Cortex

Research report

Eye dominance influences triggering action: The Poffenberger paradigm revisited

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ABSTRACT

Our dominant eye (DE) is the one we unconsciously choose when performing a monocular task. Although it has been recognized for centuries, eye dominance and its behavioral consequences remain poorly understood. Here we used the simple and well-known Poffenberger paradigm (1912) in which participants press a button with the right or left index finger, in reaction to the appearance of a lateralized visual stimulus. By selecting participants according to their DE and handedness, we were able to decipher the impact of eye dominance on visuomotor transformation speed. We show, for the first time, that in right-handers simple reaction times (RT) in response to a lateralized visual target are shorter when it appears in the contralateral visual hemifield with respect to the DE. In left-handers, only those with a right DE exhibit a shorter RT with the left hand and they show no hemifield difference. Additionally, the Poffenberger paradigm has been used to estimate the interhemispheric transfer time (IHTT) in both directions, from the right to the left hemisphere or the reverse, by comparing hand RTs following stimulation of each visual hemifield. The present study demonstrates that this paradigm leads to biased estimations of these directionally considered IHTT and provides an explanation to the often reported IHTT negative values that otherwise appear implausible. These new findings highlight the need to consider eye dominance in studies investigating the neural processes underlying visually-guided actions. More generally, they demonstrate a substantial impact of eye dominance on the neural mechanisms involved in converting visual inputs into motor commands.

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1. Introduction

Behavioral studies, and particularly measurement of reaction time (RT), can provide information concerning the neural processes involved in sensorimotor transformations but can also shed light on general brain organization and lateralization. The production of hand movements based on visual information is a valuable part of such behavioral studies, particularly when the neural configuration of the visual and reach systems are carefully considered during experimental design. To elaborate, first consider three well-known

a Poffenberger Paradigm and classical RT predictions

Left hand responses   *Right hand responses*

Left Visual Field ●—
Right Visual Field ●—

Mean RT

Left Hand   Right Hand

	Left Hand	Right Hand
RT LVF	DP	DP + IT
RT RVF	DP + IT	DP
CUD	IT	IT

b Results of Marzi et al. meta-analysis

CUD L→R = 5.3 ms   CUD R→L = 2.3 ms

Left Hand   Right Hand

Adapted from Marzi et al. (1991)

c Predictions with a left DE

Left hand responses   *Right hand responses*

Left Visual Field ●—
Right Visual Field ●—

Mean RT

Left Hand   Right Hand

	Left Hand	Right Hand
RT LVF	DP	DP + IT
RT RVF	DP - DEA + IT	DP - DEA
CUD	-DEA + IT	DEA + IT

d Predictions with a right DE

Left hand responses   Right hand responses

Left Visual Field ●—
Right Visual Field ●—

Mean RT

Left Hand   Right Hand

	Left Hand	Right Hand
RT LVF	DP - DEA	DP - DEA + IT
RT RVF	DP + IT	DP
CUD	DEA +IT	-DEA + IT

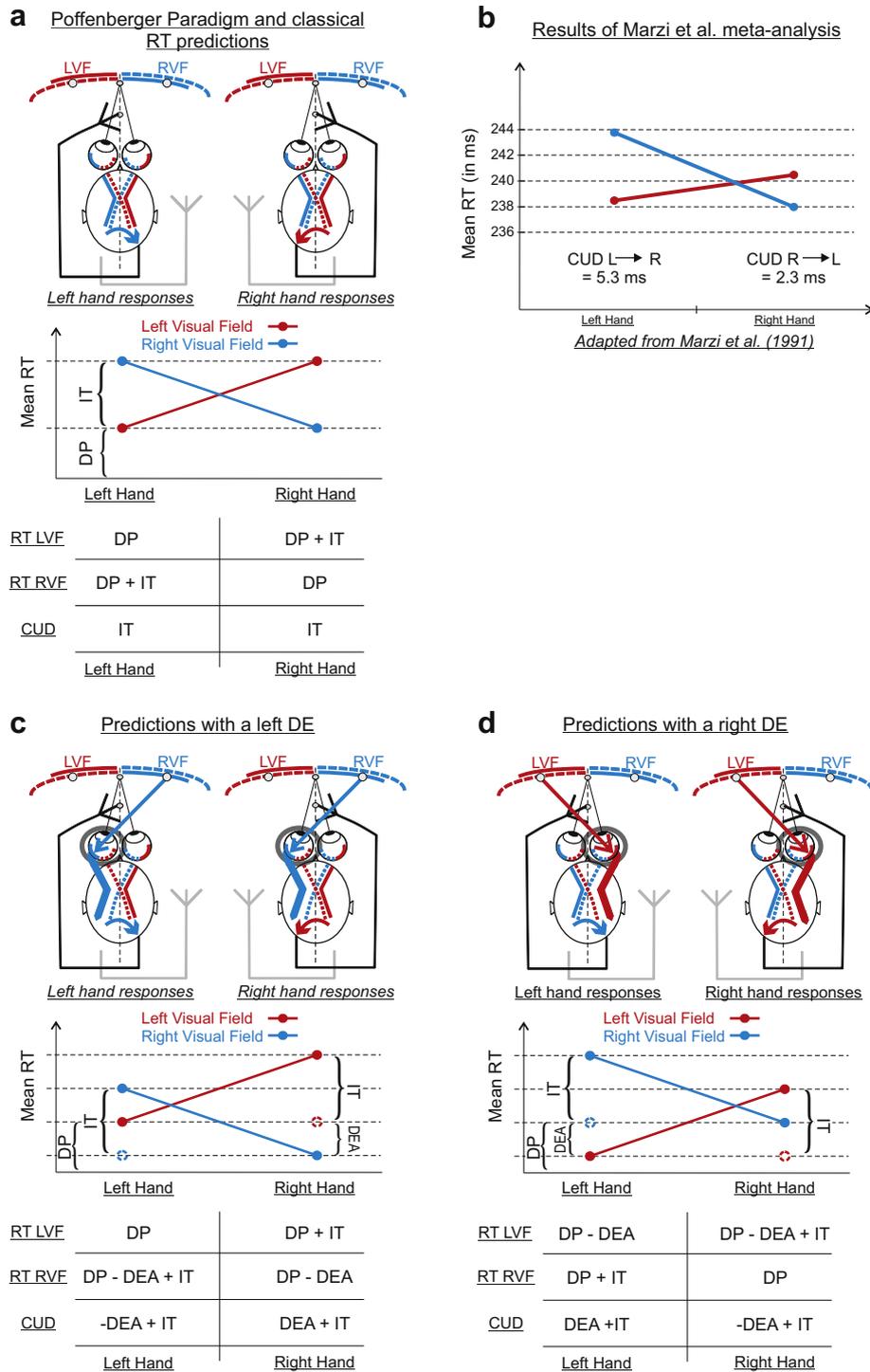**Fig. 1** − **Experimental schemes and reaction time (RT) predictions. (a) Poffenberger paradigm simple predictions. Two white LEDs (74 cd/m², 1.2° in visual angle, with their centers at a horizontal angular distance of 7° to the left or to the right of a smaller green fixation LED (6 cd/m²; .4° in visual angle) were used. Participants had to press on a central button aligned with their body midline as quickly as possible after lateral LED onset. Four conditions were tested: two uncrossed conditions, in which the hand used to respond, and the visual field wherein the stimulation appeared, were on the same side (LHa-LVF and RHa-RVF), and two crossed conditions, in which they were on opposite sides (LHa-RVF and RHa-LVF). "DP" (direct pathway) corresponds to the time required for the direct pathway without transfer (uncrossed condition). "IT" corresponds to the supplementary time for the interhemispheric transfer (crossed condition). RT difference between the two conditions involving the same hand gives a value referred to as Crossed-Uncrossed difference (CUD), either from left to right (blue arrow, left hand) or from right to left (red arrow, right hand). (b) Results of Marzi et al.'s (1991) meta-analysis (16 studies considered). Overall mean RT was 1.5 msec faster when the stimulus appeared in the LVF (red line) compared to the RVF**

characteristics of the visuomotor system: 1) each hemisphere processes information coming from the contralateral visual hemifield, 2) each hemisphere controls contralateral hand movements, and 3) each hand can respond to stimuli presented in either visual hemifield. Taking these characteristics into account, one can attain valuable information regarding the control of visually-guided movements by contrasting different combinations of visual hemifield stimulated and hand required for response. Poffenberger (1912) was the first to study RT under these different combinations to evaluate the time required for a transfer of information from one hemisphere to the other (e.g., by comparing in a block of trials with left hand responses the RTs when the stimulus is presented in the left or the right hemifield, see below for further details).

In the present study we also consider the fact that our two eyes differ. One eye is usually preferred when we have to align a target in peripersonal space with a more distant point or when performing a monocular task such as looking through a small hole. This particular type of eye dominance has been referred to as *sighting dominance* (Porac & Coren, 1976), but will be referred to simply as eye dominance from here forth in the present paper. In a meta-analysis, Bourassa, McManus, and Bryden (1996) reported that among right-handers (representing 90% of the population) 66% have a right dominant eye (DE) and 34% a left DE. According to their meta-analysis, 40% of left-handers have a right DE and 60% a left DE. Although the functions and behavioral consequences of this ocular lateralization have intrigued generations of scientists, they remain poorly understood (Carey, 2001; Mapp, Ono, & Barbeito, 2003; Wade, 1998; Wardrop, 1808, p. 245).

A seminal study by Minucci and Connors (1964) showed that movements triggered in response to monocular stimulations of the DE have shorter RTs than those evoked by stimulations of the non-DE. Using a simple RT task, the authors found that RTs of right-handers (4 with a left DE and 6 with a right DE) to a flash stimulus were systematically faster after foveal monocular stimulations of the DE than after similar stimulations of the non-DE for the four photopic intensity levels tested. These findings indicate that the influence of eye dominance is not restricted to perceptual processes but extends to sensorimotor mechanisms (see also Shneor & Hochstein, 2006; Walls, 1951). Interestingly, studies have revealed that stimulation of the DE activates a larger cerebral network and with shorter latency than stimulation of the non-DE (Rombouts, Barkhof, Sprenger, Valk, & Scheltens, 1996; Seyal, Sato, White, & Porter, 1981; but see Mendola & Conner, 2007). More specifically, recent results of Shima et al. (2010) suggest that the influence of the DE on visual activations would be related to the temporal retina of the DE

connected to its ipsilateral hemisphere. They studied activations of the primary visual cortex (V1) in response to peripheral visual stimulations in monocular condition using magnetoencephalography (MEG) overlaid on each subject's MRI scan for source localization. While the authors did not find a significant impact of eye dominance on the magnitude of V1dipole moment response after stimulation of nasal hemiretina, the stimulation of the temporal hemiretina of the DE led to greater activation compared to the stimulation of the temporal hemiretina of the non-DE. Hence, although the neurophysiological basis of eye dominance has yet to be confirmed, the larger and quicker visual activation when stimulating the DE could mainly concern its ipsilateral hemisphere which receives input from the temporal hemiretina.

The aim of the present study was to assess whether, during binocular viewing, there is a speed advantage for stimuli presented in the contralateral visual hemifield with respect to the DE (i.e., involving the temporal hemiretina of the DE). Indeed, if the larger and quicker activation recorded after DE stimulation holds in binocular viewing and is restricted to the hemisphere ipsilateral to the DE, the contralateral visual hemifield with respect to the DE should benefit from a speed advantage. In other words, processing a visual stimulus presented in this contralateral hemifield should be faster and more efficient, leading to a faster simple RT when participants are asked to react to the stimulus. To test this hypothesis, we recorded finger simple RT (button press) to the appearance of a lateralized visual stimulus. Given the crossed organization of visual and motor neural pathways, a visual hemifield advantage will not have the same consequences for both hands (see detailed predictions below). Hence we used the Poffenberger paradigm as it provides a methodology to compare response to each visual hemifield with each hand (Braun, 1992; Marzi, Bisiacchi, & Nicoletti, 1991; Poffenberger, 1912). In this paradigm, participants are asked to fixate a point straight ahead and to respond as quickly as possible to the appearance of a lateralized visual stimulus by pressing on a centrally located button, alternately with the right or the left hand.

Fig. 1a illustrates the Poffenberger paradigm-based predictions that one should take slightly longer time to react when the responding hand is on the side opposite to the visual hemifield in which the stimulation appears, than when both the stimulation and responding hand are on the same side (Braun, 1992; Corballis, 2002; Marzi et al., 1991). Indeed, if the visual stimulus and the responding hand are on the same side (referred to as the uncrossed condition), the processing of the sensory input and the organization of the motor execution are performed within the same hemisphere (i.e., through intrahemispheric pathways). If not (referred to as the crossed

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(blue line) (Wilcoxon test $T = 23$, $p < .02$). CUD was smaller from right to left (2.3 msec) than from left to right (5.3 msec) (Wilcoxon test $T = 25$, $p < .05$). (c) and (d) Poffenberger paradigm predictions with the integration of the DE influence. The gray, bold circles correspond to the DE. The postulated beneficial relationship between the temporal hemiretina of this DE and its ipsilateral hemisphere is shown by the large filled arrow. It should result in a dominant eye advantage (DEA) in stimulus processing speed for the contralateral visual hemifield. Consequently, when the temporal hemiretina of the DE was stimulated (i.e., stimuli contralateral to the DE), the value of DP should decrease (DP-DEA). Dashed circles correspond to the DP value before the IT in crossed conditions. As a starting point IT is considered longer than DEA (see text for further details).

condition), an interhemispheric transfer, from the hemisphere that receives the sensory input to the hemisphere that controls the motor response, is required (Braun, 1992; Corballis, 2002; Marzi et al., 1991). This interhemispheric transfer via the corpus callosum should lead to a longer RT in the crossed condition than in the uncrossed condition (Poffenberger, 1912; Savazzi et al., 2007). Transcribing these predictions in an algebraic model in which we noted "DP" (for direct pathway) the time required to produce a response through the direct pathway without transfer (the uncrossed condition), "IT" the supplementary time corresponding to the interhemispheric transfer (the crossed condition), and "LVF/RVF" the left/right visual hemifield, we should obtain:

<u>Left Hand responses :</u>$\quad \left. \begin{array}{l} \text{RT for LVF stimulation} : RT_{\text{LHa\_LVF}} = \textbf{DP} \\ \text{RT for RVF stimulation} : RT_{\text{LHa\_RVF}} = \textbf{DP} + \textbf{IT} \end{array} \right\}$ LVF advantage

<u>Right Hand responses :</u>$\quad \left. \begin{array}{l} \text{RT for LVF stimulation} : RT_{\text{RHa\_LVF}} = \textbf{DP} + \textbf{IT} \\ \text{RT for RVF stimulation} : RT_{\text{RHa\_RVF}} = \textbf{DP} \end{array} \right\}$ RVF advantage

Since the pioneering work by Poffenberger (1912) the speed difference value between crossed and uncrossed conditions, the so-called crossed-uncrossed difference (CUD), is thought to be a behavioral estimate of the interhemispheric transfer time (IHTT; Bashore, 1981; Marzi et al., 1991). Two ways are classically used to compute CUD: they consist in comparing crossed and uncrossed conditions that involve either the same hand (e.g., $(RT_{\text{LHa\_RVF}}) - (RT_{\text{LHa\_LVF}})$) or the same hemifield (e.g., $(RT_{\text{RHa\_LVF}}) - (RT_{\text{LHa\_LVF}})$). In our experiment we used the former to compare one hemifield with the other in order to eliminate the bias introduced by the well-established difference in speed between the left and the right hand in such simple visuo-motor tasks (Annett & Annett, 1979; Barthelemy & Boulinguez, 2001). This issue regarding CUD computation will be further discussed in the section 2.3. Hence we have:

made this suggestion after noting that in studies employing the Poffenberger paradigm an overall speed advantage for the LVF (11 over 16 studies; see also Marzi, 2010; Savazzi et al., 2007) and CUDs with smaller values from right to left than from left to right was often observed (see Fig. 1b). Because this advantage was not observed for the two direct pathways in their meta-analysis, the authors concluded that this advantage for the LVF was the result of a faster IHTT from right to left hemispheres. However, it is worth noting that the eye dominance, and a fortiori the possible specific relationship between the DE and its ipsilateral hemisphere through the temporal hemiretina (Shima et al., 2010, see above), have never been taken into account in studies using Poffenberger paradigm. Yet, we think that the DE could be critically important if eye dominance influences hemifield advantage and hence CUDs.

One could integrate, in the simple prediction scheme shown in Fig. 1a, the hypothetical special relationship between the DE and its ipsilateral hemisphere[1] (see above). This relationship would result in a speed advantage for the contralateral visual hemifield stimulating the temporal hemiretina of the DE. Taking this relationship into consideration leads to the following modified predictions (Fig. 1c and d). RTs when stimulations appear in the contralateral hemifield with respect to the DE should decrease, giving rise to larger RT differences between the two hemifields for the hand contralateral to the DE. In our algebraic model, we note "Dominant Eye Advantage" (DEA) the speed advantage that should be

<u>CUD from left to right :</u>$\quad (RT_{\text{LHa\_RVF}}) - (RT_{\text{LHa\_LVF}}) = (\textbf{DP} + \textbf{IT}) - (\textbf{DP}) = \textbf{IT}$

<u>CUD from right to left :</u>$\quad (RT_{\text{RHa\_LVF}}) - (RT_{\text{RHa\_RVF}}) = (\textbf{DP} + \textbf{IT}) - (\textbf{DP}) = \textbf{IT}$

Thus, simply considering predictions of a Poffenberger paradigm, CUD should be similar for right to left and for left to right directions.

Nevertheless, after their meta-analysis based on 16 studies where the Poffenberger paradigm was used (mainly with right-handers), Marzi et al. (1991) suggested that there could actually be an asymmetry in IHTT with faster transfer from right to left hemisphere than in the reverse direction. They

given by the stimulation of the temporal hemiretina of the DE. Importantly, as a starting point, we consider that the IT value is larger than the DEA value. Equations for RT values for each

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[1] The influence of eye dominance has not been specifically investigated in left-handers, hence we give here predictions without taking into account handedness.

hemifield and each hand, and for CUD values for both directions are written in the tables in the bottom part of panels **c** and **d** of Fig. 1. In participants with a **left DE** (Fig. 1c), an overall advantage for RVF and a smaller CUD from left to right (−DEA + IT) than from right to left (DEA + IT) should be observed. In participants with a **right DE** (Fig. 1d), an overall advantage for LVF and a smaller CUD from right to left (−DEA + IT) than from left to right (DEA + IT) should be observed. Hence, there should be an asymmetry between the CUD values obtained for each hand, the direction of which would depend on the side of the DE.

Interestingly, our prediction for right DE is strongly similar to the results of Marzi et al. (1991) (compare panels **b** and **d** of Fig. 1) but form a totally opposite pattern for left DE. One possibility would be that the results of Marzi et al. were obtained because none of the studies included in their meta-analysis, as well as other studies on this issue, took into account the participants' eye dominance. Indeed, given that a vast majority among the 16 studies included only right-handers, the LVF advantage could be ascribed to the over-representation of right-handers with right DE in each of these studies (according to Bourassa et al. (1996), 66% of right-handers have right DE). In the same meta-analysis, the authors also mentioned that handedness might affect CUDs values. Although few studies have investigated left-handers in such tasks, this meta-analysis showed that results depended on whether participants have normal or inverted posture for the writing hand: no asymmetry was reported in left-handers with normal hand posture whereas left-handers with inverted hand posture showed paradoxical negative CUDs (Marzi et al., 1991; Marzi, 2010; Pellicano, Barna, Nicoletti, Rubichi, & Marzi, 2013).

The aim of the present study was to investigate whether eye dominance influences visuomotor transformations and, if it is the case, how this could explain CUD differences reported in studies involving the Poffenberger paradigm. We conducted separate experiments with right-handers and with left-handers.

2. Experiment 1: right-handers

2.1. Material and methods

2.1.1. Participants
Thirty-eight right-handers (mean age = 26.8 years, SD = ±6.5; 22 females) participated in this experiment after having provided a signed written consent for their inclusion. All participants were healthy, reported normal or corrected-to-normal vision and showed no sign of neurological disorders. The study was performed in accordance with the local ethics committee and the ethical standards laid down in the Declaration of Helsinki (last modified, 2004). The eye dominance was assessed by the hole-in-card test (Miles, 1930) repeated three times. This test is known to be the most reliable to determine eye dominance (Taghavy & Kügler, 1987) and is not influenced by handedness. The handedness of each participant was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; score = lateralization quotient) According to this test a lateralization quotient of +100% represents extreme

right hand preference and −100% extreme left hand preference; the mean value obtained here was 70.1% (SD = ±23.7%; range from 20 to 100%). The eye dominance test allowed us to classify participants in 2 experimental groups: right-handers with left or right DE (18 and 20 participants, respectively). Supplementary Table A.1 summarizes the features of the right-handers.

2.1.2. Experimental setup
In a dimly lit room, participants were comfortably installed in a chair in front of a table on which a very sensitive response button (sampling rate: 1000 Hz) was aligned with their body midline. Depending on the condition (see section 2.1.3), either their left or right index finger was resting on this button. The participants were facing, at a viewing distance of 80 cm, a panel containing two lateralized white LEDs (74 cd/m^2, 1.2° in visual angle), with their centers at a horizontal angular distance of 7° to the left and to the right of a smaller green central fixation LED (6 cd/m^2; .4° in visual angle).

2.1.3. Task, protocol and stimulations
A trial started with the illumination of the fixation LED. Then, after a variable delay (i.e., 600–1200 msec in 200 msec steps) either the left or the right target was presented for 100 msec. The task of participants was to press on the centrally placed button as quickly as possible after the LED illumination, whatever its side (i.e., left or right visual hemifield) while keeping their gaze on the fixation LED. Each participant performed 10 blocks of 100 trials alternately with their left or right hand. The hand used in the first block was counterbalanced across participants. A short break was given between each block. Among the 500 trials performed for each hand, 224 stimulations in the LVF and 224 in the RVF were pseudo-randomly mixed. In the remaining 52 trials, no stimulus appeared after the illumination of the fixation target. These 'catch-trials', pseudo-randomly scattered within the 5 blocks, helped to prevent target anticipation. To help participants maintaining central fixation, the green LED remained lighted throughout the trial. Nevertheless, gaze position was checked by electro-oculography and trials with saccades were rejected from the analyses.

2.1.4. Statistical analysis
Trials in which RT was smaller than 150 msec (anticipatory responses, .6% of the trials; see Iacoboni & Zaidel, 2000; Jensen, 2006) or larger than 800 msec (lack of attention, 1% of the trials) were discarded. For each participant, the median RT was then computed for each of the four experimental conditions. Data for these right-handed participants passed the O'Brien's test for homogeneity of variances (p = .41; O'Brien, 1979). Therefore, medians of RT were submitted to a 2 (DE: Left, Right) × 2 (Hand: Left, Right) × 2 (stimulated Hemifield: Left, Right) mixed ANOVA, with repeated measured on the last two factors. Newman–Keuls post-hoc tests were used to perform specific comparisons. For each participant group, means of the medians across participants were computed. Finally, CUD values for both directions (i.e., from right to left or from left to right) were obtained from these means.

A randomization test (permutation test) was also used to assess whether the pattern of CUD values obtained for the two

groups of right-handers (right or left DE) was due to chance (null hypothesis) or was actually related to eye dominance (Manly, 1997). Each participant with his/her two CUD values (i.e., left to right and right to left) was randomly reassigned to one of the two groups (right or left DE) and mean CUD values were then recomputed. This procedure of random shuffling and mean computation was repeated 10000 times. Finally the original observed mean CUD values were compared to the randomization distributions giving the probability that observed values were obtained by chance.

2.2. Results

Means of the median RTs obtained by right-handers with left DE or right DE are shown on the Fig. 2. Median values were submitted to a three factor mixed ANOVA to evaluate the impact on the hand RT of the DE (Left DE/Right DE), of the responding Hand (Left hand/Right hand), and of the Hemifield of presentation (Left visual field/Right visual field). It revealed no significant main effects of Eye ($p = .8$), Hand ($p = .4$), or Hemifield ($p = .86$) and no significant interaction between Hand and Eye ($p = .4$). However, the ANOVA showed a significant interaction between the Hand and Hemifield factors [$F(1,36) = 16.81$; $p = .0002$]. The breakdown of the interaction (*Newman–Keuls test*) showed that RTs were significantly faster in the uncrossed condition than in crossed condition ($p = .019$ and $p = .018$ for the left and right hand, respectively). These results are in line with the basic predictions of the Poffenberger paradigm. More interestingly, we found a significant interaction between DE and Hemifield factors [$F(1,36) = 10.31$; $p = .0028$] suggesting that stimuli presented in the contralateral hemifield with respect to the DE led to shorter RTs. Post-hoc comparisons revealed a tendency to faster RTs when the stimulus appeared in contralateral than ipsilateral hemifield to the DE ($p = .09$ and $p = .055$ for right-handers with right and

left DE, respectively). The reasons for falling just short of the conventional .05 cut-off value for statistical significance could be found by analyzing the *post-hoc* comparisons of the second level interaction between Hand, Hemifield and Eye ($p = .42$). Although this interaction was not significant here, inspection of the post-hoc comparisons is informative (Hsu, 1996, p. 177). These comparisons of the second level interaction allowed to differentiate the hand used to respond and revealed that in agreement with predictions formalized with our algebraic model (see Fig. 1c, d), significant differences between the two hemifields were only found when participants with left DE responded with the right hand ($p = .0003$) and when right DE participants responded with the left hand ($p = .001$).

Some right-handers included in the present study were weakly lateralized (Edinburgh Handedness Inventory score < 50%: 2 and 4 right-handers with left and right DE, respectively; see Supplemental Table 1). The results described above were not influenced by these weakly lateralized subjects. Indeed, we performed the same analysis as reported above with only participants having a score ≥ 50% and obtained similar results as when all participants were included in the analyses (see Supplementary Material).

Finally, the randomization test conducted with all 38 participants (see Material and methods) revealed that the pattern of observed CUD values was strongly related to the eye dominance since the null hypothesis (pattern obtained by chance) is rejected for each of the four cases (i.e., CUD from right to left and from left to right for each group of right-handers) with $p < .01$ (see Supplemental Fig 1).

2.3. Discussion

The algebraic model described in the introduction (see section 1.) predicted the impact of eye dominance on visuo-motor processing for targets in each visual hemifield. This
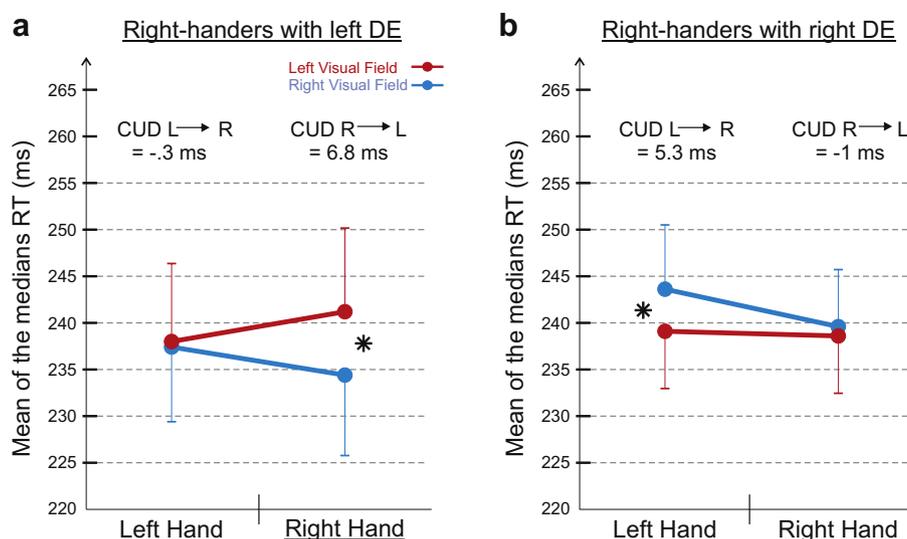

Fig. 2 — **Averaged median RTs for right-handers. A mixed ANOVA revealed a significant interaction between DE and Hemifield factors [$F(1,36) = 10.31$; $p = .0028$]: right-handers with left DE (a) tended to show faster RTs when the stimulus appeared in right visual field (blue line) whereas right-handers with right DE (b) tended to show a left visual field (red line) advantage. Furthermore,** *Post-hoc comparisons* **showed that this difference was statistically significant (*, $p < .05$) only when participants used their contralateral hand with respect to the DE. Error bars correspond to SEM.**

prediction, consisting of a speed advantage for the hemifield contralateral with respect to the DE, was completely fulfilled in right-handers. Indeed, right-handers with right DE show a speed advantage for the LVF whereas right-handers with left DE show a speed advantage for the RVF. From a general point of view, the results demonstrate the influence of the eye dominance in the processing of visual information for hand movements production in right-handers.

As stated in the introduction, some neurophysiological studies already tried to characterize the influence of eye dominance and brought data in favor of a larger and a quicker visual activation when the DE is monocularly stimulated (Rombouts et al. 1996; Seyal et al. 1981). The speed advantage observed here for the contralateral hemifield with respect to the DE corroborates the special relationship between the DE and its ipsilateral hemisphere proposed by Shima et al. (2010). It indeed supports the assumption that the temporal hemi-retina of the DE could be responsible for the greater activation of the hemisphere ipsilateral to the DE. Nevertheless we note that the neurophysiological basis of the eye dominance phe-nomenon is far from clear. For example, contrary to the traditional assumption of a hard-wired trait, the eye domi-nance has been shown to depend on horizontal gaze position. Indeed, Khan and Crawford (2001) and Carey and Hutchinson (2013) showed that the eye dominance switches when the gaze is contralaterally oriented with respect to the DE: in this condition, subjects tend to prefer the other eye to realize an alignment between a ring and distant target. In the context of the present RT study, a contralateral gaze deviation with respect to the DE should be associated with a change of the hemifield for which a speed advantage is observed. This pre-diction has to be tested in further experiments.

When compared to previous work concerning visuo-motor asymmetries, the present results may appear somewhat contradictory with classical reports of naso-temporal asym-metries (the term "naso-temporal" is here used for monocular condition in which the temporal hemifield corresponds to what is processed by the nasal hemiretina and the nasal hemifield to what is processed by the temporal hemiretina). Indeed, in tasks where subjects choose themselves the di-rection of their saccades performed in monocular conditions, they tend to prefer targets presented in the temporal hemi-field (e.g., Bompas, Sterling, Rafal, & Sumner, 2008; Posner & Cohen, 1980). Such results are in line with an advantage for the ipsilateral hemifield with respect to the eye, whereas in the present study the advantage was for the contralateral hemifield with respect to the DE. Nevertheless, naso-temporal asymmetry was not observed in the latencies of the saccades (Bompas et al. 2008; Honda, 2002; Jóhannesson, Asgeirsson, & Kristjánsson, 2012; Rafal, Smith, Krantz, Cohen, & Brennan, 1990; Rafal, Henik, & Smith, 1991; Walker, Mannan, Maurer, Pambakian, & Kennard, 2000; see however Kristjánsson, Vandenbroucke, & Driver, 2004). The fact that the present study deals exclusively with RT values could be a clue to resolve the contradiction. In addition, these naso-temporal asymmetries were mostly observed for eye movements whereas the present study focused on hand movements. Finally, one could also ask whether the retino-tectal pro-jections could play a role in the results obtained here. Indeed, ganglion cells of the retina in addition to projecting into the

lateral geniculate nucleus giving rise to the geniculocortical pathway, also project directly on the superior colliculus (Perry & Cowey, 1984; Williams, Azzopardi, & Cowey, 1995). The work of Sylvester, Josephs, Driver, and Rees (2006) examined the retino-tectal projections in humans with fMRI. Studying only subjects with right DE, they showed that the retino-tectal projections are stronger between the nasal hemiretina and the contralateral superior colliculus. This pattern is opposite to the one required to explain the effects observed in the present study. In sum, our results would rather support a specific organization related to the DE than previously described naso-temporal asymmetries or asymmetries in retino-tectal projections.

The present results may also shed new lights on classical views concerning CUD values. As briefly described in the introduction (see section 1), we hypothesized that results from Marzi et al. (1991); see Fig. 1b) could be due to an over-representation of right-handers with right DE (two-thirds in a random population; Bourassa et al., 1996). Indeed, none of the studies included in their meta-analysis took into account eye dominance. Results of the present experiment obtained in right-handers with right DE largely corroborate those obtained in the meta-analysis by Marzi et al. (1991). Both patterns showed an overall LVF speed advantage and faster CUDs from right to left than in the reverse direction. The only difference is that negative CUDs as those revealed in our experiment were not reported in the Marzi et al. meta-analysis. One pos-sibility is that the presence of right-handers with a left DE in the 16 studies included in the Marzi et al. (1991) meta-analysis (i.e., ~34% as estimated by Bourassa et al. (1996) in random samples of the population), who showed in the present study the opposite pattern of results compared to those obtained by our participants with right DE may have prevented negative CUD values.

To specifically test this hypothesis, we conducted a Monte-Carlo simulation (Mooney, 1997). Given that Marzi et al. (1991) compiled numerous studies using the Poffenberger paradigm that did not take into account the DE, we simulated what should be the result of such a compilation of a large set of studies using this paradigm while not taking into account the DE in a population of right-handers, which by definition in-cludes a given percentage of left DE. The basic idea was to evaluate if the results shown by Marzi et al. (1991), i.e., a trend toward RT values for participants with right DE but with no negative CUDs, see Fig. 1b) could be obtained by not taking into account the DE. We simulated 10000 experiments in which 20 right-handers would have been studied. We first drew a random distribution of the number of participants with right DE (out of the 20 participants) for these 10,000 experi-ments which gave us the composition in right-handers with right DE and left DE for each of our simulated experiments. This distribution was assumed to be normal with a mean of 65.57% and an SD of 7.64% (Bourassa et al., 1996).[2] Then, from the present study we had at our disposal mean RT values for each of the 4 possible conditions (2 hands for response × 2 hemifields for stimulus presentation) for right-handers with

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[2] This Standard Deviation was not given in Bourassa et al. (1996). We computed it from the distribution of the means for the 29 studies considered in this meta-analysis.

right DE and for right-handers with left DE. We randomly drew from distributions based on these results (also assumed to be normal, see Supplementary Material for means and SDs) RT values for each participant of these 10000 iterations, depending on their eye dominance. Then, for each iteration we computed the average value for each of the four hand–visual field combinations without taking into account the eye dominance, i.e., merging the 20 subjects. Finally, as it would have been done for a meta-analysis, we computed the grand averages for these RT values from these 10000 theoretical experiences (Fig. 3). Results showed very similar values to those obtained in the Marzi et al. (1991) meta-analysis (compare Fig. 3 with the panel b of the Fig. 1). As in Marzi et al. (1991), we tested the statistical significance of differences between LVF and RVF stimulations and between the two

CUD directions from the means of each simulated experiment. However, given that we simulated 10000 studies, we used Student's *t*-tests rather than the Wilcoxon tests used in Marzi et al.'s (1991) study which involved only 16 studies (the nonparametric Wilcoxon test is best suited for small sample size). Results from these tests showed an overall speed advantage for LVF compared to RVF (*p* < .001 in our simulation; *p* < .02 in Marzi et al. 1991) and smaller CUD, but not negative, for the right to the left direction than for the left to the right direction (*p* < .001 in our simulation; *p* < .05 in Marzi et al. 1991). Although not a demonstration, this simulation fully supports the idea that not taking into account eye dominance biases average measurements toward the results obtained by right-handers with right DE and leads to the absence of negative CUDs in inter-subject means. Moreover, the non-negligible proportion of right-handers with left DE could explain the rather large and poorly understood inter-individual variability reported in studies based on the Poffenberger paradigm (e.g., Hasbroucq, Kornblum, & Osman, 1988; Iacoboni & Zaidel, 2000).

Our data strongly suggest that asymmetry in IHTT described in several studies based on behavioral data (Aglioti, Dall'Agnola, Girelli & Marzi, 1991; Marzi, 2010; Milner, Jeeves, Ratcliff, & Cunnison, 1982; Savazzi et al., 2007) is to some extent due to the eye dominance acting as a hidden factor. Nevertheless, crucially, we are not questioning the observation of IHTT asymmetry made from ERP studies. For a lateralized visual stimulation, visually evoked potentials (VEP) over contralateral visual areas occur slightly earlier than VEP over the ipsilateral hemisphere (from 5 to 20 msec; Brown, Larson, & Jeeves, 1994; Marzi, 2010 for reviews). This ipsilateral activation is the consequence of information transfer through the corpus callosum after the contralateral activation as evidenced by its absence in acallosal patients (Rugg, Milner, & Lines, 1985; Zaidel & Iacoboni, 2003). Hence the timing difference between the two VEP waves (i.e., contralateral and ipsilateral sites to the stimulation) gives an accurate measure of IHTT (Nowicka, Grabowska, & Fersten, 1996; Rugg, Lines, & Milner, 1984). It has repeatedly been shown that this latency difference is shorter from right to left than from left to right direction (Iwabuchi & Kirk, 2009; Saron & Davidson, 1989; see Brown et al., 1994 for a review). This ERP method provides a more direct measurement of IHTT than behavioral CUD estimation and allows to avoid the temporal confound introduced by the eye dominance in the series of sensorimotor transformations leading to hand movements. Consequently the IHTT asymmetry demonstrated with VEP appears unquestionable. In fact our results support the idea that behavioral (e.g., hand RT) and electrophysiological (e.g., VEP) variables reflect partly distinct processes (Saron & Davidson, 1989; Savage & Thomas, 1993).

Importantly, in these right-handed participants, whatever their DE, the crossed pathway for the hand ipsilateral to the DE unexpectedly led to shorter RTs than the uncrossed pathway, resulting in negative CUDs. In its current stage, the algebraic model remains inadequate to explain these illogical values. However, negative CUDs for the ipsilateral hand observed in our right-handers can become intelligible if one considers that the speed advantage due to the eye dominance (DEA) could actually be larger than the time required to
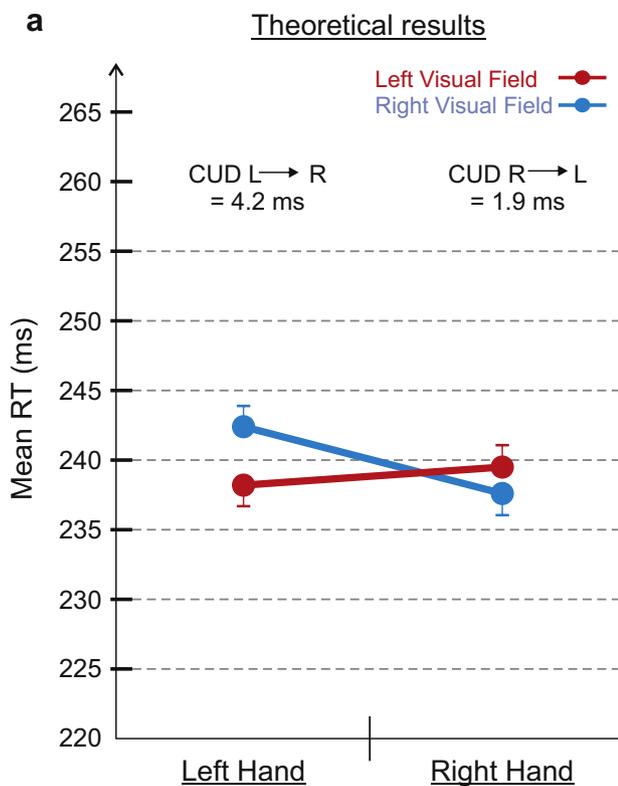

a

Theoretical results

Fig. 3 – **Results of the Monte-Carlo simulation (N = 10000 iterations) conducted to illustrate the effect of not taking into account the DE in a Poffenberger paradigm. The simulation was based on the known proportion of Right-handers with a left DE in a random population of Right-handers (Bourassa et al., 1996) as well as on the data of the present study for the RT values in the two types of Right-handers (see text for details). Grand averages for each of the four hand–visual field combinations from these 10000 iterations are shown. The pattern of result is very similar to the one obtained in Marzi et al.'s meta-analysis (1991): overall mean RT was 1.2 msec shorter when the stimulus appeared in LVF than RVF (t-test: p < .001). CUD was smaller from right to left (1.9 msec) than from left to right (4.2 msec) as shown by a t-test (p < .001). Results are to be compared with panel (b) of Fig. 1.**

transfer the information from one hemisphere to the other (IT). Indeed, if we assume in our algebraic model that DEA value is larger than IT value, we obtain for right-handers with a **left DE** a smaller and negative CUD for the left to right direction:

$$CUD\ left\ to\ right = (-DEA) + IT \rightarrow Negative\ CUD\ (IT < DEA)$$

$$CUD\ right\ to\ left = DEA + IT \rightarrow Large\ CUD$$

For the right-handers with a **right DE** we obtain a smaller and negative CUD for the right to left direction:

$$CUD\ left\ to\ right = DEA + IT \rightarrow Large\ CUD$$

$$CUD\ right\ to\ left = (-DEA) + IT \rightarrow Negative\ CUD (IT < DEA)$$

Hence, the results obtained in right-handed participants are in agreement with the assumption of a larger value for DEA than the supplementary time caused by interhemispheric transfer (IT; the crossed condition). The crossed condition would remain faster than the uncrossed condition leading to negative CUDs.

Finally, by demonstrating the speed impact of the eye dominance on simple RTs to lateralized targets, our results and the suggested algebraic model provide an alternative explanation to the two postulates drawn by Braun from his review of 49 studies involving a Poffenberger paradigm (Braun, 1992, p. 343). This author noted that CUD was always larger when computed from the ipsilateral hand and, conversely, negative when computed from the contralateral hand with respect to the advantaged visual hemifield (see also Braun & Daigneault, 1994 for detailed discussion). Braun (1992) suggested that the modulation of CUD values for each hand could be the result of hemispheric specialization differences in the processing visual inputs and he proposed a scheme in which fast and slow channels from each side of the brain to the other can coexist. The present experiment shows that eye dominance could be sufficient to explain the two main postulates raised in Braun's (1992) review. Indeed Fig. 2a and b show that CUD obtained in the two groups of right-handers are exactly in agreement with the pattern described in Braun (1992). The larger visual activation of the hemisphere ipsilateral to the DE (Shima et al., 2010, see section 1) could in fact correspond to the specialization hypothesized by Braun (1992).

3. Experiment 2: left-handers

To our knowledge, no study has specifically investigated the influence of the eye dominance during a sensori-motor task in a left-handed population. This could be related to the difficulty in recruiting left-handed individuals with either right or left DE and also due to the fact that left-handers show generally less hemispheric lateralization for controlling visuo-spatial skills than right-handers (Eviatar, Hellige, & Zaidel, 1997; Hécaen, De Agostini, & Monzon-Montes, 1981; Hellige et al., 1994). Thus, to gain a more complete understanding of the eye dominance effect, we performed exactly the same Poffenberger paradigm employed in Experiment 1 but with left-handed participants.

3.1. Material and methods

3.1.1. Participants
Twenty-two left-handers (mean age = 24.4 years, SD = 5.2; 12 females) participated in this experiment. They were all left-handed (mean = −60% SD = ±24% range from −20 to −100%) as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). The eye dominance test (see section 2.1.1) allowed us to classify participants in 2 experimental groups: left-handers with left or right DE (12 and 10 participants, respectively). Hand posture during writing was also determined (non-inverted vs inverted) (Levy & Reid, 1976). Supplementary Table A.2 summarizes the features of the left-handers.

We used exactly the same experimental setup, task, protocol and stimulations as in the Experiment 1 (see sections 2.1.2 and 2.1.3).

3.1.2. Statistical analysis
Trials in which RT was smaller than 150 msec or larger than 800 msec were discarded (rejection rates: .7% and .6%, respectively), the median RT was then computed for each of the four experimental conditions. Data for left-handers also passed the O'Brien's test (1979) for homogeneity of variances ($p = .67$) and then were submitted to the same three-factor mixed ANOVA as in experiment 1 (see section 2.1.4).

3.2. Results

Means of the median RTs obtained by left-handers with left DE or right DE are shown on the Fig. 4. As for right-handers, median RTs obtained by left-handers with left DE or right DE were submitted to a three-factor mixed ANOVA. A significant interaction between the factors Hand and Hemifield [$F(1,21) = 4.39$; $p = .049$] indicated that the basic predictions of the Poffenberger paradigm were fulfilled. Nevertheless, unlike for right-handers, there was no interaction between the DE and Hemifield factors. Rather we found a significant interaction between factors Hand and DE [$F(1,21) = 6.12$; $p = .022$] which suggests that the fastest hand depends on the side of the DE. In fact, *Post-Hoc* comparisons showed that this significant interaction was due to shorter RTs when left-handers with right DE used their left hand ($p = .006$).

3.3. Discussion

In left-handers, predictions provided in the introduction are only marginally respected. Only left-handers with left DE tend to show faster RTs when target appeared in the contralateral hemifield (i.e., RVF). This non-statistically significant trend ($p = .12$) was also accompanied, as in right-handers, by a larger difference of RT between hemifields for the contralateral hand (i.e., the right hand) with respect to the DE. Finally, for these participants the crossed pathway also led to shorter RTs than the uncrossed one, leading to a negative CUD. Conversely, results obtained by left-handers with right DE in the conditions with right hemifield stimulation are not consistent with our predictions. For this hemifield, which is not supposed to be influenced by the DE, participants nevertheless displayed shorter RTs for the crossed condition (left-hand response to RVF stimulation) than for the uncrossed one (right-hand
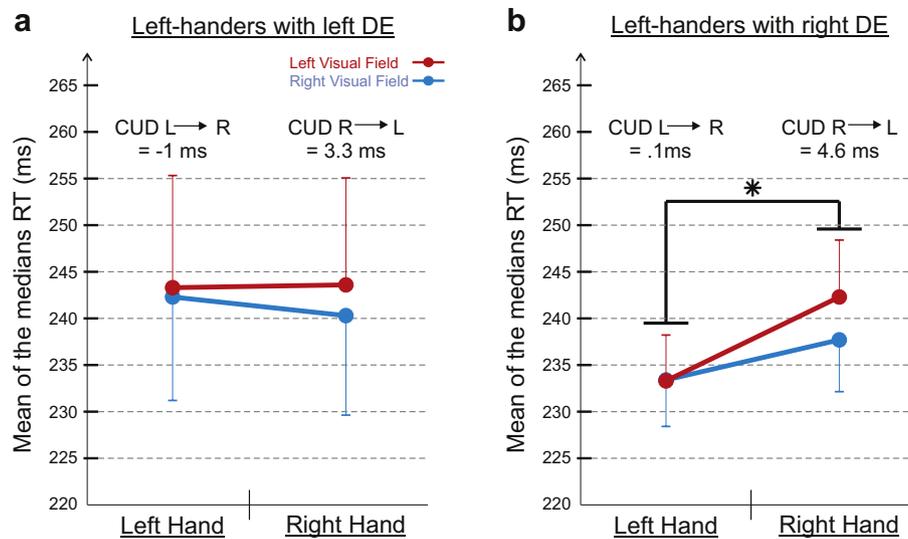
Fig. 4 – Averaged median RTs for left-handers. A mixed ANOVA revealed a significant interaction between DE and Hand factors [$F(1,21) = 6.12$; $p = .022$]. *Post-hoc comparisons* did not show a significant difference between hands ($p > .6$) in left-handers with left DE (a) whereas left-handers with right DE (b) showed faster RTs when they used their left hand ($p = .006$). Error bars correspond to SEM.

response to RVF stimulation). In sum, this pattern resulted in a statistically significant advantage for the left hand in left-handers with right DE, irrespectively of the stimulated hemifield. It is interesting to note that the RTs recorded in these conditions (i.e., left hand responses to left or right visual field stimulation) for these participants were the lowest RTs recorded for all combinations of groups and conditions of the present experiment. This could provide an explanation for the reported over-representation of left-handers with right DE in top-level sports involving high spatio-temporal constraints and uncertainty such as fencing (Azemar, 2003, p. 87, p. 241).

A potential important factor to analyze the performance of left-handers may also be their adopted writing posture, i.e., inverted or non-inverted. It has been suggested that left-handers who adopt an inverted writing posture could control the distal musculature mainly from the ipsilateral hemisphere (Levy & Reid, 1976, 1978; Moscovitch & Smith, 1979; but see Herron, Galin, Johnstone, & Ornstein, 1979; McKeever & VanDeventer, 1980; Teasdale & Owen, 2001). To verify whether these inverted writers (n = 7 in our group of left-handers, see Supplementary Table A2) could have influenced the results, we conducted a statistical analysis for left-handers (see section 3.1.2) while considering only participants that employ non-inverted writing posture. This new analysis resulted in a very similar pattern of effects to those observed when all left-handers were integrated: interaction between factors Hand and Hemifield ($p = .073$); interaction between factors Hand and DE ($p = .067$). In addition, in left-handers with right DE, the same tendency for faster RT with the left hand was observed ($p = .071$) as when all participants are considered. Hence, the presence of left-handers who adopt an inverted posture to write cannot account for the mismatch between the results in left-handers and our predictions.

To our knowledge, this is the first investigation of the influence of DE in left-handers. While the results evidenced that

left-handers with right DE showed a speed advantage when using the left hand, further studies will be necessary to appraise the sensorimotor transformations used by left-handers with left DE to control their movements.

4. General discussion

The present study aimed to decipher the speed influence of eye dominance on the neural mechanisms involved in converting visual inputs into motor commands. Results showed that this influence depends on the handedness of participants. In right-handers (Experiment 1 section 2), shorter RTs were found for targets presented in the contralateral visual hemifield with respect to the DE. This speed advantage indicates that eye dominance plays a key role in visuomotor transformations and could hence explain CUD differences reported in previous studies employing the Poffenberger paradigm (see algebraic model, section 1). In left-handers (Experiment 2 section3.), the impact of eye dominance seems to be weaker. Nevertheless, it is important to note that the special relationship between the DE and its ipsilateral hemisphere proposed by Shima et al. (2010) has never been searched for in left-handers. Thus, the importance of temporal hemiretina input in controlling visually-evoked hand movements in left-handers remains unknown. Moreover, left-handers show generally less hemispheric lateralization for controlling visuo-spatial skills (Eviatar et al., 1997; Hécaen et al., 1981; Hellige et al., 1994). It is possible that the visuomotor transformations of left-handers are less strictly linked to the DE than for right-handers.

In any case, the results of the present study have strong implications concerning the conclusions that can be drawn from the Poffenberger paradigm. Indeed, among the two ways classically used to compute CUD, one, the comparison

between conditions involving the same hemifield ((RT_{RHa_LVF}) − (RT_{LHa_LVF}) for example), has already been largely rejected. Indeed, for this computation of CUD, differences in the neuromuscular or sensorimotor systems of the two hands could largely bias the CUD computation (Annett & Annett, 1979; Barthelemy & Boulinguez, 2001). Importantly, the speed advantage for the contralateral visual hemifield with respect to the DE shown for right-handers in the present study implies that the second method for computing CUD, which compares RT between the crossed and uncrossed conditions involving the same hand ((RT_{LHa_RVF}) − (RT_{LHa_LVF})), is also biased. Indeed this latter CUD computation results from the comparison of the two hemifields for which difference in visuo-motor processing speed is due to the eye dominance phenomenon. In the present study, this bias has led to the prevalence of negative CUDs for the hand ipsilateral to the DE. Taken together, the disclosures of these biases (previous and present studies) bring an unequivocal demonstration to the claim that CUDs cannot be considered as a correct estimation of the IHTT (Braun & Daigneault, 1994; Hasbroucq et al., 1988). The only valid alternative to deal with the paradigm came from Poffenberger himself (Poffenberger, 1912). Indeed, he only compared RT values for direct pathways, averaging RT_{RHa_RVF} and RT_{LHa_LVF}, with RT values for indirect pathways, averaging RT_{RHa_LVF} and RT_{LHa_RVF}. Hence, he limited his approach to a global estimation of IHTT without making inference regarding IHTT values for both directions.

5.   Conclusions

In conclusion, our findings demonstrate a substantial impact of eye dominance on neural mechanisms involved in converting visual inputs into motor commands. Importantly, the effect of eye dominance strongly depended on whether the participants were right- or left-handed. In right-handers, RTs were shorter for targets presented in the contralateral visual hemifield with respect to the DE whereas in left-handers, RTs of left hand was shorter only in participants with right DE, irrespective of the stimulated hemifield. Given the relatively high proportions of crossed configuration (34% of right-handers have a left DE and 40% of left-handers have a right DE), our results imply that eye dominance has to be carefully considered in studies on visually triggered actions.

Authors contributions

RC, JB, AG discussed the results, elaborated conclusions and wrote the paper.
RC conducted the experiments and analyzed the data.
AG conceived the experiments and supervised the project.

Acknowledgments

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2014.05.009.

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