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Asymmetry in visual information processing depends on the strength of eye dominance

Romain Chaumillon[a], Nadia Alahyane[b], Patrice Senot[b], Judith Vergne[b], Christelle Lemoine-Lardennois[b], Jean Blouin[a], Karine Doré-Mazars[b], Alain Guillaume[a,1], Dorine Vergilino-Perez[b,c,*,1]

[a] Aix-Marseille Université, CNRS, Laboratoire de Neurosciences Cognitives, UMR7291, Fédération de recherche 3C, Marseille, France
[b] Laboratoire Vision Action Cognition EA no. 7326, Université Paris Descartes, Sorbonne Paris Cité, Boulogne Billancourt, France
[c] Institut Universitaire de France, France

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ABSTRACT

Unlike handedness, sighting eye dominance, defined as the eye unconsciously chosen when performing monocular tasks, is very rarely considered in studies investigating cerebral asymmetries. We previously showed that sighting eye dominance has an influence on visually triggered manual action with shorter reaction time (RT) when the stimulus appears in the contralateral visual hemifield with respect to the dominant eye (Chaumillon et al. 2014). We also suggested that eye dominance may be more or less pronounced depending on individuals and that this eye dominance strength could be evaluated through saccadic peak velocity analysis in binocular recordings (Vergilino-Perez et al. 2012). Based on these two previous studies, we further examine here whether the strength of the eye dominance can modulate the influence of this lateralization on manual reaction time. Results revealed that participants categorized as having a strong eye dominance, but not those categorized as having a weak eye dominance, exhibited the difference in RT between the two visual hemifields. This present study reinforces that the analysis of saccade peak velocity in binocular recordings provides an effective tool to better categorize the eye dominance. It also shows that the influence of eye dominance in visuo-motor tasks depends on its strength. Our study also highlights the importance of considering the strength of eye dominance in future studies dealing with brain lateralization.

1. Introduction

Lateralization is a fundamental property of the human brain that has consequences on perceptual, motor and cognitive processes (Dien, 2008; Serrien et al., 2006). One aspect of the brain lateralization that remains very poorly understood is the fact that we unconsciously choose the same eye when we have to perform a monocular task. This preference is defined as the sighting eye dominance (Coren and Kaplan, 1973; Porac and Coren, 1976). Some studies began to unravel the neural bases of this lateralization. Neurophysiological works have shown that the monocular stimulation of the dominant eye (DE) leads to a faster and larger activation of the visual cortical areas compared to the stimulation of the non-dominant eye (Seyal et al.,1981; Rombouts et al.,1996). However, Mendola and Conner (2007), on a small sample of 7 participants, found that acuity eye dominance defined as the eye having the higher visual acuity, was related to fMRI BOLD signal change in the ventral occipital area (V1v, V2v, VP and V4) between monocular stimulations, whereas sighting eye dominance was not. They pointed to the fact that other brain regions not assessed in their study might be better correlated with sighting than acuity dominance. Indeed, two other studies testing sighting eye dominance, suggested that the difference in visual activation mainly concerns the ipsilateral cortex. By studying anatomical MRI, Erdogan et al. (2002) observed that the visual cortex ipsilateral to the DE was larger in size than the contralateral one. More recently in a MEG study, Shima et al. (2010) investigated brain/V1 response to visual stimuli. They showed that there was no impact of eye dominance on the magnitude of primary visual cortex response after stimulations of nasal hemiretinas (connected to the contralateral hemisphere) but that the stimulation of the temporal hemiretina of the DE (connected to its ipsilateral hemisphere) led to a greater activation compared to the stimulation of the temporal hemiretina of the non-DE. Taken together, these past studies suggest

* Correspondence to: Laboratoire Vision Action Cognition, EA no.7326, Institut de Psychologie, 71 avenue Edouard Vaillant, 92774 Boulogne Billancourt, France.
E-mail address: dorine.vergilino-perez@parisdescartes.fr (D. Vergilino-Perez).
[1] AG and DVP should be considered as co-last authors.

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the existence of a particular relationship between the dominant eye and its ipsilateral visual cortex.

Recently, Chaumillon et al. (2014) reasoned that this specific relationship between the sighting dominant eye and the ipsilateral visual cortex could result in an asymmetry in the processing of information coming from each visual hemifield. In a simple visuomanual task, the larger visual activation in the hemisphere ipsilateral to the DE could be associated with better and quicker processing of a stimulus appearing in the visual hemifield contralateral to the DE and hence, lead to shorter reaction time (RT) of hand movement in response to this stimulus presentation. Given the crossed organization of visual and motor neural pathways, a visual hemifield advantage will not have the same consequences for both hands. Hence a thorough examination of this issue requires comparing the hemifield difference for both hands, which can be seen by using the Poffenberger paradigm (Poffenberger, 1912; see Chaumillon et al., 2014 for details). In this paradigm, participants have to press a button with their left or right index in response to a lateralized visual target appearing either to the left or to the right from a central fixation point. Using this paradigm, Chaumillon et al. (2014) were indeed able to show that manual RT was shorter in response to visual stimulation appearing in the contralateral visual hemifield with respect to the DE. These observations are consistent with a special relationship between the DE and the ipsilateral hemisphere and shed light on the influence of this lateralization of the visual system in visuo-motor transformations. Importantly, the results of this past study also evidenced that the difference in RT between the two visual hemifields (approximately 6 msec) is only observed when subjects responded with their hand contralateral to the DE. This latter observation follows logically from the articulation between the two temporal factors involved in the task: the temporal advantage due to the eye dominance and whether an interhemispheric transfer is required or not before the manual response (see Chaumillon et al., 2014 for more details).

A characteristic shared by most, if not all, lateralizations of the human brain is their continuous nature: for a given lateralized function, people are distributed on a continuum ranging from extremely lateralized in one direction to the other extreme, with an infinite number of intermediate possibilities (Beaton, 1997; Scharoun and Bryden, 2014). Nevertheless, eye dominance is generally measured by tests asking people to unconsciously choose one or the other eye (Seijas et al., 2007; Rice et al., 2008). For example, in the widely used Hole-in-card test (Miles, 1930), the participant looks at a target through the hole in a cardboard using both hands, and then slowly brings the card toward the face by keeping the target centered in the hole. The eye over which the card is centered is considered as the sighting dominant eye. Obviously, such test gives a binary result, participants having a left or a right DE. But, the idea that sighting eye dominance could be more or less robust (*i.e.* could be quantified along a continuum) has already been proposed (Carey, 2001; Johansson et al., 2015).

Different methodologies to quantify the strength of eye dominance have been proposed (Carey and Hutchinson, 2013; Johansson et al., 2015). Notably, Carey and Hutchinson (2013) suggested that the strength of eye dominance might be revealed by the eccentricity at which the switch of dominance from one eye to the other is observed in a task requiring visual alignments with different target eccentricities (see also Khan and Crawford, 2001). Recently, Vergilino-Perez et al. (2012) suggested that eye dominance could be quantified in another way, with participants categorized according to the strength of their eye dominance (i.e., strong or weak eye dominance) based on the analysis of the peak velocity of horizontal saccades. Movements of the two eyes of the participants were recorded while they made rightward or leftward saccades toward lateralized visual targets. A group of participants exhibited the classical naso-temporal asymmetries in saccadic peak velocities: temporal saccades were consistently found to have higher peak velocity than nasal saccades with a difference about 20°/sec for movements of same amplitude, hence the right eye has its higher peak velocity for rightward saccade and vice-versa for the left eye (Hyde, 1959; Robinson, 1964; Fricker, 1971; Collewijn et al., 1988). The other group exhibited higher peak velocities toward the visual field ipsilateral to the DE whatever the eye being considered. The authors proposed that these two patterns of data were related to the strength of eye dominance. The former group was considered as having weak eye dominance whereas the latter was considered as having strong eye dominance. In other words, participants could be classified relative to their eye dominance (left or right) and its strength (weak or strong). Despite these suggestions concerning the strength of eye dominance, its potential impact on visuomotor tasks has never been directly assessed, except in a recent study showing an effect of the eye dominance strength on the saccade target selection (Tagu et al., 2016).

Based on the two previous studies (Vergilino-Perez et al., 2012; Chaumillon et al., 2014), we examined here the influence of sighting eye dominance with two goals in mind: i) to confirm this method of eye dominance strength determination based on saccadic peak velocity analysis and ii) to determine whether the influence of eye dominance in a visuomotor task can vary according to its strength. We used here again the Poffenberger task but this time, we classified participants according to their pattern of saccadic peak velocities. Participants with a naso-temporal asymmetry in saccade peak velocity should have a weak eye dominance (Vergilino-Perez et al., 2012) and, consequently, should present no or a weak preference for the contralateral visual hemifield with respect to the DE. Alternatively, participants exhibiting higher peak velocities toward the visual field ipsilateral to the DE whatever the eye being considered would be participants with strong eye dominance and should consequently show a larger contralateral hemifield preference. If this pattern of predicted results is found here (i.e. the relation between the oculomotor behavior and the results in the manual task), this would validate the method of analyzing saccade peak velocity to determine the strength of eye dominance and demonstrate that the impact of eye dominance on visuomotor transformations changes according to its strength.

2. Materials and methods

2.1. Participants

Fifty participants (mean age: 24.3 years; SD=5.6, 38 females) gave their informed consent to take part in the study after an explanation of the procedure. Note that two of them also participated in the 2012 study (Vergilino-Perez et al., 2012). The study adhered to the principles of the Declaration of Helsinki and the procedure was approved by the ethics committee of Paris Descartes University (CEERB n°IRB 20130500001072). All participants were healthy, reported normal or corrected-to-normal vision and showed no sign of neurological disorders. They were all right-handed and were divided into four groups according to their eye dominance (left and right) and its strength (weak or strong). Their hand preference was determined by using the Humphrey Laterality Questionnaire modified by Hecaen and Ajuriaguerra (1963). Their eye dominance was determined by the "Hole-in-card" test (Miles, 1930) repeated three times. All the participants were consistent across the three measures (i.e. the hole in the card was aligned with the same eye). The strength of the eye dominance was determined by the criteria proposed by Vergilino-Perez et al. (2012), based on the analysis of peak velocity of horizontal saccades recorded in a preliminary block (described in the Section 2.3). For each eye, the median of the peak velocity was computed separately for rightward and leftward saccades directed to targets presented at 5°, 10° and 15°eccentricities (respective average medians of peak velocity of 252°/s ± 37; 250°/s ± 44 and 399°/s ± 48). Fig. 1 presents the indivi-

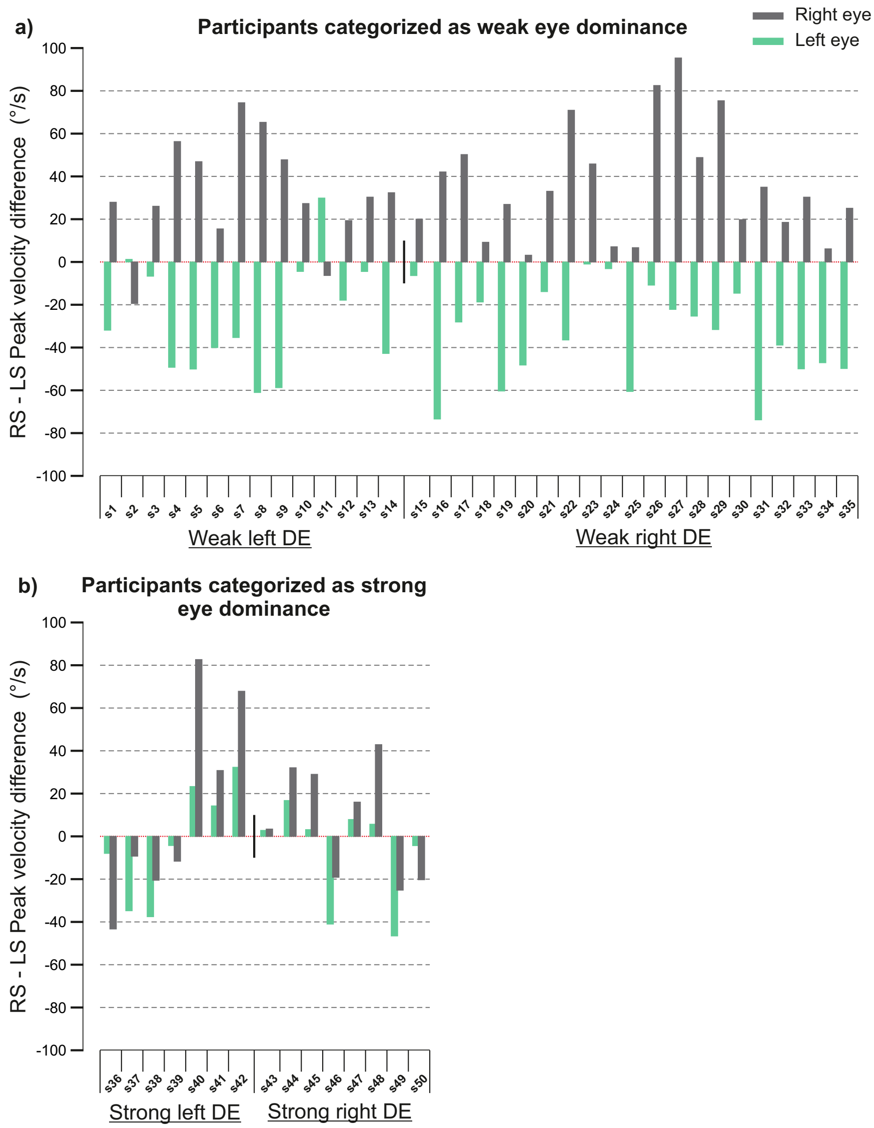

Fig. 1. Individual differences in median peak velocity between rightward (RS) and leftward (LF) saccades across the three tested target eccentricities (in °/s) for **a)** participants with weak left or right dominant eye (DE) and **b)** participants with strong left or right DE. Data were obtained in the preliminary saccade block. Recording was binocular. Data are shown for the left eye (LE; green bars) and right eye (RE; gray bars) for each subject performing saccades directed to targets lateralized 5°, 10° or 15° left or right from the initial central fixation point. Negative differences in peak velocity indicate that leftward saccades have greater peak velocities than rightward saccades. A positive difference indicates the reverse.

dual differences in median peak velocity between rightward and leftward saccades across the three target eccentricities. Participants showing naso-temporal asymmetries in saccadic peak velocity (*i.e.* faster rightward saccades with the right eye and faster leftward saccades with the left eye) were classified as having a weak eye dominance (Fig. 1A) whereas participants showing the same asymmetries in peak velocity irrespective of the recorded eye (i.e. faster rightward [or leftward] saccades with both left and right eye) were classified as having a strong eye dominance (Fig. 1B). Supplementary Fig. A.1 depicts an example of the velocity profile for leftward and rightward saccades (for a 5° target eccentricity) for a representative participant with a strong right DE and a representative participant with a weak right DE.

Eight participants had a strong right DE (8 females, mean age: 23.9 years-old, SD: ± 3.5; mean hand laterality score: 92.61%, SD: ± 5.92% range: 86.36–100%). Twenty-one participants had a weak right DE (16 females, mean age: 24.4 ± 6.7 years-old; mean hand laterality score: 90.12 ± 9.7%, range: 68.18–100%). Seven had a strong left DE (5 females; mean age: 23.2 ± 4.9 years-old; mean hand laterality score: 86.02 ± 5.93%, range: 77.27–95.45%) and fourteen had a weak left DE (9 females, mean age: 24.8 ± 5.6 years-old; mean hand laterality score: 86.19 ± 8.9%, range: 68.18–95.45%).

2.2. Experimental setup

Stimuli were presented on an Iiyama HM240DT monitor with a refresh rate of 170 Hz and a resolution of 800*600 pixels. The experimental session took place in a dimly lit room. Participants were seated 57 cm away from the screen in front of a table and their head kept stable with a chin and forehead rest. For all experimental blocks (preliminary saccade block and Poffenberger blocks), movements of the two eyes were recorded with an EyeLink 1000® (SR Research, Ontario, Canada) having a temporal resolution of 500 Hz, a spatial resolution of 0,01° and an average accuracy of .25°. Online saccade detection corresponded to above-threshold velocity (30°/s) and acceleration (8000°/s^2). For the Poffenberger blocks, a sensitive response button was aligned with the participants' body midline. Depending on the block, either their left or right index finger was resting on this button.

2.3. Tasks, protocols and stimulations

The experiment began with a preliminary block, using a reduced version of the saccade task used by Vergilino-Perez et al. (2012), in order to classify participants as having strong or weak eye dominance. Participants had to saccade toward a lateralized target presented 5°, 10° or 15° left or right from the central fixation point. The initial central fixation and the saccade target were 0,5°*0,5° white crosses with a luminance of 35 cd/m^2 displayed on a medium gray background (2.7 cd/m^2).

Each block began with a 9-point calibration over the entire screen. Before each trial, a small circle was presented at the screen center in order to compare the actual eye position with the previous calibration. The participants had to fixate the circle and to press a button of the pad. At this stage, the correspondence between the actual eye position on the central circle and the position of the preceding calibration was checked. If the eye was outside a window of .75° around the position where the eye should be, a new calibration began. Otherwise, the trial began. Each trial began with the presentation of the initial fixation cross randomly displayed during 400, 600 or 800 ms. During this delay, the eye position was checked and if the distance between eye position and the center of the cross was greater than .75°, the trial was cancelled and returned later in the session. The initial fixation cross disappeared simultaneously with the target appearance. Participants were instructed to make a saccade toward the target. Each participant performed 90 trials, 15 trials per eccentricity left or right of the fixation cross.

After a break and a new calibration procedure, participants ran the Poffenberger protocol that was very similar to that used by Chaumillon et al. (2014). The trial began with the presentation of a central 0,4°*0,4° white fixation cross (luminance of 35 cd/m^2) that remained on the screen during all the trial. After a random delay of 600, 800, 1000 or 1200 ms, a white circle of .9° (luminance of 47.5 cd/m^2) was presented for 100 ms, 7° left or right from the central fixation cross. The participants were instructed to press on the button as quickly as possible after target appearance while keeping their gaze on the central fixation cross. Gaze position was checked with the eye tracker and the calibration phase was repeated every twenty trials. Catch trials with no peripheral target presentation were also included to prevent target anticipation. Each participant performed 10 blocks of 100 trials each, by alternating the hand used for the response. The hand used in the first block was counterbalanced across participants. A short break was given between blocks. Each participant ran 500 trials with each hand, 224 with the target presented in the left visual field (LVF), 224 with the target presented in the right visual field (RVF) and 52 catch trials. Experimental and catch trials were pseudo-randomly mixed.

2.4. Statistical analysis

In the Poffenberger blocks, we excluded from subsequent analyses trials in which blinks (.04%) or saccades (10.5%) occurred and trials with manual response time (RT) shorter than 150 ms or longer than 800 ms (.99% of the trials). We computed for each participant the median RT for each of the four experimental conditions (2 Response hands x 2 Hemifields of presentation). Therefore, a non-parametric bootstrap-based ANOVA (see below) was run on the averaged median RTs with Eye dominance (left or right) and its Strength (weak or strong) as between-subject factors and Response hand (left or right) and Hemifield of presentation (left or right) as within-subject factors. Multiple pairwise comparisons were used to perform specific comparisons.

Non-parametric bootstrap-based ANOVA was used because preliminary analyses revealed that the obtained data were normally distributed (Shapiro-Wilk tests; all $p > .05$) but that the variances between the results of Weak and Strong left-eyed participants were not balanced in one experimental condition (i.e. right hand response to stimulations in the left visual field; p=.014), preventing the use of parametric ANOVAs. To deal with this issue, we used a non-parametric bootstrap-based ANOVA method (number of iterations =1000; percentile bootstrap) which allows to maintain the Type I error rate of our tests at its nominal level and to maintain the power of the tests, even when the data are heteroscedastic (Wilcox, 2011, 2012; see also Erceg-Hurn and Mirosevich, 2008).

To provide information about the magnitude of effects, the effect sizes are reported. The computation of effect sizes is subject to the same assumptions as the ANOVA. For this reason, we estimated effect sizes using the robust Cohen's d (d_r; Algina et al., 2005a, 2005b, 2006; see also Erceg-Hurn and Mirosevich, 2008 and Keselman et al., 2008) rather than the classic Cohen's d. The computation of the d_r was also be based on bootstrap method. To be consistent with non-parametric bootstrap-based ANOVA, we fixed the number of iterations to 1000.

3. Results

The statistical analysis did not reveal any main effect of the Eye dominance (F (1, 46)=1.27, p=.33; d_r=.24), of the Dominance strength ($F < 1$; d_r=.11), of the Hemifield of presentation ($F < 1$; d_r=.04), nor of the Response hand (F (1, 46)=1.01, p=.19; d_r=.1). However, as expected in a Poffenberger paradigm, we found a significant interaction between the factors Response hand and Hemifield of presentation (F (1, 46)=28.60, $p < .001$). The multiple pairwise comparisons indicated that manual RT was significantly shorter for stimuli presented in the LVF than the RVF when participants used their left hand ($p < .001$; d_r =.*16*), and shorter for stimuli presented in the RVF than the LVF when they used the right hand ($p < .001$; d_r = .14). More interestingly for our purpose, as illustrated in Fig. 2, a significant three-way interaction was found between the Hemifield of presentation, the Eye dominance and the Dominance strength factors (F (1, 46) =4.49, p=.039).

Nevertheless, the breakdown of this interaction revealed shorter manual RT for stimulation in the RVF than in the LVF for strong left-eyed participants (p=.032; d_r =.17). For strong right-eyed participants, manual RT was shorter in the LVF than the RVF but the difference was not significant (p=.16; d_r =.2). The weak left- and right-eyed participants exhibited no difference in RT between the two hemifields (p=.85; d_r =.03 in weak left-eyed and p=.99; d_r =.03 in weak right-eyed participants).

In sum, the results provided by the 4-way bootstrap-based ANOVA suggests that weak and strong eye dominance groups differed in their behavior. Although we used a non-parametric analysis, the unbalanced amount of participants between weak and strong eye dominance groups may have affected the results. Thus, in order to better characterize the impact of the dominance strength on the relationship between the response hand and the hemifield of stimulation, we conducted bootstrap-based ANOVAs on the averaged median RTs, separately for participants with strong or weak eye dominance, with the eye dominance (left or right) as a between-subject factor, and the response hand (left or right) and the hemifield of presentation (left or right) as within-subject factors.

For participants with weak eye dominance (see Fig. 3a), the bootstrap-based ANOVA revealed a significant interaction between the Response hand and the Hemifield of stimulation factors (F (1, 33) =21.36, p=.003). As classically found in the Poffenberger paradigm, post-hoc comparisons revealed that manual RT was significantly shorter in the LVF than in the RVF with the left hand (p=.023; d_r =.08) and in the RVF than in the LVF with the right hand (p=.03; d_r=.09). We found no significant effect of the Eye dominance, Response hand or Hemifield of stimulation factors (respectively F (1, 33)=1.30, p=.27, d_r =.37; F (1, 33)=1.74, p=.1, d_r =.18; $F < 1$, d_r=.03), nor significant interaction between Eye dominance and Hemifield of stimulation ($F < 1$) or between Eye dominance and Response hand ($F < 1$). The story was different for participants with strong eye dominance (Fig. 3b). No main effects of the Eye dominance,

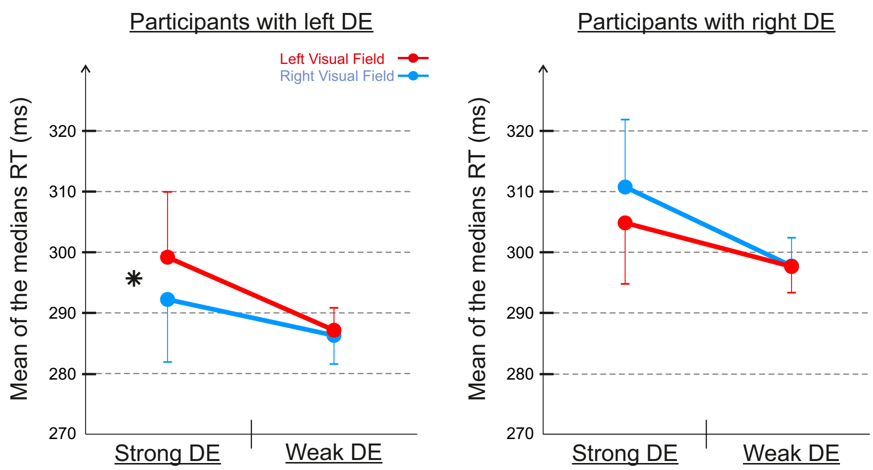

Fig. 2. Averaged median RTs obtained for stimulation in the left (LVF; red dots) or right visual field (RVF; blue dots) for participants with a strong or weak left dominant eye (DE; left panel) or a strong or weak right DE (right panel). The interaction between the hemifield of presentation, the eye dominance and the dominance strength was significant ($F\,(1, 46) = 4.49$, $p = .039$), revealing shorter RT for stimulation in the visual field controlateral to the DE (i.e. right visual field for left DE and left visual field for right DE) than in the ipsilateral one only for participants with strong eye dominance. Error bars correspond to SEM. * $p < .05$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

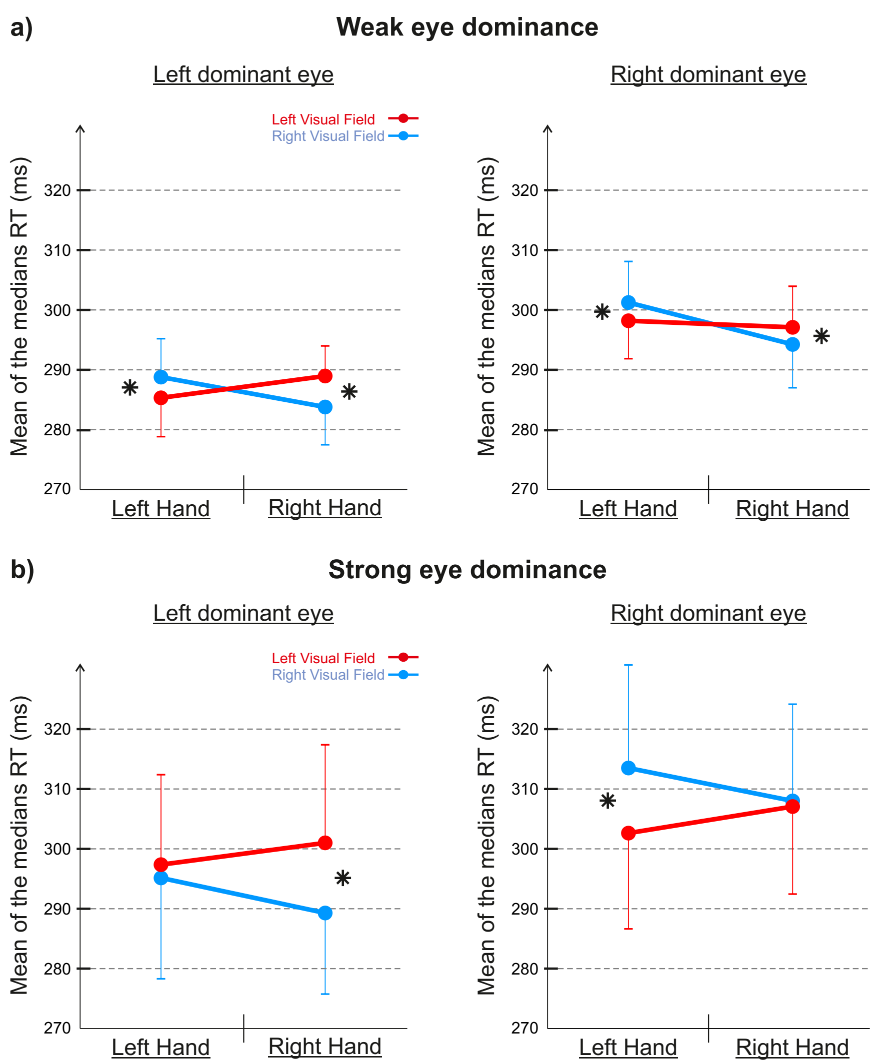

Fig. 3. Averaged median RTs obtained for **a)** participants with a weak left or right dominant eye (DE) and **b)** participants with a strong left or right DE, when they gave a manual response to a target presented either in the left (red dots) or in the right visual field (blue dots), using either the right or the left hand. For participants with a weak eye dominance, RTs were significantly shorter in the LVF than in the RVF when responding with the left hand and in the RVF than in the LVF when responding with the right hand. For participants with a strong eye dominance, RTs were shorter for stimulation presented in the visual field controlateral to the DE (i.e. RVF for left DE and LVF for right DE) than in the ipsilateral one when participants used their contralateral hand with respect to the DE. Error bars correspond to SEM. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Hemifield of presentation nor Response hand were found (all $F < 1$). On the one hand, the ANOVA revealed a significant interaction between the Response hand and the Hemifield of stimulation factors (F (1, 13) =8.92, p=.015), indicating that RT was shorter when the response hand and the hemifield of stimulation coincided. However, the breakdown performed on this interaction revealed only a strong trend toward a difference between LVF and RVF for the left hand (p=.052; d_r=.27) and did not reveal any difference for the right hand (p=.24; d_r =.12). On the other hand, the interaction between Hemifield of stimulation and Eye dominance factors was significant (F (1, 13)=5.53, p=.029), suggesting shorter RT when the targets appeared in the contralateral visual field with respect to the dominant eye. Although the breakdown of this interaction revealed shorter RT for stimulation in the RVF than in the LVF for strong left-eyed participants (p=.032; d_r=.17), there was no significant difference in strong right-eyed participants (p=.16; d_r=.2). The reasons for this non-significant difference in strong right-eyed participants could be found by analyzing the multiple comparisons of the non-significant triple interaction between the factors Eye dominance, Response Hand and Hemifield of presentation ($F < 1$). Although this interaction was not significant here, inspection of the breakdown is informative for our purpose (Hsu, 1996, P177 for justification to perform multiple pairwise comparisons of a non-significant interaction, see also Chaumillon et al., 2014). As shown in Fig. 3b, RTs were found to be shorter in the RVF than in the LVF for strong left-eyed participants only when they responded with their right hand (p= < .001; d_r =.29). On the contrary, RTs were found to be shorter in the LVF than in the RVF for strong right-eyed participants only when they responded with their left hand ($p < .001$; d_r =.36). The fact that we observed a significant effect only when participants used their contralateral hand with respect to the DE was in total accordance with previous results on the influence of eye dominance in a Poffenberger task (see also the algebraic model proposed by Chaumillon et al., 2014). In other words, as predicted, participants with strong eye dominance showed shorter manual RT to stimulation presented in the contralateral hemifield with respect to their dominant eye than in the ipsilateral hemifield whereas it was not the case for participants with weak eye dominance.

4. Discussion

The determination of the sighting dominant eye with binary tests like the "hole-in-card" test may not capture the whole phenomenon of the eye dominance as the strength of the eye dominance also appears to be an important parameter. This strength would represent a continuum from "weak" to "strong" eye dominance. We suggested that this strength of eye dominance could be assessed through a careful analysis of saccadic peak velocity for each eye (Vergilino-Perez et al., 2012). We previously showed that sighting eye dominance plays a key role in visuo-motor transformations (Chaumillon et al., 2014). Such an influence of eye dominance is revealed, in a visuo-motor task (*i.e.* Poffenberger paradigm), by lower manual RT for stimuli presented in the contralateral visual hemifield with respect to the DE. Nevertheless, the determination of the sighting DE with binary tests like the "hole-in-card" test, that we used in 2014, may not capture the whole phenomenon of the eye dominance as its strength also appears to be an important parameter. In another study, we suggested that the strength of eye dominance could be assessed through a careful analysis of saccadic peak velocity for each eye (Vergilino-Perez et al., 2012). Following these two studies, participants categorized as having weak or strong eye dominance according to their saccadic peak velocity pattern should show different result patterns in a visuo-motor task. The results from the present study are totally in line with this assumption. We indeed found here that, for a manual visuo-motor task, participants for whom the saccadic peak velocity data indicated strong eye dominance were those showing shorter RT to targets appearing in the contralateral hemifield with respect to their DE. On the contrary, this difference between the two hemifields was not found when the peak velocity data classified the participants as having a weak DE.

Results obtained in the present study represent a strong validation of our method using saccade peak velocity to determine the strength of the eye dominance. Indeed, we show here for the first time different behavioral performances in manual response times as a function of the categorization of participants as having weak or strong eye dominance. This is of particular importance if we consider how scarce the literature is about different possible degrees of eye dominance (Carey and Hutchinson 2013; Johansson et al., 2015). Concerning this categorization method, the initial proposition in our paper of 2012 (Vergilino-Perez et al., 2012) was that a strong eye dominance would be associated with higher peak velocities for both eyes for saccades toward the ipsilateral visual hemifield with respect to the DE. However, one can note here that in our group categorized as having strong eye dominance, some participants exhibited higher peak velocities toward the visual field contralateral -and not ipsilateral- to the DE whatever the eye being recorded (see Fig. 1). However, results of these participants in the Poffenberger task matched to the patterns observed for their eye dominance group as defined by the hole-in-card test. The higher peak velocities observed for saccades toward the contralateral visual hemifield with respect to the DE was also found for 2 participants in the Vergilino et al.'s study (2012), as well as for 12 participants over 32 in the Tagu et al.'s study (2016). Therefore, this suggest that the criteria for a strong eye dominance should be to exhibit higher peak velocities toward a same visual-field (be it left or right) with both eyes, and not only toward the visual field ipsilateral to the DE. In other words, people having strong eye dominance are those exhibiting an absence of naso-temporal asymmetry. It should be noted that, at this time, our procedure involving a simple saccadic task allows us to distinguish between individuals with a weak or a strong eye dominance. This categorization could probably be improved to locate each individual more precisely on the continuum from "weak" to "strong" eye dominance. We are currently conducting research in this direction.

Altogether our results suggest that the influence of the eye dominance in a visuomotor task does vary according to the strength of this dominance. We hypothesized in the introduction that due to the crossing of visual pathways, the larger activation of the ipsilateral visual cortex (Shima et al., 2010) may lead to a difference in the visual processing between the two hemifields relative to the eye dominance. Both the present study and the one of Chaumillon et al. (2014) gave for the first time evidence in favor of this hypothesis as the difference in the visual processing between the two hemifields leads to faster detection for stimulation presented in the visual field contralateral to the dominant eye. However, for participants with weak eye dominance, our present study showed that the preference for the contralateral hemifield with respect to the DE completely disappeared. Such a variable influence allows to better understand the difference between values obtained in Chaumillon et al. (2014) and the present experiment: the difference in RT between the two hemifields when the contralateral hand was used was roughly of 5 ms in this past study whereas the difference observed here was around 10 ms. This can be due to the inclusion of participants with a weak DE in the pool of subjects of Chaumillon et al. (2014). These participants showing no hemifield preference perhaps decreased the mean value at the population level.

The present results suggest that, like the other lateralizations, the eye dominance is not an “all or nothing phenomenon” but is rather expressed on a continuum from weak eye dominance to strong eye dominance. Until now, it has been considered that the sighting eye dominance may be determined with tests in which participants have to unconsciously choose one or the other of their eyes when performing a monocular task (Coren and Kaplan, 1973; Taghavy and Kugler, 1987). However, it is commonly reported that for some subjects there is a variability in this choice when different sighting tasks are used or when the same test is repeated in the same individual (Seijas et al., 2007;

Rice et al., 2008). These difficulties to find a "single dominant eye for each individual" as pointed by Mapp et al. (2003) led the authors to claim the absence of a functional role for the eye dominance. We rather suggest that these difficulties could occur when a given subject has a weak eye dominance. Other authors suggested that sighting dominance could be flexible, switching from one eye to the other relative to the horizontal gaze angle (Khan and Crawford, 2001; Carey, 2001; Carey and Hutchinson, 2013). Indeed, one parameter depending on subjects in these previous studies was the gaze eccentricity at which the switch was observed. Here again we propose that the strength of the eye dominance may contribute to this phenomenon.

Moreover, our present results should allow to remove some noise in studies searching for hemifield preference. We clearly demonstrate here the importance of taking into account the eye dominance as well as its strength in behavioral and neurosciences studies. For example, behavioral performance was investigated in numerous divided visual field studies in order to examine visual field asymmetries considered as indicators of brain lateralization (Dien, 2008; Serrien et al., 2006). Thus, the left hemisphere specialization for language and the right hemisphere specialization for spatial processing are two long-standing examples of perceptual asymmetries, leading to better processing of linguistic stimuli in the RVF as well as better processing of spatial stimuli in the LVF (e.g. Mishkin and Forgays, 1952; Kimura, 1973; Lindell, 2006). However, if these studies took into account the handedness of participants by selecting only right-handers, none were interested in eye dominance even though only 66% of right-handers are right-eye dominant (Bourassa et al., 1996). The demonstration of a different visual processing between the hemifields contralateral and ipsilateral to the dominant eye, modulated by the dominance strength, should be taken into account in any attempt to explain a superiority of one hemifield in the processing of specific stimuli.

Several questions remain concerning the mechanisms of the strength variation of the eye dominance. Our results suggest that strong eye dominance is associated with a loss of the naso-temporal asymmetries. The mechanisms underlying the disappearance of these well-known asymmetries must be elucidated. Recent imaging studies suggest some anatomical asymmetries because eye dominance affects the laterality of brain activity in the visual cortex (Constantinidis, 2003; Petit et al., 2009, 2014). Therefore, one way to explain the impact of eye dominance on naso-temporal asymmetries is related to the privileged relationship found between the dominant eye and the ipsilateral visual cortex in neuroimaging studies (Erdogan et al., 2002; Shima et al., 2010). It can be supposed that naso-temporal asymmetries are the basic trait of the oculomotor system when no other lateralization is involved (i.e. weak eye dominance). But when other lateralization, as eye dominance, is involved, this basic property might be modified leading to different behaviors. In other words, the neural mechanisms underlying the eye dominance might overshadow the naso-temporal asymmetries. Being able to dissociate weak from strong eye dominance may allow to improve the characterization of the neural bases of eye dominance.

5. Conclusion

In conclusion, our study showed that the ocular dominance strength varies from one individual to another and should not be simply determined by an "all or nothing" test involving necessarily the choice of an eye. Even if subsequent studies should be conducted to further examine the influence of eye dominance and its strength on perceptual, attentional and motor processes, it appears crucial to include these two variables as factors of interest in studies on visuo-motor transformations, in particular the ones looking at brain lateralization.

The results of the present experiment may have implications for both basic and applied research. It could represent a first step in providing a battery of tests to quantify sighting eye dominance. Such a battery could in fine be an important tool for clinical research and diagnosis as eye dominance seems is an important factor for the success and safety of some surgical operations (Jehangir et al., 2016) such as monovision surgery (Seijas et al., 2007).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2017.01.015.

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