

# Attention and Interhemispheric Communication: Implications for Language Dominance

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**Abstract**—Dominance of the left hemisphere for language processing is a prominent feature of brain organisation. Whereas structural models clarify the functional asymmetry due to direct access to local language circuits, dynamic models propose functional states of intrahemispheric activation and interhemispheric inhibition that are coupled with attentional processes. Real word settings often require modulations of lateralised neural processing and further express individual heterogeneity. In this research, we tested left- and right-handers, and used a behavioural paradigm with presentation of lateralised cue-target pairs to the same or opposite visual field. We observed that handedness distinctly affected word processing in the left hemisphere following contralateral cueing. Moreover, left-hemispheric dominance strengthened for right-handers vs abolished for left-handers, influencing behavioural efficiency. In combination with eye dominance recordings, these data suggest that attentional biases guided the processing strategies of both groups and in turn their achievements. Therefore, hand and eye dominance are both essential factors with a functional role in directing the communication of visual information between both hemispheres. Overall, the findings underline the importance of interacting hand-eye control systems in contributing to interhemispheric patterns in the context of language processing. © 2022 The Author(s). Published by Elsevier Ltd on behalf of IBRO. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

**Key words:** laterality, hemispheric activation-inhibition, handedness, eye dominance, word comprehension.

## INTRODUCTION

The cerebral hemispheres have unique functional properties that shape the lateralisation patterns of many cognitive systems. Functional lateralisation relies, however, on both intrahemispheric and interhemispheric connections (Tzourio-Mazoyer, 2016). Whereas intrahemispheric circuits facilitate local activation within one hemisphere, interhemispheric circuits underlie communication between hemispheres that can involve cooperation or competition of information exchanges, including excitatory and inhibitory functions (Bloom and Hynd, 2005; van der Knaap and van der Ham, 2011). In particular, the *excitatory* model proposes that the corpus callosum assists cross-hemispheric sharing of information (Ringo et al., 1994), which decreases hemispheric lateralisation. Conversely, the *inhibitory* model suggests that the corpus callosum offers pathway by which one hemisphere can inhibit the contralateral side (Kinsbourne, 1974; Cook, 1986), which strengthens independent processing and increases hemispheric lateralisation. A central feature of the corpus callosum is its connection of homotopic areas

between hemispheres (Chao et al., 2009). Evolutionary and developmental influences likely supported an increased intrahemispheric and reduced interhemispheric connectivity, favouring patterns of asymmetry and thus lateralisation (Nowicka and Tacikowski, 2011).

As a key cognitive function, language generally relies more heavily on the left than right hemisphere. It is argued that the corpus callosum plays an essential role in establishing the functional asymmetry of language during development, especially by suppressing cortical activity in the competing hemisphere (Jeeves and Temple, 1987). This is further supported by data from individuals with agenesis of the corpus callosum who show an increased distribution of language processing across hemispheres in addition to right-hemispheric dominance (Hinkley et al., 2016). The left-sided superiority such as for the ability to recognise written words or to extract meaning has been demonstrated in neuroimaging work (Price, 2000; Josse and Tzourio-Mazoyer, 2004), and behavioural research that has revealed performance advantages when words are presented to the right as compared to left visual field (Hunter and Brysbaert, 2008; Serrien and O'Regan, 2022). Two influential models are proposed in the literature to explain these lateralised effects. Whereas structural models clarify that hemispheric asymmetries arise due to differences of dealing with language content, dynamic models propose that

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Abbreviations:  $L_{IRT}$ , laterality index for reaction time;  $M_{AGE}$ , mean age; SE, standard error; SLF, superior longitudinal fasciculus.

each hemisphere directs attention to its contralateral visual field and simultaneously inhibits the other hemisphere, guided by intra- and interhemispheric mechanisms (i.e., opponent-processor theory; [Kinsbourne, 1974](#)). Thus dynamic models consider that both hemispheres work together in a complementary manner ([Querné et al., 2000](#)). In case of a lateralised visual input, an activation imbalance is triggered in favour of the stimulated hemisphere. That is, presenting a stimulus to the right visual field produces an attentional shift to the opposite left hemisphere, regulated through reciprocal inhibition. Each hemisphere allocates this contralateral attentional bias, although its strength differs with a stronger bias from the left hemisphere than from the right hemisphere ([Kinsbourne et al., 1977](#); [Reuter-Lorenz et al., 1990](#)).

Neuroanatomical models preserve the concept of interhemispheric inhibition, and refer to two attentional systems that rely on fronto-parietal circuitry ([Corbetta and Shulman, 2011](#)). First, the bilateral-organised dorsal network regulates shifts of spatial attention in a top-down manner, albeit according to asymmetries that are distinct for parietal and frontal regions. In particular, parietal nodes are characterised by a contralateral bias of attention and interact through interhemispheric inhibition as opposed to frontal nodes that are driven by right-hemispheric dominance ([Duecker and Sack, 2015](#)). Second, the ventral network that is strongly right-hemispheric dominant is involved in detecting behaviourally relevant stimuli and can bias the dorsal network ([Corbetta and Shulman, 2011](#)). When active, both systems display distinct recruitment and switch patterns for flexible use of attention ([Bartolomeo and Seidel Malkinson, 2019](#); [Mengotti et al., 2020](#)).

A dynamic model of functional lateralisation further addresses individual variation due to differences and responsiveness of information processing mechanisms ([Hutchinson et al., 2003](#)). One such identified factor is handedness, which represents an expression of hemispheric asymmetry for hand movement control. At the population-level, there is a strong 90:10% prevalence of right vs left handedness in humans ([Coren and Porac, 1977](#)). Both groups show distinct functionality across hemispheres for language processing ([Tzourio et al., 1998](#); [Tussis et al., 2016](#)) with the handedness-language association specifying that more right- than left-handers have typical left-hemispheric lateralisation ([Pujol et al., 1999](#); [Knecht et al., 2000](#); [Flöel et al., 2005](#)). In particular, about 95% of right-handers and 75% of left-handers express left-sided dominance for language with the remaining minority demonstrating bilateral or right-hemispheric profiles ([Mazoyer et al., 2014](#); [Tzourio-Mazoyer et al., 2016](#); [Vingerhoets, 2019](#)). With respect to attention, evidence illustrates that the ventral system is predominantly right-hemispheric lateralised in right- as opposed to left-handers who show bilateral or left-hemispheric lateralisation ([Bareham et al., 2015](#)) whereas the dorsal network is more pronounced in the right hemisphere for left-handers ([Petit et al., 2015](#)). Together, these data express that handedness associates with modifications of language and attention pro-

cessing in the brain, suggesting differences for the integration of distributed processing and information exchange between hemispheres.

The aim of this research is to investigate modulations of the activation-inhibition states during language processing and its relation with handedness. Here, we use an experimental behavioural approach of lateralised cue-target pairs that are guided by attentional shifts and implemented within a divided visual field paradigm. In particular, we examine how word processing is affected by non-instructive cues presented in the same vs opposite visual field, i.e., when cues and targets are processed by a single hemisphere vs both hemispheres. Here, we use brief cue-target intervals that support automatic spread of activation ([Chiarello, 1985](#); [Koivisto, 1998](#); [Korsnes and Magnussen, 2007](#)). The hypothesis is that processing of cue-target pairs will be distinct in the same hemisphere (intrahemispheric) vs opposite hemispheres (interhemispheric) due to attention shifts and altered interactions when both sides are involved. In addition, differences between both hemispheres are expected to occur as right-hemispheric regions tend to be more bilaterally interconnected whereas left-hemispheric regions interact more locally ([Gotts et al., 2013](#)). We further study left- and right-handers as well as their eye dominance that provides a foundation for attentional biases ([Schintu et al., 2020](#)), and investigate differences between groups and individuals. We hypothesise that cue-target processing will be differently regulated by left- than right-handed individuals due to differentiation of attentional influences that interact with interhemispheric mechanisms. Overall, we argue that studying the dynamic involvement of interhemispheric interactions will provide increased insights into the regulation of hemispheric lateralisation.

## EXPERIMENTAL PROCEDURES

### Participants

A total of 41 participants was included in the study. Their mean age ( $M_{AGE}$ ) and standard error (SE) of the mean was  $M_{AGE} = 21.2 \pm 0.5$  years. The participants had normal or corrected-to-normal vision and no history of a neurological or psychological condition as assessed by a health history questionnaire. We recruited individuals who self-identified as right-handed and non-right-handed. Participants were all informed about the procedures of the study and provided written informed consent prior to the start of the experiment. The research was approved by the School of Psychology Ethics Committee (reference: 604R) and was conducted in accordance with the Declaration of Helsinki.

### Handedness

Handedness consists of different dimensions and is typically studied by means of preference and performance assessments. Whereas preference is generally captured by self-reports, performance is measured through manual proficiency tests ([Corey](#)

et al., 2001). Here, we include an assessment of both dimensions.

**Handedness questionnaire.** Participants completed a handedness questionnaire that consisted of 15 items (i.e., write, hold toothbrush, use scissors, throw ball, hold racquet, use spoon to stir, open lid from drinks can, use computer mouse, peel apple, use comb, hold knife to cut, use needle, deal cards, use eraser, broom use - upper hand). The handedness questionnaire used a 5-point Likert scale that varied between always left (0), usually left (1), equal (2), usually right (3) and always right (4). Accordingly, the scores of the items were added for each participant, and divided by the maximum score of the questionnaire, and multiplied by 100. This gave a handedness score that ranged from 0 (extreme left-handedness) to 100 (extreme right-handedness), (Serrien and O'Regan, 2019). The handedness scores were used to categorise the participants as 20 left-handers ( $M_{AGE} = 22.4 \pm 0.8$  years;  $M_{HAND} = 22.2 \pm 3.3$ , 16 females) and 21 right-handers ( $M_{AGE} = 20.1 \pm 0.4$  years;  $M_{HAND} = 92.4 \pm 6.5$ , 15 females). The writing hand was included as an additional condition as most individuals categorise their handedness on the basis of their writing hand (Perelle and Ehrman, 2005).

**Manual proficiency.** Participants' performance was measured using a computerised finger tapping test. This required participants to tap on the spacebar of a computer keypad with the left or right index finger as quickly as possible for 10 s. There were three trials for each hand. The participants scores were calculated by obtaining the average score from the trials performed with each hand. We also calculated the difference between the right and left hand performances ( $DIF_{TAP}$ ). Positive and negative scores associated with right and left hand benefits for tapping, respectively.

### Eye dominance

Eye sighting dominance represents the behavioural preference for one eye over the other under monocular viewing conditions (analogous to hand dominance), and has been associated with activation patterns of attentional systems (Roth et al., 2002). It has a population bias like handedness with the majority of people being right eye dominant, i.e., 65% (Porac et al., 1976) albeit less pronounced (Bourassa et al., 1996).

**Eye dominance assessment.** Participants were asked their preference to look through a key hole. The scores involved a 5-point Likert scale that varied between always left (0), usually left (1), equal (2), usually right (3) and always right (4), divided by the maximum score of the questionnaire, and then multiplied by 100. This provided an eye dominance score that ranged from 0 (extreme left-eyed) to 100 (extreme right-eyed). The scores were calculated separately for left-handers ( $M_{EYE} = 31.3 \pm 5.9$ ) and right-handers ( $M_{EYE} = 73.8 \pm 5.6$ ). In our sample, 70% of left-handers showed left eye dominance whereas 76% of right-handers had right eye dominance. There were four participants with no eye dominance (two left- and two right-handers).

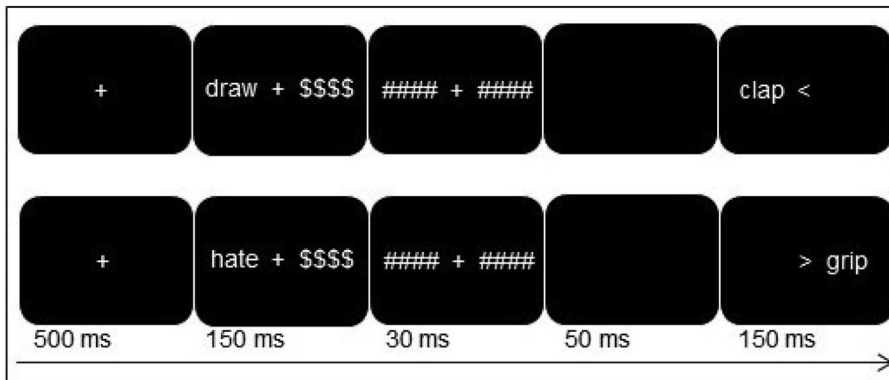
### Experimental task

**Divided visual field paradigm.** We used a divided visual field paradigm that involves presenting information to the visual fields on the basis of the neuro-anatomical organisation of the visual system. Thus, stimuli projected to the right visual field are processed initially by visual cortical regions in the left hemisphere and vice versa. Subsequent to this projection, communication between hemispheres permits transfer to the other side through direct connections, mainly via the corpus callosum. Although providing behavioural measures, the technique can be used to obtain reliable predictors of lateralisation patterns (Hunter and Brysbaert, 2008; Gerrits et al., 2020).

**Experimental paradigm.** The experimental paradigm includes cue-target pairs presented in close succession to the same (intra) or opposite (inter) visual field for investigating the contribution of attentional mechanisms to word recognition. We use non-instructive cues that are shown briefly and the cue-target presentations occur with a short stimulus onset asynchrony followed with backward masking. These experimental features support cueing due to automatic spread of activation and ensure that use of conscious strategies is limited (e.g., Chiarello, 1985; Koivisto, 1998; Korsnes and Magnussen, 2007), although the cue still captures attentional resources (Eimer, 1997; Kiefer and Brendel, 2006). It is argued that such biases before target onset can interact with interhemispheric inhibition. The stimuli are action words associated with use of the hands (i.e., draw) and abstract words referring to internal states (i.e., hope), (O'Regan and Serrien, 2018) based on the idea that their meaning is acquired through interactions with the action or process that is captured by the word (Hauk et al., 2004). Finally, the cue-target pairs comprise congruent and incongruent associations (combinations of the same or different word categories) with participants being asked to respond to the target only, as indicated by a central arrow at fixation. The participants received no instructions with respect to the stimuli combinations.

**Procedure.** Participants were seated at a viewing distance of 70 cm from a computer monitor, with their head rested on a chinrest. A trial sequence is illustrated in Fig. 1 and was presented using PsychoPy (Peirce and MacAskill, 2018). All stimuli subtended  $1.1^\circ$  of visual angle in height and were presented in white Arial font on a black background. The trial sequence started with a central fixation cross for 500 ms followed by the presentation of a cue word for 150 ms alongside a filler stimulus (\$\$\$\$) in the opposite visual field. Cue and filler stimuli were matched for length, presented at  $\pm 2^\circ$  visual angle of central fixation, and followed by a backward mask for 30 ms. Thereafter, there was a blank screen for 50 ms, followed by the presentation of a target word for 150 ms to the same (intra-hemispheric) or opposite (inter-hemispheric) visual field.

The fixation cross was replaced by an arrowhead pointing to the left or right side in order to indicate the



**Fig. 1.** Example of the schematic timeline of the experimental design with the top panel showing the intrahemispheric condition (target = action word, congruent) and the lower panel illustrating the interhemispheric condition (target = action word, incongruent).

target word. There was an inter-stimulus interval of 1000 ms. Participants were instructed to specify the category of the target word i.e. whether it was an action or an abstract word, and to respond as accurately and as quickly as possible. Bimanual responses were used in order to avoid an effect of stimulus–response compatibility, i.e., keypress responses to stimuli presented in right and left visual fields are faster for hand ipsilateral than contralateral to stimuli (Berlucchi et al., 1977). Participants pressed two keys simultaneously using their index fingers for one category and their middle fingers for the other category. There were 40 observations per participant and per condition of the intra- and interhemispheric trials. There were four blocks of 80 trials, resulting in a total of 320 trials. An equal number of intrahemispheric and interhemispheric trials were presented in each block. Half of the trials were congruent (i.e. cue-target were action words or abstract words) and the other half were incongruent (i.e. action cue with abstract target or vice versa). Trials were randomised within blocks of trials. Participants completed 16 practice trials to familiarise themselves with the task demands. Participants were offered the opportunity to take a break in between each of the blocks of trials.

Target word performance was measured using reaction time (i.e., averaged bimanual responses) and response accuracy (i.e., percentage of correct responses). We further computed a laterality index for reaction time ( $LI_{RT}$ ) according to  $[L - R]/[L + R] \times 100$  and for response accuracy ( $LI_{ACC}$ ) according to  $[R - L]/[R + L] \times 100$  where R and L stimuli presented in the right and left visual field, respectively. The LI quantifies the relative strength of lateralisation with positive scores of  $LI_{RT}$  and  $LI_{ACC}$  representing a right visual field advantage, whereas negative scores of  $LI_{RT}$  and  $LI_{ACC}$  indicate a left visual field advantage (Serrien and O'Regan, 2022).  $LI_{RT}$  and  $LI_{ACC}$  were calculated separately for intra- and interhemispheric trials. A LI cut-off score was computed to categorise individuals as left-, right- or non-lateralised. Based on the group sample across intra- and interhemispheric conditions, the cut-off score was calculated according to mean-SE if mean > 0, and mean + SE if mean < 0 and was set to 0.2. Thus, scores at +0.2 and -0.2 were used to divide right visual

field ( $LI > +0.2$ ) from left visual field ( $LI < -0.2$ ) and non-lateralised ( $-0.2 \leq LI \leq +0.2$ ) dominance.

### Statistical analyses

Effect sizes were calculated by means of partial eta squared  $\eta^2_p$  and Cohen's d as provided by SPSS statistics (version 27). A p-value of <0.05 was used as statistically significant. Means alongside the SE are reported throughout the paper.

The reaction times of the language task were analysed using mixed  $2 \times 2 \times 2 \times 2 \times 2$  ANOVAs.

There were within-subjects factors of Stimulus Presentation (intrahemispheric vs interhemispheric), Visual Field (left vs right), Target Stimulus (abstract vs action), Cue-target Congruency (congruent vs incongruent) and a between-subject factor of Handedness Group (left-hander vs right-hander). The  $LI_{RT}$  was analysed using mixed  $2 \times 2 \times 2 \times 2$  ANOVA, including within-subjects factors of Stimulus Presentation, Target Stimulus, Cue-Target Congruency and a between-subjects factor of Handedness Group. Mixed ANOVAs were followed by post-hoc analyses (two-tailed paired t-tests and independent t-tests) with Bonferroni correction for multiple comparisons where appropriate. In addition, correlations were calculated between the  $LI_{RT}$  of the target words in the intra- and interhemispheric conditions alongside the handedness scores. At the individual-level, we assessed the number of individuals who demonstrated either a left- or right-hemispheric profile as well as those who lacked a clear pattern (non-lateralised). Chi-square tests were conducted to assess the  $LI_{RT}$  frequency counts of the handedness groups.

Hemispheric functioning was further detailed by assessing the complementary organisation of the activation-inhibition states. Complementary organisation would indicate functional biases at the group- and/or individual-level. Here, we examined participants' hemispheric associations of intra- and interhemispheric conditions by correlating their  $LI_{RT}$  scores and by assessing the number of individuals with a dominant profile. In particular, right visual field superiority for intra- and interhemispheric conditions would reflect dominance of the left hemisphere whereas right visual field superiority for intrahemispheric condition alongside left visual field superiority for interhemispheric condition would reflect a shift of hemispheric dominance to the right hemisphere. Prevalence of the dominant pattern was evaluated against the null-hypothesis of five combinations (four lateralisation and one non-lateralisation pattern).

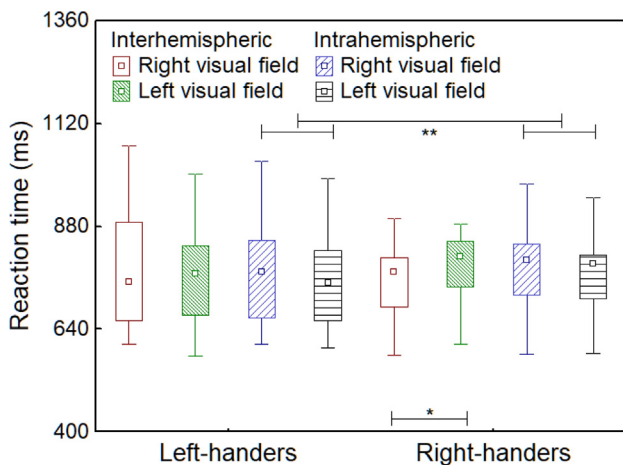
An unpaired t-test was used to assess eye dominance differences between both handedness groups. Correlation analyses were further conducted between eye and hand dominance as well as between eye

dominance across handedness groups and the  $LI_{RT}$  of the intra- and interhemispheric conditions.

## RESULTS

We report on the reaction time data of the language task as the accuracy data which were above 87% did not show significant effects,  $p > 0.05$ . In this experimental context, we argue that the timing measurement is most sensitive to the small effects associated with visual half field processing. We study group- and individual-level data on the basis that as an evolutionarily stable strategy, two levels of lateralisation are observed. Whereas lateralisation at the individual level implies a pronounced bias in single individuals, lateralisation at the population-level indicates that the majority of individuals demonstrate the same bias (Vallortigara, 2006). The data from the manual proficiency (tapping) task can be found in the [supplementary materials](#) section.

**Mean reaction time.** The analysis demonstrated a significant main effect of Visual Field,  $F(1,39) = 4.47$ ,  $p = 0.04$ ,  $\eta^2p = 0.10$ , with quicker responses when target words were presented in the right than left visual field. The three-way interaction of Handedness Group  $\times$  Stimulus Presentation  $\times$  Visual Field was significant,  $F(1,39) = 9.26$ ,  $p = 0.004$ ,  $\eta^2p = 0.19$  (Fig. 2). Post-hoc analyses revealed an overall right visual field preference in the intrahemispheric condition,  $t(40) = 2.69$ ,  $p = 0.01$ ,  $d = 0.42$ . In contrast, target word responses were distinct in the interhemispheric condition with right-handers demonstrating a right visual field advantage,  $t(20) = 3.09$ ,  $p < 0.03$ ,  $d = -0.68$ , whereas left-handers tended towards a left visual field advantage  $t(19) = 1.56$ ,  $p = 0.07$ ,  $d = 0.35$ .

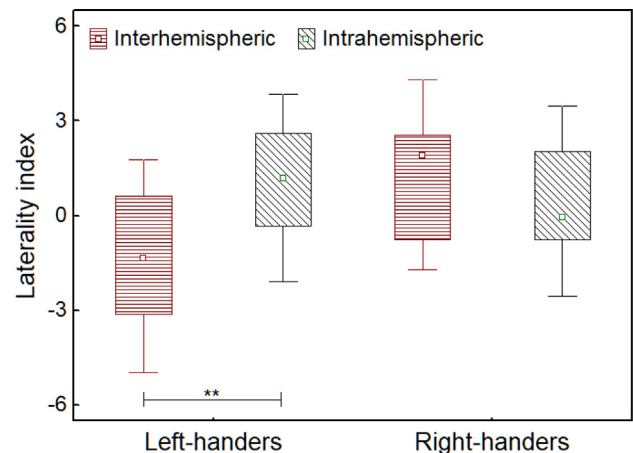


**Fig. 2.** Reaction times for the target words in both handedness groups as a function of the stimulus presentation (interhemispheric vs intrahemispheric condition), and visual field of presentation (right vs left visual field). Box-and-whiskers plots with the box representing the median with 25th and 75th percentiles whereas the whiskers represent the 5th and 95th percentiles. There was a right visual field preference across handedness groups in the intrahemispheric condition. However, in the interhemispheric condition, right-handers showed a right visual field advantage whereas left-handers tended towards a non-significant left visual field advantage. Significant effects (\*\* $p \leq 0.01$ ; \* $p < 0.05$ ).

Examining more in detail, the left–right visual field difference in the interhemispheric condition was significantly distinct between left-handers ( $-16 \pm 10$  ms) and right-handers ( $22 \pm 7$  ms),  $t(39) = 3.09$ ,  $p = 0.002$ ,  $d = 0.97$ , whereas in the intrahemispheric condition there was no difference between left-handers ( $-18 \pm 7$  ms) and right-handers ( $-8 \pm 7$  ms),  $p > 0.05$ . No other main effects or interactions were significant ( $p > 0.05$  for all). The mean  $\pm$  SE scores for left-handers were for interhemispheric  $773 \pm 36$  ms (LVF) and  $789 \pm 35$  ms (RVF) vs for intrahemispheric  $764 \pm 33$  ms (LVF) and  $782 \pm 33$  ms (RVF). The scores for right-handers were for interhemispheric  $778 \pm 22$  ms (LVF) and  $756 \pm 22$  ms (RVF) vs for intrahemispheric  $771 \pm 27$  ms (LVF) and  $778 \pm 26$  ms (RVF).

**$LI_{RT}$ .** The analysis showed a significant main effect of Handedness Group,  $F(1,39) = 4.64$ ,  $p = 0.038$ ,  $\eta^2p = 0.11$ , alongside a significant interaction of Handedness Group  $\times$  Stimulus Presentation,  $F(1,39) = 17.06$ ,  $p = 0.0002$ ,  $\eta^2p = 0.30$  (Fig. 3). Post-hoc analyses indicated that the  $LI_{RT}$  of the right-handers had left-hemispheric dominance for the interhemispheric ( $1.40 \pm 0.47$ ) and intrahemispheric ( $0.50 \pm 0.44$ ) condition ( $p > 0.05$ ) albeit with the proportional magnitude with respect to the LI cut-off score (0.20) being stronger for the inter- than intrahemispheric condition,  $\chi^2_1 = 10.25$ ,  $p < 0.002$ . Conversely, the  $LI_{RT}$  of the left-handers was distinct for both conditions,  $t(19) = -4.85$ ,  $p < 0.001$ ,  $d = -1.09$  and showed opposite tendencies with dominance of the left hemisphere for intrahemispheric ( $1.14 \pm 0.41$ ) vs dominance of the right hemisphere for interhemispheric ( $-1.35 \pm 0.49$ ) condition. No other main effects or interactions were significant ( $p > 0.05$  for all).

**$LI_{RT}$  and handedness.** For the intrahemispheric condition, a correlation analysis showed no significant



**Fig. 3.** The laterality index as a function of interhemispheric and intrahemispheric conditions for left- and right-handers. Box-and-whiskers plots with the box representing the median with 25th and 75th percentiles whereas the whiskers represent the 5th and 95th percentiles. Right-handers showed left-hemispheric dominance for both intra- and interhemispheric conditions whereas left-handers demonstrated an opposite pattern of hemispheric dominance. Significant effects (\*\* $p < 0.01$ ).

association,  $p > 0.05$ ,  $R^2 = 0.04$  (Fig. 4, left panel). The scatter plot indicates that right-handed individuals demonstrated dominance of the right visual field (N = 10, 48%) and left visual field (N = 9, 43%) vs non-lateralisation (N = 2, 9%). A large number of left-handed individuals showed right visual field (N = 14, 70%) as opposed to left visual field (N = 6, 30%) dominance. For the interhemispheric condition, a correlation analysis provided a positive association.  $r(39) = 0.52$ ,  $p < 0.001$ ,  $R^2 = 0.28$  (Fig. 4, right panel), revealing that increased right-handedness associated with stronger dominance of the right visual field. The scatter plot illustrates that the majority of right-handed individuals demonstrated superiority of the right visual field (N = 15, 71%) whereas a smaller number obtained left visual field dominance (N = 6, 29%). Conversely, a large number of left-handed individuals had superiority of the left visual field (N = 12, 60%) as opposed to right visual field (N = 6, 30%) and non-lateralisation (N = 2, 10%).

These results at an individual-level organisation illustrate that more left- than right-handed individuals had right visual field dominance for the intrahemispheric condition,  $\chi^2_1 = 10.00$ ,  $p < 0.002$  whereas this was reversed for the interhemispheric condition with more right- than left-handed individuals demonstrating right visual field dominance,  $\chi^2_1 = 33.82$ ,  $p < 0.0001$ . Also, the number of right-handed individuals with right visual field dominance was lower for the intra- than interhemispheric condition,  $\chi^2_1 = 4.07$ ,  $p = 0.04$ , whereas this was reversed for the number of left-handed individuals with right visual field dominance being lower for the inter- than intrahemispheric condition,  $\chi^2_1 = 15.21$ ,  $p = 0.0001$ .

***L<sub>IRT</sub> intra- and interhemispheric.*** The correlation analysis between the L<sub>IRT</sub> scores did not show a significant association,  $p > 0.05$ ,  $R^2 = 0.003$  (Fig. 5). The scatter plot illustrates that various combinations were observed across participants, but many right-handers (N = 8, 38%) showed right visual field dominance for both intra- and interhemispheric conditions. Moreover, there was prevalence of this

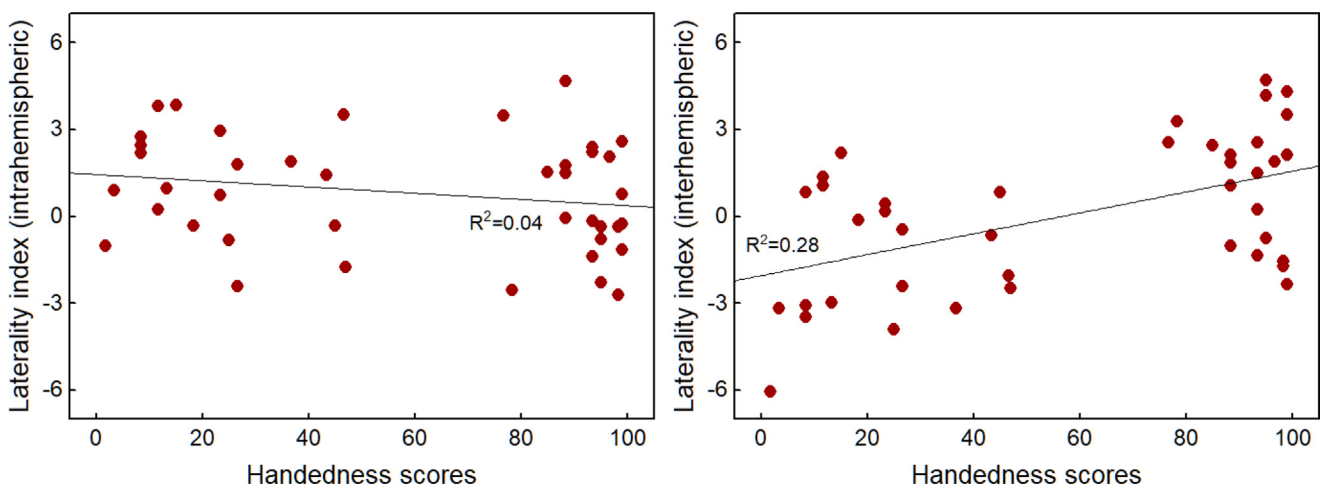
combination against the null-hypothesis with 20% according to five categories,  $z = 2.06$ ,  $p < 0.04$ , CI: 18.03–61.47%. In contrast, many left-handers (N = 8, 40%) demonstrated right visual field dominance for intrahemispheric condition and left visual field dominance for interhemispheric condition. Moreover, there was prevalence of this combination against the null-hypothesis with 20% according to five categories,  $z = 2.24$ ,  $p < 0.003$ , CI: 19.12–63.95%. No other combinations obtained significance,  $p > 0.05$ .

***Eye and hand dominance.*** An unpaired t-test revealed a significant difference for eye dominance between both handedness groups,  $t(39) = -5.21$ ,  $p < 0.0001$ ,  $d = -1.63$ . A correlation analysis between eye and hand dominance was significant,  $r(39) = 0.68$ ,  $p < 0.001$ ,  $R^2 = 0.46$ , indicating a positive association between the preference of eye and hand. However, of note is that both handedness groups showed variation, i.e., 70% of left-handers had left eye dominance whereas 76% of right-handers demonstrated right eye dominance.

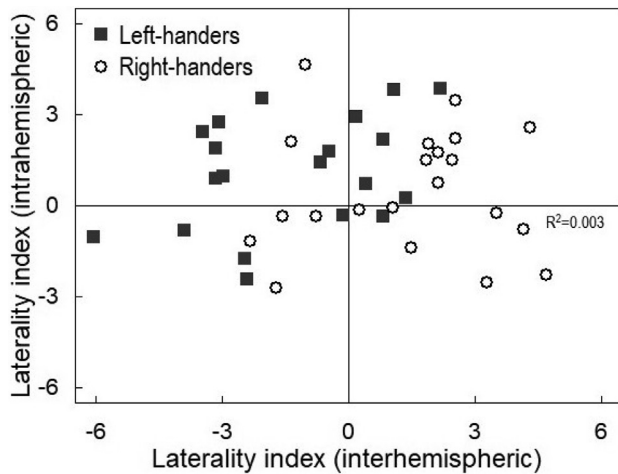
***Eye dominance and L<sub>IRT</sub> intra- and interhemispheric.*** Correlation analyses between the eye dominance score across handedness groups and the L<sub>IRT</sub> of the intrahemispheric condition was not significant,  $p > 0.05$ , whereas there was a significant association with the L<sub>IRT</sub> of the interhemispheric condition,  $r(39) = 0.56$ ,  $p < 0.001$ ,  $R^2 = 0.31$  (Fig. 6). Correlation analyses that included only the individuals with typical eye dominance for each handedness group revealed no significance with the L<sub>IRT</sub> of the intrahemispheric condition,  $p > 0.05$ , whereas there was a significant association with the L<sub>IRT</sub> of the interhemispheric condition,  $r(28) = 0.66$ ,  $p < 0.0001$ ,  $R^2 = 0.45$ .

## DISCUSSION

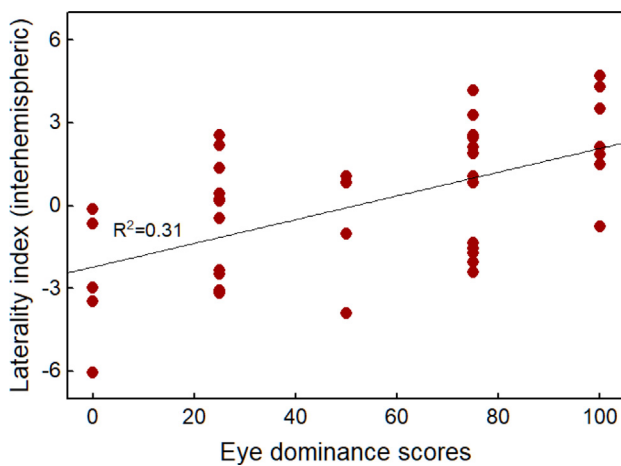
Hemispheric lateralisation underlines that cognitive processes such as language are lateralised in the brain, and relies on specialisation of the hemispheres alongside interhemispheric communication pathways



**Fig. 4.** Scatter plots of the laterality index with handedness scores for the intrahemispheric (left panel) and interhemispheric (right panel) conditions. Language responses with positive score represent superiority of the right visual field, left-handed < 50 and right-handed > 50.



**Fig. 5.** Scatter plot of the laterality index for the complementary intra- and interhemispheric conditions with positive/negative scores representing superiority of the right/left visual field. The quadrants show the different combinations of complementary organisation.



**Fig. 6.** Scatter plot of the laterality index for the interhemispheric condition alongside eye dominance scores. Language responses with positive score represent superiority of the right visual field, left eye dominance < 50 and right eye dominance > 50.

(Hellige, 1993; Gazzaniga, 2000; Bloom and Hynd, 2005). In this work, we adopt a dynamic model of functional lateralisation that underlines that hemispheric asymmetries are sensitive to attentional processes guided by an activation-inhibition synergy that acts as a regulatory mechanism. We address influences of task parameters and individual variation by means of contralateral vs ipsilateral cueing together with the study of individuals with different hand and eye dominance.

### Language processing and activation-inhibition processes

Language processing strongly relies on the left hemisphere as evidenced from behavioural, imaging and clinical research (Springer et al., 1999; Knecht et al., 2000; Szafarski et al., 2002; Hunter and

Brysbaert, 2008; Skeide and Friederici, 2016). Under normal circumstances, word and meaning processing are optimised through facilitation of the left hemisphere alongside inhibition of the right hemisphere (Kinsbourne, 1974; Chiarello and Maxfield, 1996). However, left-hemispheric dominance is a dynamic feature and can vary as a result of factors that modulate the interhemispheric balance (Smith-Conway et al., 2012; Hartwigsen et al., 2013). Using resting state measurements, it has been shown that differences in language lateralisation associate with those in homotopic interhemispheric connectivity (Tzourio-Mazoyer et al., 2016). We used an experimental design that included lateralised non-instructive cues with brief stimulus duration that further minimise eye movements to spatial locations (Landis and Regard, 1988; Hunter and Brysbaert, 2008). We observed no effect of cueing congruency on target processing, suggesting that changes of attentional asymmetries did not significantly influence task performance. There was further no impact of word type (abstract vs action), which underlines dominance of left-hemispheric processing and is in line with previous work (O'Regan and Serrien, 2018).

The reaction time data showed different effects on intra- and interhemispheric regulation. In the intrahemispheric condition, word targets presented in the right visual field were processed quicker than those presented in the left visual field, underlining the functional superiority of the left hemisphere. That word processing is less efficient in the non-dominant vs dominant hemisphere has been addressed in the literature by two main models. Whereas the callosal relay model suggests that information is transferred to the dominant side via the corpus callosum, the direct access model proposes that information is processed by the right hemisphere only (Iacoboni and Zaidel, 1996; Olk and Hartje, 2001). These models imply reduced processing in the non-dominant hemisphere which leads to inferior performance, and there is research that supports both viewpoints (Chu et al., 2018).

In the interhemispheric condition, the changes indicated that transfer between both hemispheres is a fundamental mechanism of information integration that steers neural processes, particularly for tasks that support sensorimotor and perceptual control (Koch et al., 2011; Chaumillon et al., 2018; Schintu et al., 2021). Yet, the reaction times of the target responses differed as a function of the visual field of presentation and further interacted with handedness. That is, whereas target processing in the right hemisphere was similar for both groups, this was not the case for the left hemisphere. In particular, targets presented to the right visual field were affected by cues initially presented to the opposite visual field, suggesting modulation of the interhemispheric balance by attentional resources, and in turn left-hemispheric functioning. Previous work has shown that interhemispheric transfer of visual information is fastest from the right to left side, and thus links with the specialisation of the right hemisphere for visuospatial attention (Marzi et al., 1991). However, the left-hemispheric reaction times in our study revealed characteristic effects as a function of handedness. In particular, right-handers showed faster reaction times whereas left-handers

tended to slow down their reaction times. This suggests that initial handling in the right hemisphere triggered release of interhemispheric inhibition, influencing efficiency of processing. The laterality index further detailed these handedness-related influences, with right-handers strengthening left-hemispheric dominance as opposed to left-handers who demonstrated elimination of its superiority. Therefore, the switch between right- and left-sided processing elicited distinct interactions between hemispheres and rebalancing of resources.

The association of handedness with the inter- but not intrahemispheric condition points to modulations of attentional resources. Moreover, both handedness groups have different neural circuits that underlie attentional control with the ventral network showing right-hemispheric lateralisation in right-handers vs bilateral or left-hemispheric lateralisation in left-handers (Bareham et al., 2015) whereas the bilateral-organised dorsal network is more pronounced in the right hemisphere in left-handers (Petit et al., 2015). A critical component is the dorsal system with its distinct parietal nodes (but not frontal nodes) for which attentional allocation occurs towards the contralateral side while both hemispheres maintain mutual inhibition, suggesting regional differences of hemispheric asymmetries as proposed by a hybrid model of attentional control (Duecker and Sack, 2015). In addition, the ventral system can bias the dorsal system, for example due to a significant stimulus that triggers a reorientation of attention (Corbetta and Shulman, 2011), illustrating that both circuits cooperate for flexible use of attention as a result of the task or contextual requirements (Vossel et al., 2014; Bartolomeo and Seidel Malkinson, 2019; Mengotti et al., 2020). The foundation of these attentional networks is facilitated by the superior longitudinal fasciculus (SLF), a major bidirectional association tract that connects various premotor and parietal areas, with branches that are closely linked with their functional role; dorsal (SLF I, partly SLF II) and ventral (SLF III, partly SLF II), (Koch et al., 2011; Thiebaut de Schotten et al., 2011; Budisavljevic et al., 2021). In particular, SLF I and SLF II are involved in top-down modulation of selective attention and online movement control (Budisavljevic et al., 2021) with the anatomical characteristics of SLF I prominently associating with handedness (Howells et al., 2018). Clinical work has further revealed that the resection of SLF II in surgical patients results in postoperative changes of selective attention and hand preference for goal-directed tasks, suggesting a relationship between attentional processing and handedness (Howells et al., 2020).

Besides handedness, eye dominance as an index of attentional systems has a relevant role in interhemispheric transfer of visual information at the level of posterior parietal circuitry. Moreover, right-handers (with dominant right eye) show faster right-to-left transfer whereas left-handers (with dominant left eye) lack a clear asymmetry (Chaumillon et al., 2018). These effects would thus lead to a strong right-to-left drive for right-handers vs an unbalanced drive for left-handers. Our results revealed that left- and right-handers had pronounced left and right eye dominance, respectively. That the majority of both handedness groups expressed typical

eye dominance suggests that the release of interhemispheric inhibition likely boosted left-sided processing and facilitation of target identification for right-handers. In contrast, unstructured interhemispheric influences would weaken left-sided processing and delay target identification for left-handers.

Studies about the neural basis of eye dominance have shown that stimulation of each eye reaches both cerebral hemispheres. However, due to anatomic-functional association between the dominant eye and ipsilateral primary visual cortex (Erdogan et al., 2002; Rombouts et al., 1996; Seyal et al., 1981; Shima et al., 2010), visual information is processed more efficiently in the contralateral vs ipsilateral visual hemifield to dominant eye (Chaumillon et al., 2014, 2017; Tagu et al., 2016). Furthermore, the asymmetric activation and priority of visual processing captured by the dominant eye may modulate visuospatial attention circuitry (Shneur and Hochstein, 2008). This proposes that for participants with right eye dominance, the relationship with its ipsilateral hemisphere (right hemisphere; Shima et al., 2010) is consistent with a right-sided asymmetry of attentional networks. In contrast, in participants with left eye dominance, the relationship with its ipsilateral hemisphere (left hemisphere) neutralises the right-hemispheric dominance for visuospatial attention (Chaumillon et al., 2018; Schintu et al., 2020). Combined, the data illustrate that eye and hand dominance are central factors that associate with attentional control and interhemispheric communication, influencing functional lateralisation properties. Their interaction may be linked through an evolutionary origin that steers visually-guided activities to spatial settings through an exploration of the environment with hand and eyes (Petit et al., 2015).

### Individual handedness-language and complementary intra-interhemispheric associations

Handedness is an essential trait of motor control, and represents the dominance to use one hand over the other for skilled manual activities. Throughout history, a preferential bias of right- vs left-handers has been noted in humans at the population level according to a 90–10% ratio (Coren and Porac, 1977). Both groups demonstrate variation of intrahemispheric sensorimotor representations as well as interhemispheric interactions that are particularly critical through inhibitory regulation, with right-handers demonstrating modulations that tend to support control of the dominant (left) hemisphere whereas both hemispheres show more equal capabilities in left-handers (Reid and Serrien, 2012; Tazoe and Perez, 2013; Pool et al., 2014).

Left-hemispheric lateralisation for language is prominent in about 95% of right-handers and 75% of left-handers, indicating that atypical language superiority is more frequent in individuals characterised by non-right-handedness (Pujol et al., 1999; Knecht et al., 2000). Two additional language-related variants have been confirmed through neuroimaging work: no hemispheric dominance with bilateral representations, a pattern that is rather equally present in both handedness groups, in addition to right-hemispheric dominance that



is usually only observed in a small subgroup of left-handers (Tzourio-Mazoyer et al., 2016; Vingerhoets, 2019). Taking these differences into account, it is therefore relevant to consider the profiles that characterise their behaviour (Serrien and O'Regan, 2022). Our data revealed that the participants from both handedness groups had distinct sensitivity during intra- and interhemispheric conditions. In particular, left-hemispheric dominance of target words was strongest during the interhemispheric condition for right-handed individuals as opposed to the intrahemispheric condition for left-handed individuals. This confirms heterogeneity as a function of the hemispheric processing demands.

The concept of complementary organisation has especially been addressed in the literature for assessing whether lateralisation of one cognitive function can predict the asymmetric processing of another one (Cai et al., 2013; Brederoo et al., 2020; Serrien and O'Regan, 2022). We used the premise of complementarity to examine more closely the activation-inhibition synergy. In particular, theoretical viewpoints propose that intrahemispheric activation and interhemispheric inhibition are two separate mechanisms (Kinsbourne, 1974) or are components of the same mechanism that support processing priorities within and between hemispheres (Querné et al., 2000). In examining complementarity, our results revealed a range of combinations, indicating flexibility of information processing. However, we noted a characteristic pattern for both groups. Whereas many right-handed individuals demonstrated left-sided dominance across conditions, left-handed individuals revealed left-sided dominance for intrahemispheric condition versus right-sided dominance for interhemispheric condition. This suggests that right-handed individuals tended to process information more robustly within unilateral left circuitry whereas left-handed individuals are more guided by bilateral circuits. Thus, there is pronounced individual variation that associates with distinctive hemispheric mechanisms as a function of handedness. In conclusion, our data showed that handedness distinctly affected word processing in the left hemisphere following contralateral cueing. This result was further supported by a prominent role of eye dominance, suggesting that characteristic attentional biases guided the processing strategies of both groups. Therefore, hand and eye dominance are both key factors with a functional role in directing transfer of information between both hemispheres alongside an impact on processing resources. Overall, the findings underline the importance of interacting hand-eye control systems in contributing to interhemispheric patterns in the context of language processing.

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## CONFLICT OF INTEREST

None.

## REFERENCES

- Bareham CA, Bekinschtein TA, Scott SK, Manly T (2015) Does left-handedness confer resistance to spatial bias? *Sci Rep* 5:9162. <https://doi.org/10.1038/srep09162>.
- Bartolomeo P, Seidel Malkinson T (2019) Hemispheric lateralization of attention processes in the human brain. *Curr Opin Psychol* 29:90–96. <https://doi.org/10.1016/j.copsyc.2018.12.023>.
- Berlucchi G, Crea F, di Stefano M, Tassinari G (1977) Influence of spatial stimulus-response compatibility on reaction time of ipsilateral and contralateral hand to lateralized light stimuli. *J Exp Psychol Hum Percept Perform* 3:505–517. <https://doi.org/10.1037/0096-1523.3.3.505>.
- Bloom JS, Hynd GW (2005) The role of the corpus callosum in interhemispheric transfer of information: excitation or inhibition? *Neuropsychol Rev* 15:59–71. <https://doi.org/10.1007/s11065-005-6252-y>.
- Bourassa DC, McManus IC, Bryden MP (1996) Handedness and eye-dominance: a meta-analysis of their relationship. *Laterality* 1:5–34. <https://doi.org/10.1080/713754206>.
- Brederoo SG, Van der Haegen L, Brysbaert M, Nieuwenstein MR, Frans W, Cornelissen FW, Lorist MM (2020) Towards a unified understanding of lateralized vision: A large-scale study investigating principles governing patterns of lateralization using a heterogeneous sample. *Cortex* 133:201–214. <https://doi.org/10.1016/j.cortex.2020.08.029>.
- Budisavljevic S, Castiello U, Begliomini C (2021) Handedness and white matter networks. *Neuroscientist* 27:88–103. <https://doi.org/10.1177/1073858420937657>.
- Cai Q, Van der Haegen L, Brysbaert M (2013) Complementary hemispheric specialization for language production and visuospatial attention. *Proc Natl Acad Sci USA* 110:E322–E330. <https://doi.org/10.1073/pnas.1212956110>.
- Chao YP, Cho KH, Yeh CH, Chou KH, Chen JH, Lin CP (2009) Probabilistic topography of human corpus callosum using cytoarchitectural parcellation and high angular resolution diffusion imaging tractography. *Hum Brain Mapp* 30:3172–3187. <https://doi.org/10.1002/hbm.20739>.
- Chaumillon R, Blouin J, Guillaume A (2014) Eye dominance influences triggering action: the Poffenberger paradigm revisited. *Cortex* 58:86–98. <https://doi.org/10.1016/j.cortex.2014.05.009>.
- Chaumillon R, Alahyane N, Senot P, Vergne J, Lemoine-Lardennois C, Blouin J, Doré-Mazars K, Guillaume A, Vergilino-Perez D (2017) Asymmetry in visual information processing depends on the strength of eye dominance. *Neuropsychologia* 96:129–136. <https://doi.org/10.1016/j.neuropsychologia.2017.01.015>.
- Chaumillon R, Blouin J, Guillaume A (2018) Interhemispheric transfer time asymmetry of visual information depends on eye dominance: An electrophysiological study. *Front Neurosci* 12. <https://doi.org/10.3389/fnins.2018.00072>.
- Chiarello C (1985) Hemisphere dynamics in lexical access: automatic and controlled priming. *Brain Lang* 26:146–172. [https://doi.org/10.1016/0093-934x\(85\)90034-3](https://doi.org/10.1016/0093-934x(85)90034-3).
- Chiarello C, Maxfield L (1996) Varieties of interhemispheric inhibition, or how to keep a good hemisphere down. *Brain Cogn* 30:81–108. <https://doi.org/10.1006/brcg.1996.0006>.
- Chu R, Meltzer JA, Bitan T (2018) Interhemispheric interactions during sentence comprehension in patients with aphasia. *Cortex* 109:74–91. <https://doi.org/10.1016/j.cortex.2018.08.022>.
- Cook ND (1986) *The brain code: The mechanisms of information transfer and the role of the corpus callosum*. London: Methuen.
- Corbetta M, Shulman GL (2011) Spatial neglect and attention networks. *Ann Rev Neurosci* 34:569–599. <https://doi.org/10.1146/annurev-neuro-061010-113731>.
- Coren S, Porac C (1977) Fifty centuries of right-handedness: the historical record. *Science* 198:631–632. <https://doi.org/10.1126/science.335510>. PMID: 335510.
- Corey DM, Hurley MM, Foundas AL (2001) Right and left handedness defined: a multivariate approach using hand preference and hand

- performance measures. *Neuropsychiatry Neuropsychol Behav Neurol* 14:144–152.
- Duecker F, Sack AT (2015) The hybrid model of attentional control: New insights into hemispheric asymmetries inferred from TMS research. *Neuropsychologia* 74:21–29. <https://doi.org/10.1016/j.neuropsychologia.2014.11.023>.
- Eimer M (1997) Uninformative symbolic cues may bias visual-spatial attention: behavioral and electrophysiological evidence. *Biol Psychol* 46:67–71. [https://doi.org/10.1016/s0301-0511\(97\)05254-x](https://doi.org/10.1016/s0301-0511(97)05254-x).
- Erdogan AR, Ozdikci M, Aydin MD, Aktas O, Dane S (2002) Right and left visual cortex areas in healthy subjects with right-eye and left-eye dominance. *Int J Neurosci* 112:517–523.
- Flöel A, Jansen A, Deppe M, Kanowski M, Konrad C, Sommer J, Knecht S (2005) Atypical hemispheric dominance for attention: functional MRI topography. *J Cereb Blood Flow Metab* 25:1197–1208. <https://doi.org/10.1038/sj.jcbfm.9600114>.
- Gazzaniga MS (2000) Cerebral specialization and interhemispheric communication: does the corpus callosum enable the human condition? *Brain* 123:1293–1326. <https://doi.org/10.1093/brain/123.7.1293>.
- Gerrits R, De Clercq P, Verhelst H, Vingerhoets G (2020) Evaluating the performance of the visual half field paradigm as a screening tool to detect right hemispheric language dominance. *Laterality* 25:722–739. <https://doi.org/10.1080/1357650X.2020.1854279>.
- Gotts SJ, Jo HJ, Wallace GL, Saad ZS, Cox RW, Martin A (2013) Two distinct forms of functional lateralization in the human brain. *Proc Natl Acad Sci USA* 110:E3435–E3444. <https://doi.org/10.1073/pnas.1302581110>.
- Hartwigsen G, Saur S, Price CJ, Ulmer S, Baumgaertner A, Siebner HR (2013) Perturbation of the left inferior frontal gyrus triggers adaptive plasticity in the right homologous area during speech production. *Proc Natl Acad Sci USA* 110:16402–16407. <https://doi.org/10.1073/pnas.1310190110>.
- Hauk O, Johnsrude I, Pulvermüller F (2004) Somatotopic representation of action words in human motor and premotor cortex. *Neuron* 41:301–307. [https://doi.org/10.1016/S0896-6273\(03\)00838-9](https://doi.org/10.1016/S0896-6273(03)00838-9).
- Hellige JB (1993) *Hemispheric asymmetry: What's right and what's left*. Harvard University Press.
- Hinkley LBN, Marco EJ, Brown EG, Bukshpun P, Gold J, Hill S, Findlay AM, Jeremy RJ, Mari L, Wakahiro ML, Barkovich AJ, Mukherjee P, Sherr EH, Nagarajan SS (2016) The contribution of the corpus callosum to language lateralization. *J Neurosci* 36:4522–4533. <https://doi.org/10.1523/JNEUROSCI.3850-14.2016>.
- Howells H, Thiebaut de Schotten M, Dell'Acqua F, Beyh A, Zappalà G, Leslie A, Simmons A, Declan G, Murphy D, Catani M (2018) Frontoparietal tracts Linked to lateralized hand preference and manual specialization. *Cereb Cortex* 28:2482–2494. <https://doi.org/10.1093/cercor/bhy040>.
- Howells H, Puglisi G, Leonetti A, Viganò L, Fornia L, Simone L, Forkel S, Rossi M, Cerri G, Bello L (2020) The role of left fronto-parietal tracts in hand selection: evidence from neurosurgery. *Cortex* 128:297–311. <https://doi.org/10.1016/j.cortex.2020.03.018>.
- Hunter ZR, Brysbaert M (2008) Visual half-field experiments are a good measure of cerebral language dominance if used properly: Evidence from fMRI. *Neuropsychologia* 46:316–325. <https://doi.org/10.1016/j.neuropsychologia.2007.07.007>.
- Hutchinson A, Whitman RD, Abeare C, Raiter J (2003) The unification of mind: Integration of hemispheric semantic processing. *Brain Lang* 87:361–368. [https://doi.org/10.1016/s0093-934x\(03\)00133-0](https://doi.org/10.1016/s0093-934x(03)00133-0). PMID: 14642539.
- Iacoboni M, Zaidel E (1996) Hemispheric independence in word recognition: Evidence from unilateral and bilateral presentations. *Brain Lang* 53:121–140. <https://doi.org/10.1006/brln.1996.0040>.
- Jeeves MA, Temple CM (1987) A further study of language function in callosal agenesis. *Brain Lang* 32:325–335. [https://doi.org/10.1016/0093-934x\(87\)90131-3](https://doi.org/10.1016/0093-934x(87)90131-3).
- Josse G, Tzourio-Mazoyer N (2004) Hemispheric specialization for language. *Brain Res Rev* 44:1–12. <https://doi.org/10.1016/j.brainresrev.2003.10.001>.
- Kiefer M, Brendel DJ (2006) Attentional modulation of unconscious “automatic” processes: evidence from event-related potentials in a masked priming paradigm. *Cogn Neurosci* 18:184–198. <https://doi.org/10.1162/089892906775783688>. PMID: 16494680.
- Kinsbourne M (1974) *Mechanisms of hemispheric interaction in man*. In: Kinsbourne M, Smith WL, editors. *Hemispheric disconnection and cerebral function*. Charles C Thomas. p. 260–285.
- Kinsbourne M, Swanson JM, Ledlow A (1977) Measuring interhemispheric transfer time in man. *Trans Am Neurol Assoc* 102:163–167.
- Knecht S, Dräger B, Deppe M, Bobe L, Lohmann H, Flöel A, Ringelstein E, Henningsen H (2000) Handedness and hemispheric language dominance in healthy humans. *Brain* 123:2512–2518. <https://doi.org/10.1093/brain/123.12.2512>.
- Koch G, Cercignani M, Bonni S, Giacobbe V, Bucchi G, Versace V, Caltagirone C, Bozzali M (2011) Asymmetry of parietal interhemispheric connections in humans. *J Neurosci* 31:8967–8975. <https://doi.org/10.1523/JNEUROSCI.6567-10.2011>.
- Koivisto M (1998) Categorical priming in the cerebral hemispheres: automatic in the left hemisphere, postlexical in the right hemisphere? *Neuropsychologia* 36:661–668. [https://doi.org/10.1016/s0028-3932\(97\)00147-4](https://doi.org/10.1016/s0028-3932(97)00147-4).
- Korsnes MS, Magnussen S (2007) Automatic semantic priming in the left and right hemispheres. *Scand J Psychol* 48:197–202. <https://doi.org/10.1111/j.1467-9450.2007.00557>.
- Landis T, Regard M (1988) *The right hemisphere's access to lexical meaning: a function of its release from left-hemisphere control*. In: Chiarello C, editor. *Right hemisphere contributions to lexical semantics*. New York: Springer. p. 33–46.
- Marzi CA, Bisiacchi P, Nicoletti R (1991) Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a metaanalysis. *Neuropsychologia* 29:1163–1177. [https://doi.org/10.1016/0028-3932\(91\)90031-3](https://doi.org/10.1016/0028-3932(91)90031-3).
- Mengotti P, Käsbaauer A-S, Fink GR, Vossel S (2020) Lateralization, functional specialization, and dysfunction of attentional networks. *Cortex* 132:206–222. <https://doi.org/10.1016/j.cortex.2020.08.022>.
- Nowicka A, Tacikowski P (2011) Transcallosal transfer of information and functional asymmetry of the human brain. *Laterality* 16:35–74. <https://doi.org/10.1080/13576500903154231>.
- O'Regan L, Serrien DJ (2018) Individual differences and hemispheric asymmetries for language and spatial attention. *Front Hum Neurosci* 12:380. <https://doi.org/10.3389/fnhum.2018.00380>.
- Olk B, Hartje W (2001) The bilateral effect: callosal inhibition or intrahemispheric competition? *Brain Cogn* 45:317–324. <https://doi.org/10.1006/brcg.2000.1258>.
- Peirce JW, MacAskill MR (2018) *Building experiments in PsychoPy*. London: Sage.
- Perelle IB, Ehrman L (2005) On the other hand. *Behav Genet* 35:343–350. <https://doi.org/10.1007/s10519-005-3226-z>.
- Petit L, Zago L, Mellet E, Jobard G, Crivello F, Joliot M, Mazoyer B, Tzourio-Mazoyer N (2015) Strong rightward lateralization of the dorsal attentional network in left-handers with right sighting-eye: an evolutionary advantage. *Hum Brain Mapp* 36:1151–1164. <https://doi.org/10.1002/hbm.22693>.
- Pool EM, Rehme AK, Fink GR, Eickhoff SB, Grefkes C (2014) Handedness and effective connectivity of the motor system. *Neuroimage* 99:451–460. <https://doi.org/10.1016/j.neuroimage.2014.05.048>.
- Porac C, Whitford FW, Coren S (1976) The relationship between eye dominance and monocular acuity: an additional consideration. *Am J Optom Physiol Opt* 53:803–806. <https://doi.org/10.1097/00006324-197612000-00007>.
- Price CJ (2000) The anatomy of language: contributions from functional neuroimaging. *The Journal of Anatomy* 197:335–359. <https://doi.org/10.1046/j.1469-7580.2000.19730335.x>.

- Pujol J, Deus J, Losilla JM, Capdevila A (1999) Cerebral lateralization of language in normal left-handed people studied by functional MRI. *Neurology* 52:1038–1043. <https://doi.org/10.1212/wnl.52.5.1038>.
- Querné L, Eustache F, Faure S (2000) Interhemispheric inhibition, intrahemispheric activation, and lexical capacities of the right hemisphere: A tachistoscopic, divided visual-field study in normal subjects. *Brain Lang* 74:171–190. <https://doi.org/10.1006/brln.2000.2333>.
- Reid CS, Serrien DJ (2012) Handedness and the excitability of cortical inhibitory circuits. *Behav Brain Res* 230:144–148. <https://doi.org/10.1016/j.neuroscience.2014.04.005>.
- Reuter-Lorenz PA, Kinsbourne M, Moscovitch M (1990) Hemispheric control of spatial attention. *Brain Cogn* 12:240–266. [https://doi.org/10.1016/0278-2626\(90\)90018-j](https://doi.org/10.1016/0278-2626(90)90018-j).
- Ringo JL, Doty RW, Demeter S, Simard PY (1994) Time is of the essence: a conjecture that hemispheric specialization arises from interhemispheric conduction delay. *Cereb Cortex* 4:331–343. <https://doi.org/10.1093/cercor/4.4.331>.
- Rombouts SA, Barkhof F, Sprenger M, Valk J, Scheltens P (1996) The functional basis of ocular dominance: functional MRI (fMRI) findings. *Neuroscience Letters* 221:1–4. [https://doi.org/10.1016/s0304.3940\(96\)13260-2](https://doi.org/10.1016/s0304.3940(96)13260-2).
- Roth HL, Lora AN, Heilman KM (2002) Effects of monocular viewing and eye dominance on spatial attention. *Brain* 125:2023–2035. <https://doi.org/10.1093/brain/awf210>.
- Schintu S, Chaumillon R, Guillaume A, Salemme R, Reilly KT, Pisella L, Farné A (2020) Eye dominance modulates visuospatial attention. *Neuropsychologia* 141. <https://doi.org/10.1016/j.neuropsychologia.2019.107314> 107314.
- Schintu S, Cunningham CA, Freedberg M, Taylor P, Gotts SJ, Shomstein S, Wassermann EM (2021) Callosal anisotropy predicts attentional network changes after parietal inhibitory stimulation. *Neuroimage* 226. <https://doi.org/10.1016/j.neuroimage.2020.117559> 117559.
- Serrien DJ, O'Regan L (2022) The interactive functional biases of manual, language and attention systems. *Cogn Res: Principles Implicat* 20. <https://doi.org/10.1186/s41235-022-00365-x>.
- Serrien DJ, O'Regan L (2019) Stability and flexibility in cognitive control: Interindividual dynamics and task context processing. *PLoS One* 4:e0219397.
- Seyal M, Sato S, White BG, Porter RJ (1981) Visual evoked potentials and eye dominance. *Electroencephalogr Clin Neurophysiol* 52:424–428. [https://doi.org/10.1016/0013-4694\(81\)90025-0](https://doi.org/10.1016/0013-4694(81)90025-0).
- Shima H, Hasegawa M, Tachibana O, Nomura M, Yamashita J, Ozaki Y, Kawai J, Higuchi M, Kado H (2010) Ocular dominance affects magnitude of dipole moment: an MEG study. *Neuroreport* 21:817–821. <https://doi.org/10.1097/WNR.0b013e32833ce5d7>. PMID: 20613677.
- Shneur E, Hochstein S (2008) Eye dominance effects in conjunction search. *Vision Res* 48:1592–1602. <https://doi.org/10.1016/j.visres.2008.04.021>.
- Skeide MA, Friederici AD (2016) The ontogeny of the cortical language network. *Nat Rev Neurosci* 17:323–332. <https://doi.org/10.1038/nrn.2016.23>.
- Smith-Conway ER, Chenery HJ, Angwin AJ, Copland DA (2012) A dual task priming investigation of right hemisphere inhibition for people with left hemisphere lesions. *Behav Brain Funct* 8:14. <https://doi.org/10.1186/1744-9081-8-14>.
- Springer JA, Binder JR, Hammeke TA, Swanson SJ, Frost JA, Bellgowan PS, Brewer CC, Perry HM, Morris GL, Mueller WM (1999) Language dominance in neurologically normal and epilepsy subjects: a functional MRI study. *Brain* 122:2033–2046. <https://doi.org/10.1093/brain/122.11.2033>.
- Szaflarski JP, Binder JR, Possing ET, McKiernan KA, Ward BD, Hammeke TA (2002) Language lateralization in left-handed and ambidextrous people: fMRI data. *Neurology* 59:238–244. <https://doi.org/10.1212/wnl.59.2.238>.
- Tagu J, Doré-Mazars K, Lemoine-Lardennois C, Vergilino-Perez D (2016) How eye dominance strength modulates the influence of a distractor on saccade accuracy. *Invest Ophthalmol Vis Sci* 57:534–543. <https://doi.org/10.1167/iovs.15-18428>.
- Tazoe T, Perez MA (2013) Speed-dependent contribution of callosal pathways to ipsilateral movements. *J Neurosci* 33:16178–16188. <https://doi.org/10.1523/JNEUROSCI.2638-13.2013>. PMID:24107950.
- Thiebaut de Schotten M, Dell'Acqua F, Forkel SJ, Simmons A, Vergani F, Murphy DGM, Catani MC (2011) A lateralized brain network for visuospatial attention. *Nat Neurosci* 14:1245–1246. <https://doi.org/10.1038/nn.2905>.
- Tussis L, Sollmann N, Boeckh-Behrens T, Meyer B, Krieg SM (2016) Language function distribution in left-handers: A navigated transcranial magnetic stimulation study. *Neuropsychologia* 82:65–73. <https://doi.org/10.1016/j.neuropsychologia.2016.01.010>.
- Tzourio N, Crivello F, Mellet E, Nkanga-Ngila B, Mazoyer B (1998) Functional anatomy of dominance for speech comprehension in left handers vs right handers. *Neuroimage* 8:1–16. <https://doi.org/10.1006/nimg.1998.0343>.
- Tzourio-Mazoyer N, Joliot M, Marie D, Mazoyer B (2016) Variation in homotopic areas' activity and inter-hemispheric intrinsic connectivity with type of language lateralization: an fMRI study of covert sentence generation in 297 healthy volunteers. *Brain Struct Funct* 221:2735–2753. <https://doi.org/10.1007/s00429-015-1068-x>.
- Tzourio-Mazoyer N (2016) Intra- and inter-hemispheric connectivity supporting hemispheric specialization. In: Kennedy H, Van Essen DC, Christen Y, editors. *Micro-, meso- and macro-connectomics of the brain. Research and Perspectives in Neurosciences*. Cham: Springer. doi: 10.1007/978-3-319-27777-6\_9.
- Vallortigara G (2006) The evolutionary psychology of left and right: Costs and benefits of lateralization. *Dev Psychobiol* 48:418–427. <https://doi.org/10.1002/dev.20166>.
- van der Knaap LJ, van der Ham IJM (2011) How does the corpus callosum mediate interhemispheric transfer? A review. *Behavioral Brain Research* 223:211–221. <https://doi.org/10.1016/j.bbr.2011.04.018>.
- Vingerhoets G (2019) Phenotypes in hemispheric functional segregation? Perspectives and challenges. *Phys Life Rev* 30:1–18. <https://doi.org/10.1016/j.plevr.2019.06.002>.
- Vossel S, Geng JJ, Fink GR (2014) Dorsal and ventral attention systems: distinct neural circuits but collaborative roles. *Neuroscientist* 20:150–159. <https://doi.org/10.1177/1073858413494269>.

## APPENDIX A. SUPPLEMENTARY MATERIAL

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