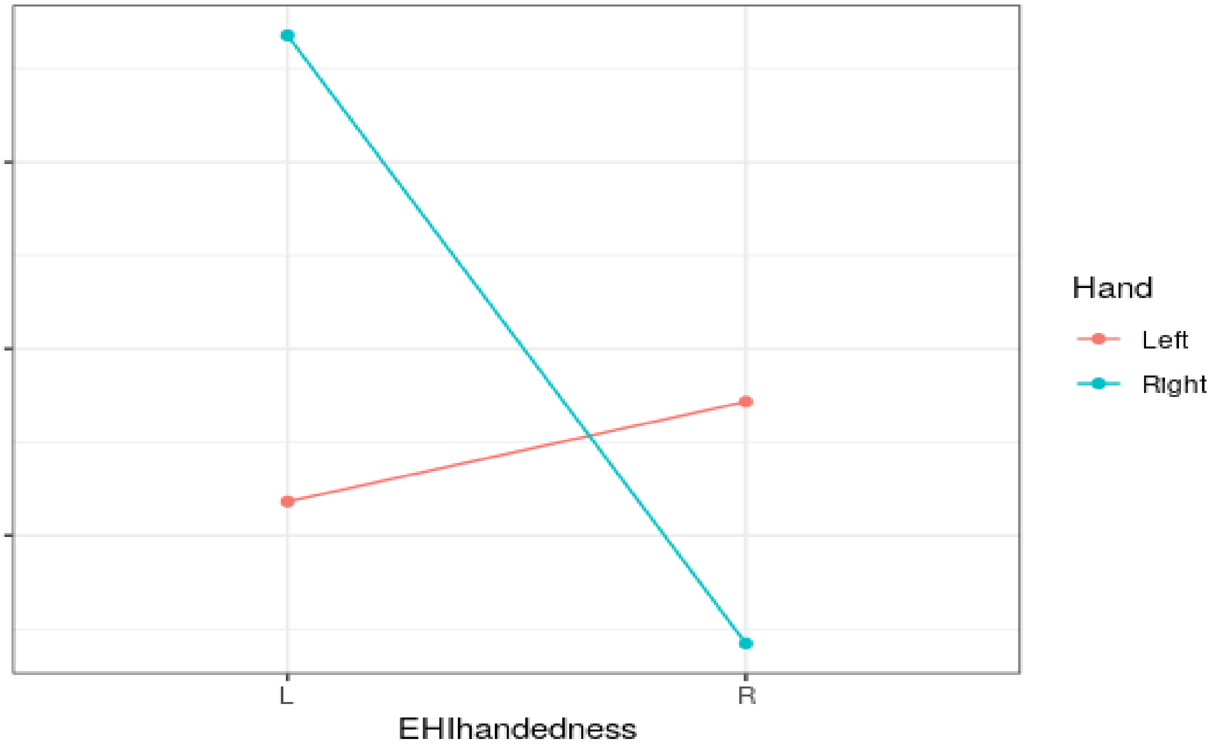

Figure 2: Interaction plot of overall mean RTs for all participants in ms as a function of handedness, determined using EHI and response hand

Figure 3 shows the interaction of VF and responding hand, where mean RTs were quicker when responding hand and VF were controlled by the same hemisphere (uncrossed condition). Differences in both are negligible, though slightly larger in LH. Given the three independent variables, a Student T test would be inappropriate in this situation and hence was not used. There was a main effect of handedness [$F(1,89) = 10.29$, $p < 0.05$]. There was no main effect of VF or response hand and also no interaction between VF and handedness, hence no further analysis of these relationships was conducted. Mean RTs of handedness and responding hand as well as responding hand and VF are shown in bar graphs (Figures 4 and 5).

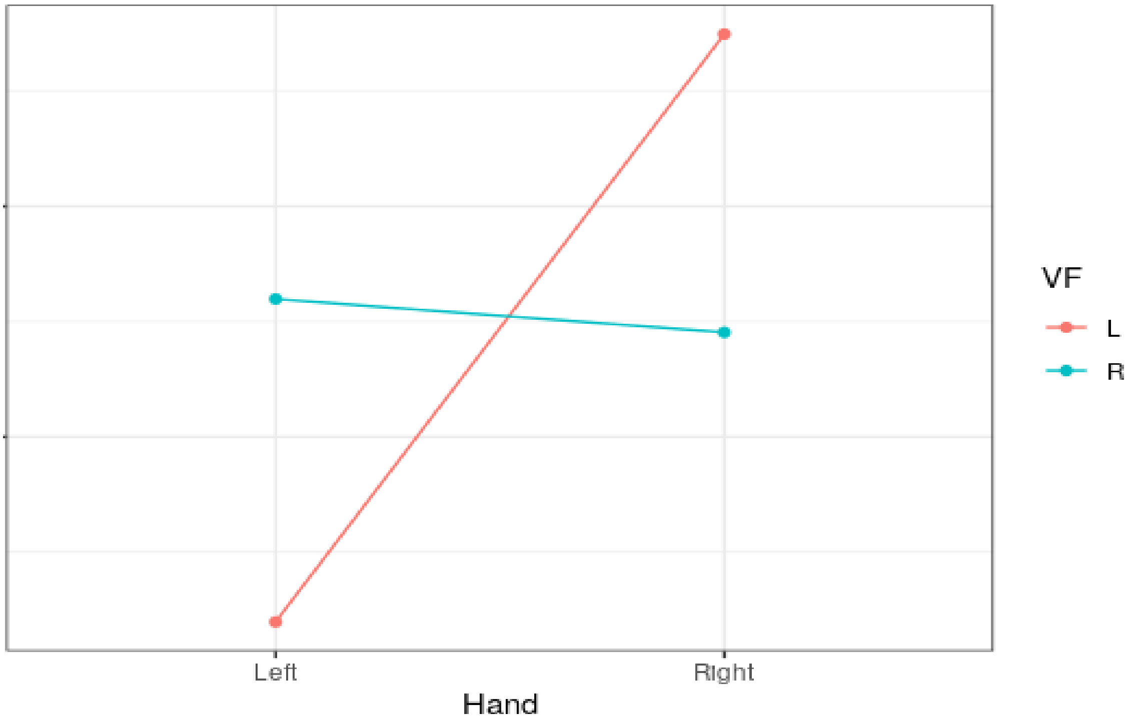

Figure 3: Interaction plot of mean RTs for all participants in ms as a function of responding hand and visual field

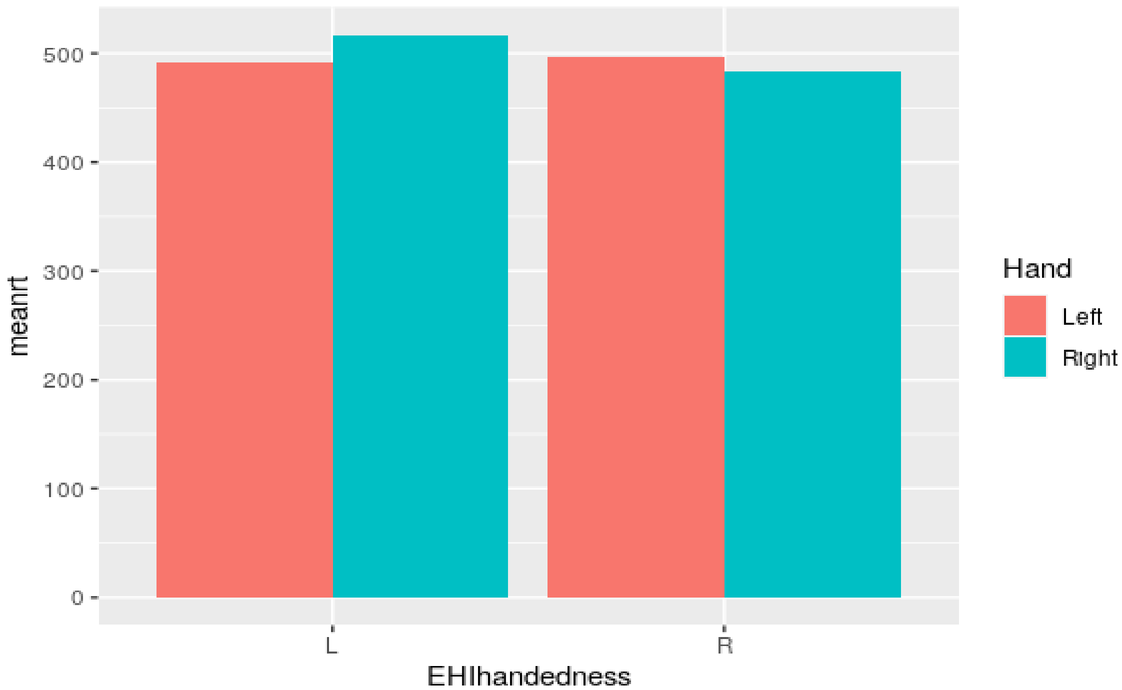

Figure 4: Bar graph representation of overall mean RTs in ms as a function of handedness and response hand

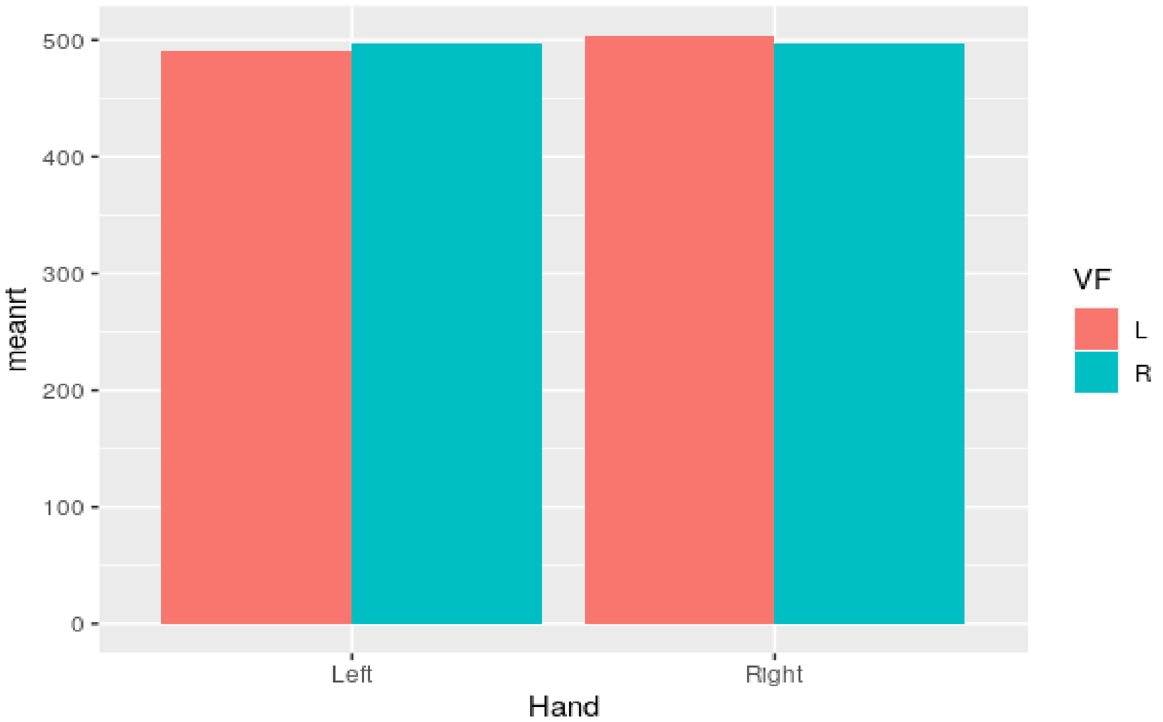

Figure 5: Bar graph representation of mean RTs of all subjects in ms as a function of responding hand and visual field

Discussion

The purpose of this research was to assess the effect of handedness on IHTT.

Reaction times

Without handedness considered, RT for LH was faster than RH (Table 1), supporting the expectation of LHs having more efficient transfer. However, when handedness was taken into account, RHs were faster than LHs, contrary to the expected prediction. Cherbuin & Brinkman (2006a; 2006b) used a letter matching task as a measure of IHT and Poffenberger's paradigm as a measure of IHTT to verify the effect of handedness on IHTT but in this study, a letter matching task was not used. Although the number of LHs and RHs were matched using LQs and the sample number was reasonable, when handedness was incorporated, RHs are faster than LHs. One explanation for this may relate to the handedness measure used which shifted some LHs to mixed handedness; this will be discussed later.

CUDs

The mean overall CUD of 6.5 was within the range reported by previous research reported of 1 – 10 / 28.5 ms (Marzi, Bisiacchi & Nicoletti., 1991; Fendrich, Hutsler & Gazzaniga, 2004; Bashore, 1981). The mean CUD of 6 for RH (RH / LVF [C] – RH / RVF [UC]) is only slightly faster than a mean CUD of 7 for LH (LH /RVF [C] – LH /LVF [UC]). Although the difference is small, it suggests asymmetric transfer through CC with faster right to left transfer and is in keeping with the existing evidence reported (Barnett & Corballis, 2005). The LH produces faster motor response (faster RT) in response to the visual stimulus in PP. This suggests that integration of visuomotor response rather than visual detection or motor response remains asymmetric (Marzi, Bisiacchi & Nicoletti., 1991) and there are 2 different callosal pathways in the crossed state as proposed by Saron (2003). Although CUD is expectedly positive due to longer RTs from crossing the CC in keeping with congruency of neural and behavioural handedness in most people (Annett, 2002), in this study 36% of the individual participant CUDs were negative in keeping with previous reports. Negative CUDs due to inconsistent behavioural (professed preference) and neural handedness has been reported in 20% (Derakhshan, 2006). Saron & Davidson (1989) reported 33% with CUDs in the opposite direction to anatomic prediction. Another small study reported negative CUDs in 44% of the participants (Davidson et al., 1990). Considering that the participants were all university students with similar cognitive abilities this is unlikely to explain the higher degree of negative CUDs due to a lack of understanding.

Saron et al. (2003) suggested that using RT methods to measure IHTT may not be valid due to the uncertain causes of negative CUDs. The use of PP in this study to measure RT may have led to this issue. PP is a behavioural measure based on observed behaviours and therefore has high validity and is also not affected by electrode positioning like ERP method (Cherbuin, 2005). It has been suggested that CUD measures are stable after 2000 trials in PP to be reliable as IHTT measure (Iacaboni & Zaidel, 2000) or for larger number of participants 600 – 800 would be adequate (Cherbuin, 2005). Considering that only 176 trials were done in this study it may have resulted in the significant number of negative CUDs vs due to stability of the paradigm. However, having higher number of trials of 600 – 800 would have risked issues with attention during the conduct of the study.

Handedness

The laterality quotients calculated from the EHI generated bimodal distribution and the ‘J’ shaped curve that is synonymous with preference measures, aiding division of handedness groups. Though the RT task itself is a performance measure of handedness, it was designed to measure CUDs using reaction times and not for accurately assessing handedness. A lack of interaction between handedness and RTs may be the result of the items in the EHI. Factor analysis of the items in the EHI have shown that at least 2 items “broom” and “opening box lid” to measure something else apart from handedness (Dragovic, 2004; McFarland & Anderson, 1980) and it has been suggested that these 2 items should be excluded as the EHI otherwise showed good test retest reliability and does measure handedness as a unidimensional measure (Dragovic, 2004) or different loadings should be used to score the items (McFarland & Anderson, 1980). The use of a broom also requires bimanual activity and is not an activity that university students would be performing regularly. Hence when responding to such an item that has never been performed, LHs may state this as either hand. This has been shown in a study comparing Annett’s handedness (AH) questionnaire (Annett, 1970) with an EHI which showed that for this item, 27% scored either hand on EHI and 11% scored LH, whilst for AH for this item 11% scored either hand and 21% scored LH. This implies that instructions in EHI are more likely to generate either hand when LH would have been the response and thus, to detect trace of left handedness, AH may be a preferable (Williams, 1991) measure of handedness. When the two items: broom and opening a lid were removed from the EHI data and the distribution of LQ’s checked, this shifted the distribution to strongly left or right handed in this study. However, as this was not predefined in the method before the study was conducted, further analysis of the effect of this change of distribution on RT & CUD was not carried out. Future research using both a performance & a preference measure would be beneficial. If the EHI is used it should have the 2 items removed as they do not contribute to the unidimensional measure of handedness that requires bimanual activity.

Strengths and limitations

The strength of the study is in the number of participants (n = 102) which is greater than all the studies in Marzi, Bisiacchi & Nicoletti's (1991) review and closely matches the study by Cherbuin & Brinkman, 2006a; 2006b) which together had 100 participants although were conducted at separate times. The current study had a disproportionate number of males to females although gender has not shown an effect (Cherbuin &. Brinkman, 2006b). In future research, it may be beneficial to recruit similar numbers to control for any gender effects. In this study there were equal number of RH & LH unlike other studies (Cherbuin & Brinkman, 2006a; 2006b) [80 RH, 20 LH], (Iacoboni & Zaidel, 2004) [5 RH] and (Bernard & Seidler, 2008) [7RH, 4LH]. The disproportionate numbers of LH and RH, makes direct comparison between groups difficult. In this study there was no control over culture/ race and it remains unknown whether this could have an impact due to suppression of left handed behaviours in some cultures (Banich & Compton, 2018) and indicates a partial lack of population validity of this sample. Further work is required to establish cross cultural validity to be applicable to the wider population.

All precautions were taken to ensure that the research was conducted reliably, and biases eliminated. As the study was conducted online, some conditions could not be controlled, which would have otherwise been possible if it was conducted in the laboratory. Participants could have been distracted during stimulus presentation, a fact that has been shown to have some effect on the Poffenberger RT task (Zaidel & Iacoboni, 2002a, as cited in Cherbuin, 2005). There was also no control of stimulus presentation since in the laboratory, stimuli would have been presented on the same type of computer mounted at a fixed height from participants' eyes. Additionally, the stimuli would be presented at the same visual angle for all participants, with each subject seated the same distance from the screen. The lack of control over these factors could also be an explanation for lack of interaction between handedness and VF condition and secondly, the observed pattern of CUDs. It is crucial for future studies to consider and control these variables.

Conclusions

This research study found that LHs (mean RT 490 ms) are faster than RHs (mean RT 494 ms) in the uncrossed state and in the crossed state as well (LH – 497ms; RH – 500 ms) but the CUD of 6ms is faster for RH (RH / LVF [C] – RH / RVF [UC] compared to 7 ms for LH (LH / RVF [C] – LH / LVF [UC] indicating faster right to left transfer and is in keeping with previous research. However, when handedness is taken into account, there was no interaction with the visual field, indicating that the handedness measure may have had an effect and this needs to be investigated more thoroughly in the future. To summarise, there is an effect of handedness on IHTT and although the results of this study are promising, further work is crucial to gain further insight into the precise neurological foundations and precise extent of this effect.

Future Research

Despite having a balanced number LH & RH and a large sample size, due to the limitations resulting from online as well as issues with EHI this may have impacted on the handedness distribution and likely on the RT & CUD. Future research should incorporate both a preference and a performance measure for measuring handedness at the same time. A preference measure should exclude items with bimanual activities such as the broom. If PP is used, the number of stimulations need to increase in order to be considered as a stable measure, else ERP should be used.

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Abbreviations
AH: Annett's handedness (from Annett, handedness questionnaire)
C: Crossed
CC: Corpus callosum
CD: Cerebral dominance
CUD: Crossed uncrossed difference
EHI: Edinburgh handedness inventory
ERP: Event related potentials
IHT: Interhemispheric Transfer
IHTT: Interhemispheric transfer time
LH: Left hand
LHs: Left Handers
LVF: Left Visual Field
MS: Milliseconds
PP: Poffenberger's paradigm
RH: Right hand
RHs: Right handers
RVF: Right Visual Field
RS Theory: Right Shift Theory
RT: Reaction Time
SD: Standard deviation
UC: Uncrossed
VF: Visual Field

References

Annett, M. (1970). A classification of hand preference by association analysis. *British journal of psychology*, *61*(3), 303-321.

Annett, M. (1998). Handedness and cerebral dominance: the right shift theory. *The Journal of Neuropsychiatry and Clinical Neurosciences*, *10*(4), 459-469.

Annett, M. (2002). *Handedness and brain asymmetry: The right shift theory*. Psychology Press.

Annett, M., & Alexander, M. P. (1996). Atypical cerebral dominance: Predictions and tests of the right shift theory. *Neuropsychologia*, *34*(12), 1215-1227.

Banich, M. T., & Compton, R. J. (2018). *Cognitive neuroscience*. Cambridge University Press.

Banich, M. T., Goering, S., Stolar, N., & Belger, A. (1990). Interhemispheric processing in left-and right-handers. *International Journal of Neuroscience*, *54*(3-4), 197-208.

Barnett, K. J., & Corballis, M. C. (2005). Speeded right-to-left information transfer: the result of speeded transmission in right-hemisphere axons? *Neuroscience letters*, *380* (1-2), 88-92.

Bashore, T. R. (1981). Vocal and manual reaction time estimates of interhemispheric transmission time. *Psychological Bulletin*, *89*(2), 352.

Bernard, J. A., & Seidler, R. D. (2008). Relationships between handedness and interhemispheric transfer time. *Brain Stimulation: Basic, Translational, and Clinical Research in Neuromodulation*, *1*(3), 266.

Brown, W. S., Larson, E. B., & Jeeves, M. A. (1994). Directional asymmetries in interhemispheric transmission time: evidence from visual evoked potentials. *Neuropsychologia*, *32*(4), 439-448.

Brown, S. G., Roy, E. A., Rohr, L. E., Snider, B. R., & Bryden, P. J. (2004). Preference and performance measures of handedness. *Brain and cognition*, *55*(2), 283-285.

Brown, W. S., Bjerke, M. D., & Galbraith, G. C. (1998). Interhemispheric transfer in normals and acallosals: Latency adjusted evoked potential averaging. *Cortex*, *34*(5), 677-692.

Cherbuin, N., & Brinkman, C. (2006a). Efficiency of callosal transfer and hemispheric interaction. *Neuropsychology*, *20*(2), 178.

Cherbuin, N., & Brinkman, C. (2006b). Hemispheric interactions are different in left-handed individuals. *Neuropsychology*, *20*(6), 700.

Cherbuin, N. (2005). Hemispheric interaction: when and why is yours better than mine?.

Clarke, J. M., & Zaidel, E. (1994). Anatomical-behavioral relationships: corpus callosum morphometry and hemispheric specialization. *Behavioural brain research*, *64*(1-2), 185-202.

Corey, D. M., Hurley, M. M., & Foundas, A. L. (2001). Right and left handedness defined: a multivariate approach using hand preference and hand performance measures. *Cognitive and Behavioral Neurology*, *14*(3), 144-152.

Davidson, R. J., Leslie, S. C., & Saron, C. (1990). Reaction time measures of interhemispheric transfer time in reading disabled and normal children. *Neuropsychologia*, *28*(5), 471-485.

Derakhshan, I. (2006). Crossed–uncrossed difference (CUD) in a new light: anatomy of the negative CUD in Poffenberger's paradigm. *Acta neurologica scandinavica*, *113*(3), 203-208.

Dragovic, M. (2004). Towards an improved measure of the Edinburgh Handedness Inventory: A one-factor congeneric measurement model using confirmatory factor analysis. *Laterality: Asymmetries of Body, Brain and Cognition*, *9*(4), 411-419.

Eviatar, Z., Hellige, J. B., & Zaidel, E. (1997). Individual differences in lateralization: Effects of gender and handedness. *Neuropsychology*, *11*(4), 562.

Fendrich, R., Hutsler, J. J., & Gazzaniga, M. S. (2004). Visual and tactile interhemispheric transfer compared with the method of Poffenberger. *Experimental Brain Research*, *158*(1), 67-74.

Fleishman, E. A. (1972). On the relation between abilities, learning, and human performance. *American Psychologist*, *27*(11), 1017.

Hatta, T., & Yoshizaki, K. (1996). Interhemispheric Cooperation of Left-and Righthanders in Mental Calculation Tasks. *Laterality: Asymmetries of Body, Brain and Cognition*, *1*(4), 299-314.

Iacoboni, M., & Zaidel, E. (2000). Crossed–uncrossed difference in simple reaction times to lateralized flashes: between-and within-subjects variability. *Neuropsychologia*, *38*(5), 535-541.

Iacoboni, M., & Zaidel, E. (2004). Interhemispheric visuo-motor integration in humans: the role of the superior parietal cortex. *Neuropsychologia*, *42*(4), 419-425.

Marzi, C. A., Bisiacchi, P., & Nicoletti, R. (1991). Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. *Neuropsychologia*, *29*(12), 1163-1177.

Marzi, C. A. (1999). The Poffenberger paradigm: a first, simple, behavioural tool to study interhemispheric transmission in humans. *Brain research bulletin*.

McFarland, K., & Anderson, J. (1980). Factor stability of the Edinburgh Handedness Inventory as a function of test-retest performance, age and sex. *British Journal of Psychology*, *71*(1), 135-142.

McManus, I. C., & Bryden, M. P. (1992). The genetics of handedness, cerebral dominance, and lateralization. *Handbook of neuropsychology*, *6*, 115-115.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*(1), 97-113.

Raczkowski, D., Kalat, J. W., & Nebes, R. (1974). Reliability and validity of some handedness questionnaire items. *Neuropsychologia*, *12*(1), 43-47.

Ramachandran, V. S. (2012). *Encyclopedia of human behavior*. Academic Press.

Rasmussen, T., & Milner, B. (1977). The role of early left-brain injury in determining lateralization of cerebral speech functions. *Annals of the New York Academy of Sciences*, *299*(1), 355-369.

RStudio Team (2020) Rstudio: Integrated Development Environment for R. Studio [Computer Software]: Retrieved from: http:// www.rstudio.com/.

Rugg, M. D., Lines, C. R., & Milner, A. D. (1984). Visual evoked potentials to lateralized visual stimuli and the measurement of interhemispheric transmission time. *Neuropsychologia*, *22*(2), 215-225.

Saron, C. D., & Davidson, R. J. (1989). Visual evoked potential measures of interhemispheric transfer time in humans. *Behavioral neuroscience*, *103*(5), 1115.

Saron, C. D., Foxe, J. J., Schroeder, C. E., & Vaughan Jr, H. G. (2003). Complexities of interhemispheric communication in sensorimotor tasks revealed by high-density event-related potential mapping.

Savazzi, S., Fabri, M., Rubboli, G., Paggi, A., Tassinari, C. A., & Marzi, C. A. (2007). Interhemispheric transfer following callosotomy in humans: role of the superior colliculus. *Neuropsychologia*, *45*(11), 2417-2427.

Somers, M., Ophoff, R. A., Aukes, M. F., Cantor, R. M., Boks, M. P., Dauwan, M., ... & Sommer, I. E. (2015). Linkage analysis in a Dutch population isolate shows no major gene for left-handedness or atypical language lateralization. *Journal of Neuroscience*, *35*(23), 8730-8736.

Springer, S., & Deutsch, G. (1998). Left brain, right brain: Perspectives from cognitive neuroscience.

van der Knaap, L. J., & van der Ham, I. J. (2011). How does the corpus callosum mediate interhemispheric transfer? A review. *Behavioural brain research*, *223*(1), 211-221.

Westerhausen, R., Kreuder, F., Sequeira, S. D. S., Walter, C., Woerner, W., Wittling, R. A., ... & Wittling, W. (2004). Effects of handedness and gender on macro- and microstructure of the corpus callosum and its subregions: a combined high-resolution and diffusion-tensor MRI study. *Cognitive brain research*, *21*(3), 418-426.

Whitford, T. J., Kubicki, M., Ghorashi, S., Schneiderman, J. S., Hawley, K. J., McCarley, R. W., ... & Spencer, K. M. (2011). Predicting inter-hemispheric transfer time from the diffusion properties of the corpus callosum in healthy individuals and schizophrenia patients: a combined ERP and DTI study. *Neuroimage*, *54*(3), 2318-2329.

Williams, S. M. (1991). Handedness inventories: Edinburgh versus Annett. *Neuropsychology*, *5*(1), 43.

Witelson, S. F. (1985). The brain connection: the corpus callosum is larger in left-handers. *Science*, *229*(4714), 665-668.

Witelson, S. F. (1989). Hand and sex differences in the isthmus and genu of the human corpus callosum: a postmortem morphological study. *Brain*, *112*(3), 799-835.

Zaidel, E., & Iacoboni, M. (2003). *The parallel brain: the cognitive neuroscience of the corpus callosum*. MIT press.

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