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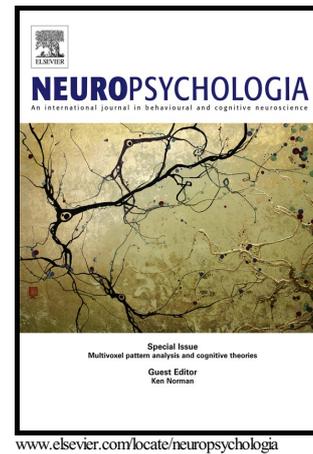
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Quantifying eye dominance strength - New insights into the neurophysiological bases of saccadic asymmetries

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Abstract

The saccadic system presents asymmetries. Notably, saccadic peak velocity is higher in temporal than in nasal saccades, and in centripetal than in centrifugal saccades. It has already been shown that eye dominance strength relates to naso-temporal asymmetry, but

its links with centripetal-centrifugal asymmetry has never been tested. The current study tested both naso-temporal and centripetal-centrifugal asymmetries simultaneously to provide a finer and continuous measure of eye dominance strength. We asked 63 participants to make centripetal and centrifugal saccades from five different locations. Analysis of saccadic peak velocity shows that eye dominance strength modulates every saccadic asymmetry tested. For the first time, we propose a graduated measure of eye dominance strength on a continuum model. The model ranges from weak to very strong eye dominance. Weak eye dominance corresponds to increased saccadic asymmetries whereas strong eye dominance corresponds to no asymmetries. Furthermore, our results provide new insights into the neurophysiological origins of saccadic asymmetries. Modulation of both naso-temporal and centripetal-centrifugal asymmetries by eye dominance strength supports the involvement of V1 in these saccadic asymmetries.

Keywords: Eye dominance, Quantification, Asymmetries, Saccadic eye movements, Peak Velocity, V1

1. Introduction

When someone is asked to report his dominant hand, she/he unhesitatingly knows what to answer, but few people are able to indicate their eye dominance (ED). This is probably because ED is a complex property that can take several forms. By evaluating thirteen different ED tests, Coren & Kaplan (1973) indeed revealed three types of ED: the *sighting* dominant eye is the eye preferentially used when performing a monocular task; the *sensory* dominant eye is the eye for which the percept is stronger during binocular rivalry; and the *acuity* dominant eye is the eye with the best visual acuity. As the authors showed that the most robust and less variable ED within participants and between tests is *sighting* ED, we decided to focus on this ED type. Sighting ED is usually assessed with tests providing a binary categorization (dominant left vs. dominant right eye). One of the most commonly used tests to assess sighting ED is the “hole-in-card-test” (Durand & Gould, 1910; Miles, 1930), in

which participants sight a dot through a hole in a cardboard held at arm's length, and bring the cardboard close to their face. In this situation, the cardboard is preferentially moved toward the dominant eye. This test is very robust and has great test-retest reliability (Coren & Kaplan, 1973; Crider, 1944; Ho, Thompson, Babu, & Dalton, 2017; Seijas et al., 2007). However, by comparing four sighting ED tests, Rice, Leske, Smestad, & Holmes (2008) and Seijas et al. (2007) have shown that while each individual test has great test-retest reliability, these tests do not globally correlate very well with each other. Contrary to handedness questionnaires - which provide a continuous percentage-based measure - tests of sighting ED only provide binary information, as they merely force participants to favor one eye. Moreover, while handedness questionnaires have revealed that some people have no hand preference, current sighting ED tests provide no opportunity to identify participants with no ED. However, a number of recent studies have been carried out to develop a continuous measure of ED strength (Carey & Hutchinson, 2013; Chaumillon et al., 2015; Dalton, Guillon, & Naroo, 2015; Ho et al., 2017; Johansson, Seimyr, & Pansell, 2015; Vergilino-Perez et al., 2012).

Interestingly, Khan & Crawford (2001) have shown that sighting ED varies as a function of gaze angle. Using a paradigm adapted from the hole-in-card test, they showed that ED switches from gaze angle of 15.5° from the straight-ahead direction. On the basis of these findings, Carey & Hutchinson (2013) proposed an estimation of sighting ED strength. They suggested that the gaze angle from which the participant's sighting eye begins to switch could be used as an estimate of ED strength - the higher the gaze angle, the greater the ED strength. In their study, participants were seated in front of a semi-circular array of rings arranged at 10° intervals from 50° in both directions from the straight-ahead. Each trial required participants to use either their left or right hand to bring the target close to their face, forcing them to sight from one eye only. However, the authors found that their estimate of ED strength depended on the hand used to perform the task: in fact, participants tended to use their left eye when using their left hand and vice-versa. In their studies, Dalton and

colleagues (Dalton et al., 2015; Ho et al., 2017) proposed to measure ED strength based on the near-far alignment test, another test of sighting ED. Participants were exposed to a graduated chart and had to align their joined forefingers with a cross situated at the center of the chart. As participants used both hands, any possible influence of the hand used on the ED strength measure was excluded. Then, participants had to close one eye and report the graduation on which their fingers had moved on the chart. Indeed, when one closes one's dominant eye, one is under the impression that one's fingers have moved ipsilaterally on the chart. The authors suggested that greater deviation reflected stronger ED, but they have shown that their ED strength measure varied as a function of the testing distance (Dalton et al., 2015; Ho et al., 2017; see also Rice et al., 2008).

Vergilino-Perez et al. (2012) proposed to quantify sighting ED strength based on asymmetric saccadic peak velocities between leftward and rightward saccades. It is well known that peak velocity is higher when saccades are directed toward the temple (i.e., leftward for the left eye and rightward for the right eye) than toward the nose (i.e., rightward for the left eye and leftward for the right eye) (Collewijn, Erkelens, & Steinman, 1988; Cook, Stark, & Zuber, 1966; Fricker, 1971; Hyde, 1959; Jóhannesson & Kristjánsson, 2013; Robinson, 1964; Tagu, Doré-Mazars, Vergne, Lemoine-Lardennois, & Vergilino-Perez, 2018). This asymmetry is referred to as naso-temporal asymmetry (NTA). Examples of temporal and nasal saccades are illustrated in Figure 1 by solid and dotted arrows, respectively. Note that while NTA has been widely found in peak velocity, its expression in other saccadic parameters is not so clear (Bompas, Sterling, Rafal, & Sumner, 2008; Honda, 2002; Jóhannesson, Ásgeirsson, & Kristjánsson, 2012; Rafal, Henik, & Smith, 1991). A possible explanation is that peak velocity is less sensitive to top-down influences than other parameters such as saccade latency (Galley, 1989; see also: Di Stasi et al., 2013; Leigh & Zee, 2006). Therefore, asymmetries may exist in other saccadic parameters; but their presence may be masked by other massive effects linked to top-down influences (for similar arguments, see discussions in Bompas et al., 2008; Tagu et al., 2018). Vergilino-Perez et al.

(2012) have shown that while some participants exhibited the standard NTA, others exhibited higher peak velocities toward the hemifield ipsilateral to their dominant eye (as measured using the hole-in-card test). They suggested that the former participants had a weak ED whereas the latter ones had a strong ED. Note that this initial criterion based on the data from eighteen participants has recently been refined thanks to studies involving larger samples of participants (Chaumillon et al., 2017; Tagu, Doré-Mazars, Lemoine-Lardennois, & Vergilino-Perez, 2016). Strong ED would be reflected in higher peak velocities toward the same hemifield, regardless of the eye, not just toward the hemifield ipsilateral to the dominant eye. In other words, participants with strong ED are those who do not exhibit NTA in saccadic peak velocity. Importantly, ED strength, as measured via this criterion, has been shown to affect perceptual (Chaumillon et al., 2017) and visuo-motor (Tagu et al., 2016) processes. Indeed, Chaumillon et al. (2017) used a Poffenberger task (Poffenberger, 1912) to show that participants with strong ED, i.e., with no NTA in saccadic peak velocity, detected a lateralized target in the hemifield contralateral to their dominant eye faster than in the other hemifield. Interestingly, this asymmetry was not found in participants with weak ED, i.e., with NTA in saccadic peak velocity. Similarly, Tagu et al. (2016) found that participants with strong ED made more accurate saccades toward the hemifield contralateral to their dominant eye than toward the ipsilateral hemifield. Again, this result was not found in participants with weak ED. Taken together, these studies suggest (1) that ED strength as estimated by the criterion proposed by Vergilino-Perez et al. (2012) clearly affects perceptual and visuo-motor abilities and (2) that the hemifield contralateral to the dominant eye is processed in a privileged manner by participants with strong ED. This can be explained in terms of neural correlates of sighting ED. Indeed, using functional magnetic resonance imaging (MRI), Rombouts, Barkhof, Sprenger, Valk, & Scheltens (1996) have shown that stimulating the dominant eye led to enhanced activation of the primary visual cortex (V1) than stimulating the non dominant eye. Moreover, anatomical MRI has led Erdogan, Özdikici, Aydin, Aktas, & Dane (2002) to notice that the visual cortex ipsilateral to the dominant eye was larger than the contralateral one. Functional imaging using magneto-encephalography (MEG) has

corroborated this structural asymmetry: Shima et al. (2010) found that presenting a diode to the dominant eye led to greater activation of its contralateral V1 than of its ipsilateral one. On the other hand, stimulating the non dominant eye did not result into such an asymmetry. These studies suggest a special relationship between the dominant eye and the ipsilateral V1. We propose that this relationship induces better perceptual (Chaumillon et al., 2017) and visuo-motor (Tagu et al., 2016) performance in the hemifield contralateral to the dominant eye in participants with strong ED. This implies that participants with weak ED should not show such a relationship between their dominant eye and its ipsilateral V1. This hypothesis deserves to be tested using neuroimaging techniques.

ED strength, as estimated by Vergilino-Perez et al. (2012), could therefore have neural correlates in V1. Indeed, this estimation is based on the presence or absence of NTAs, NTA being known to be present in the retinotectal pathway (Hubel, LeVay, & Wiesel, 1975) as well as at every step of the geniculostriate pathway. The nasal hemiretina - which receives information from the temporal hemifield - presents a higher density of cones and ganglion cells than the temporal hemiretina - which receives information from the nasal hemifield (Curcio & Allen, 1990). This asymmetry is also observed in the projections from the retina to the lateral geniculate nucleus of the thalamus (Connolly & Van Essen, 1984; Williams, Azzopardi, & Cowey, 1995) and in V1 (Toosy et al., 2001; Tychsen & Burkhalter, 1997).

However, this estimation of ED strength lacks continuity. Coupled with the hole-in-card test, it merely allows distinguishing between left/strong, left/weak, right/strong, and right/weak ED. To provide a continuous measure, we propose to study the influence of ED strength on other asymmetries of the saccadic system. Indeed, if ED strength modulates NTA (Vergilino-Perez et al., 2012), it should also modulate other asymmetries. For instance, peak velocity is also known to be higher in centripetal saccades, i.e., directed toward the straight-ahead direction, than in centrifugal saccades, i.e., directed away from the straight-ahead direction

(Abel, Dell'Osso, Daroff, & Parker, 1979; Camors, Trotter, Pouget, Gilardeau, & Durand, 2016; Collewijn et al., 1988; Frost & Pöppel, 1976; Inchingolo, Spanio, & Bianchi, 1987; Jürgens, Becker, & Kornhuber, 1981; Pelisson & Prablanc, 1988; Tagu et al., 2018). Examples of centrifugal and centripetal saccades are shown in Figures 1a and 1b, respectively. In Tagu et al. (2018), participants were asked to make saccades from five different starting positions on the horizontal axis (as illustrated in Figure 1). This allowed us to examine centripetal (Figure 1b) as well as centrifugal (Figure 1a) saccades. Moreover, by using binocular recordings of eye movements, saccades could also be compared according to their temporal (solid lines in Figure 1) or nasal (dotted lines in Figure 1) nature. Hence, four saccade directions were examined: centripetal-temporal saccades (solid lines in Figure 1b), centripetal-nasal saccades (dotted lines in Figure 1b), centrifugal-temporal saccades (solid lines in Figure 1a) and centrifugal-nasal saccades (dotted lines in Figure 1a). Using this paradigm, we showed (Tagu et al., 2018) that centripetal saccades (Figure 1b) had higher peak velocity than centrifugal ones (Figure 1a) only for temporal saccades (solid lines in Figure 1), not for nasal ones (dotted lines in Figure 1). Based on the well-known neurophysiological correlates of NTA and centripetal-centrifugal asymmetry (CCA), we assumed that the link between NTA and CCA might be due to asymmetries in V1. One of the explanations for CCA is that centripetal saccades bring the gaze back to the straight-ahead direction, which represents a default gaze direction in which eye-centered and head-centered reference frames are aligned (Durand, Trotter, & Celebrini, 2010; Kardamakis & Moschovakis, 2009; Tatler, 2007). Moreover, stimuli presented straight-ahead have been shown to induce higher activity in V1 than stimuli presented elsewhere (Durand et al., 2010). The connection between NTA and CCA (Tagu et al., 2018) and their common neurophysiological origins in V1 jointly support the view that ED strength may also modulate CCA. This modulation could help to compute an even finer quantification of ED strength. In the present study, we tested the influence of ED strength on NTA and CCA by using the same paradigm as in Tagu et al. (2018, illustrated in Figure 1) to induce centripetal-nasal, centripetal-temporal, centrifugal-nasal, and centrifugal-temporal saccades. Note that NTA

has been shown to sometimes vary between reactive and voluntary saccades elicited by different paradigms (Kristjánsson, Vandenbroucke, & Driver, 2004). This is the reason why we here tested NTA and CCA in both reactive and voluntary saccades elicited in step- and overlap paradigms, respectively. Moreover, we tested the influence of ED strength on saccadic asymmetries over a large range of conditions (2 saccade direction x 2 recorded eyes x 2 block types x 5 starting position) and a large number of trials per condition (40) to identify the main factors on which ED strength had the greater influence (i.e., the ones that should be used to measure ED) and those that were unaffected by ED strength.

2. Methods

2.1. Subjects

Sixty-three subjects participated in this study, including fifty-eight naive undergraduate students from the Institute of Psychology at Paris Descartes University, and five non-naive members of the Laboratory, with twenty-eight of them having already participated in the study by Tagu et al. (2018). All the participants reported normal or corrected-to-normal vision and no history of psychiatric or neurological disorders. They were classified based on handedness (Humphrey's questionnaire modified by Hécaen & de Ajuriaguerra, 1963) and on ED (hole-in-card test repeated three times, Durand & Gould, 1910; Miles, 1930). Each group was subdivided into two ED strength subgroups (strong and weak) based on saccadic peak velocity as proposed by Vergilino-Perez et al. (2012). This was done by analyzing leftward and rightward saccades made from the central starting position (0°). We only chose these saccades because previous studies using this classification (Chaumillon et al., 2015, 2017; Tagu et al., 2016; Vergilino-Perez et al., 2012) did not test saccades made from locations other than the center. Participants exhibiting NTA in the peak velocity of these saccades (i.e., showing higher peak velocity for leftward compared to rightward saccades of the left eye and for rightward compared to leftward saccades of the right eye) were included in the weak ED group; whereas participants exhibiting no NTA (i.e., showing higher peak velocity for leftward compared to rightward saccades for both eyes or higher peak velocity for

rightward compared to leftward saccades for both eyes) were included in the strong ED group. So in the end, participants were divided into eight groups: (1) nine Right-handed with strong Right ED (RR+, eight females, mean age: 22 ± 2.2 years, mean laterality score: $91\pm 4\%$), (2) twelve Right-handed with weak Right ED (RR-, eight females, mean age: 24 ± 4.9 years, mean laterality score: $92\pm 6\%$), (3) thirteen Right-handed with strong Left ED (RL+, 13 females, mean age: 21 ± 2.6 years, mean laterality score: $89\pm 6\%$), (4) ten Right-handed with weak Left ED (RL-, seven females, mean age: 31 ± 12.8 years, mean laterality score: $88\pm 7\%$), (5) four Left-handed with strong Right ED (LR+, three females, mean age: 22 ± 3.6 years, mean laterality score: $44\pm 25\%$), (6) five Left-handed with weak Right ED (LR-, four females, mean age: 23 ± 3.6 years, mean laterality score: $38\pm 24\%$), (7) three Left-handed with strong Left ED (LL+, two females, mean age: 29 ± 7.8 years, mean laterality score: $25\pm 18\%$), and (8) seven Left-handed with weak Left ED (LL-, five females, mean age: 26 ± 5.4 years, mean laterality score: $30\pm 23\%$). The smaller size of the left-handed and left ED groups is due to their low frequency in the population: 10% of the population is left-handed and 33% of the population is left eye dominant (Bourassa, McManus, & Bryden, 1996).

Prior to their inclusion in the study, the experimental procedure was clearly explained to the participants and they gave informed consent. The study was approved by the Paris Descartes University ethics committee (IRB number 20130500001072), and was completed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

2.2. Instruments and Materials

Stimuli were displayed on an Iiyama HM240DT monitor (Iiyama, Nagano, Japan) with a refresh rate of 170 Hz and a resolution of 800x600 pixels. The experimental sessions took place in a dimly lit room. Subjects were seated 57 cm away from the screen and their heads were immobilized using a chin and forehead rest.

Binocular recordings of eye movements were made using an Eyelink 1000[®] (SR Research, Ontario, Canada) sampled at 500 Hz. Online saccade detection corresponded to above-threshold velocity (30°/s) and acceleration (8000°/s²).

Each trial involved a fixation cross and a saccade target. Both were a 0.5°x0.5° white cross (luminance of 35 cd/m²) displayed on a medium-grey background of 4.5 cd/m².

2.3. Procedure

The procedure was the same as in Tagu et al. (2018). Each session began with a 9-point calibration filling the screen. Before each trial, eye position was checked and if the eye was outside a 0.75° window around the starting position of the next saccade, a new calibration began. The trial began with the fixation cross displayed pseudo-randomly for 400 or 800 milliseconds. During this time, if eye position was more than 0.75° away from the center of the fixation cross, the trial was cancelled and repeated later in the session. As illustrated in Figure 1, the fixation cross could appear at five random locations on the horizontal axis: at the center (0°), 5° to the left (-5°), 10° to the left (-10°), 5° to the right (+5°) or 10° to the right (+10°). The saccade target appeared five degrees to the left or to the right of the fixation cross. Thus, the target could appear at the following locations: -15°, -10°, -5°, 0°; +5°, +10° and +15°. This led to ten different saccades, which could be either centripetal-temporal, or centripetal-nasal, or centrifugal-temporal or centrifugal-nasal. The time course of a trial is presented in Figure 2. Participants were requested to make a saccade toward the target as soon as the fixation-cross disappeared. The target remained on the screen for 800 ms after the fixation-cross disappeared, then a blank screen was displayed for 1000 ms between each trial.

The ten different saccades were tested in a step block followed by an overlap block so as to explore saccadic asymmetries in both reactive and voluntary saccades. In the step block (Figure 2a), the target appeared as soon as the fixation-cross disappeared. In the overlap

block (Figure 2b), the target appeared 600 ms before the fixation-cross disappeared. Each block included 400 trials (40 for each experimental condition: 5 starting positions x 2 saccade directions) randomly distributed within each block. Ten additional training trials - one for each condition - preceded each block. Note that 6 out of the 63 participants completed the step block only (1 RR+, 1 RR-, 1 RL+, 1 LR-, 1 LL+ and 1 LL-); they were not included in the ANOVAs presented below but their data were examined in the individual analyses.

2.4. Data analysis

Firstly, to examine how NTA and CCA were related and whether they were globally modulated by ED strength, we performed repeated-measure ANOVAs in two experimental designs:

- A first ANOVA was conducted over the ten different saccades tested in the experiment, in a 2 (Saccade direction: leftward, rightward) by 2 (Recorded eye: left, right) by 2 (Block type: Step, Overlap) by 5 (Starting position: -10° , -5° , 0° , $+5^\circ$, $+10^\circ$) design;
- A second ANOVA, designed to directly compare NTA and CCA, was only focused on saccades starting from eccentric locations (saccades from $\pm 5^\circ$ and from $\pm 10^\circ$ in Figure 1). Saccades from the center of the screen were excluded because they can only be centrifugal. This ANOVA was conducted in a 2 (Recorded eye: left, right) by 2 (Block type: step, overlap) by 2 (Target hemifield: temporal, nasal) by 2 (Saccade direction relative to the straight-ahead: centripetal, centrifugal) by 2 (Eccentricity of starting position relative to the straight-ahead: 5° , 10°) design.

For both ANOVAs, post-hoc comparisons were based on Tukey's HSD. Note that these ANOVAs were performed on latency, amplitude, duration, average velocity and peak velocity, but NTA and CCA were significantly observed in peak velocity only. Hence, the result section only presents the peak velocity data, with mean \pm standard deviations. Moreover, the analyses described above initially included three between-subject factors: handedness (left/right), ED (left/right), and ED strength (strong/weak). However, as no effect

of handedness reached significance (all $p > .25$), the data from left-handed and right-handed participants have been averaged so that between-subject factors included ED and ED strength only.

Secondly, to provide a continuous measure of ED strength, we computed a percentage of ED based on the analysis of each individual's peak velocity data: for each starting position and each block type, the presence of NTA was assessed by comparing peak velocities of leftward and rightward saccades for each eye. In this analysis, standard NTA corresponds to higher peak velocity in leftward saccades for the left eye and in rightward saccades for the right one. Importantly, for each eye and each starting-position eccentricity relative to the straight-ahead (0° , 5° and 10° from the straight-ahead), we compared centrifugal-temporal saccades (solid arrows in Figure 1a) to centrifugal-nasal ones (dotted arrows in Figure 1a), as well as centripetal-temporal saccades (solid arrows in Figure 1b) to centripetal-nasal ones (dotted arrows in Figure 1b). These comparisons were designed to compare temporal and nasal saccades for centripetal and centrifugal saccades separately. Accordingly, our measure of NTA did not include any CCA measure. Similarly, for each eye and each eccentricity, the presence of CCA was assessed by comparing centripetal-temporal saccades (solid arrows in Figure 1b) to centrifugal-temporal saccades (solid arrows in Figure 1a) and by comparing centripetal-nasal saccades (dotted arrows in Figure 1b) to centrifugal-nasal ones (dotted arrows in Figure 1a). Accordingly, our measure of CCA involved no measure of NTA. All these comparisons were conducted separately for reactive and voluntary saccades, respectively elicited by the step block and the overlap block.

For each participant, we discarded trials with saccade latency shorter than 80 ms (2.57%) or longer than 800 ms (0.15%), and outliers in latency (4.10%), amplitude (1.06%), duration (2.24%), and peak velocity (0.09%). Overall, 10.2% of the trials were discarded. For each block, the outliers were values below ($Q1 - 2.3 \times IQR$) or above ($Q3 + 2.3 \times IQR$), where $Q1$ and $Q3$ are the first and third quartiles respectively, and IQR the interquartile range (Tukey boxplot, Carling, 2000).

3. Results

3.1. Group analyses: Asymmetries of the saccadic system

Analysis of the whole set of data over the ten different saccades showed a main effect of block type ($F[1,53]=21.54, p<.0001$) with higher peak velocity in the step block ($227\pm 37^\circ/\text{s}$) than in the overlap block ($217\pm 37^\circ/\text{s}$). Analysis showed neither effect of the recorded eye ($F[1,53]=1.42, p=.24$), nor effect of saccade direction ($F<1$). The between-subject factors (ED and ED strength) did not show any significant main effect either (*both* $p>.14$). The main effect of starting position ($F[4,212]=9.83, p<.0001$) showed that saccades initiated from $+10^\circ$ had lower peak velocity than saccades starting from other locations. However, the observed differences are very close to the resolution limits of our eyetracker (about $4^\circ/\text{s}$).

More importantly we found NTA, signed by the interaction between recorded eye (left/right) and saccade direction (leftward/rightward) ($F[1,53]=54.93, p<.0001$): peak velocity was higher in temporal- than nasal saccades (i.e., left eye: $228\pm 39^\circ/\text{s}$ leftward vs. $215\pm 35^\circ/\text{s}$ rightward; right eye: $230\pm 39^\circ/\text{s}$ rightward vs. $215\pm 32^\circ/\text{s}$ leftward; both $p<.0002$). Note that ED did not interact with these factors ($F<1$), suggesting that NTA was found similarly in both ED groups.

The investigation of CCA via the interaction between saccade direction and starting position ($F[4,212]=46.35, p<.0001$) showed higher peak velocity in centripetal- than centrifugal saccades, but only for saccades initiated at locations 10° away from the straight-ahead (leftward: $227\pm 39^\circ/\text{s}$ centripetal vs. $216\pm 34^\circ/\text{s}$ centrifugal; rightward: $229\pm 39^\circ/\text{s}$ centripetal vs. $211\pm 33^\circ/\text{s}$ centrifugal, both $p<.0002$). No CCA was found for saccades starting at locations 5° away from the straight-ahead (all $p>.05$). Saccade direction and starting position interacted with ED ($F[4,212]=2.99, p<.02$), but post-hoc comparisons showed that CCA did not differ between participants with left- and right ED (all $p>.05$). Interestingly however, the triple interaction between starting position, saccade direction, and ED strength ($F[4,212]=5.71, p<.0002$) showed that CCA depended on ED strength: indeed, CCA was

present in participants with weak ED (all $p < .0001$) but not in participants with strong ED (all $p > .40$). Therefore, just as NTA, CCA co-occurs with weak ED.

Interestingly, as in Tagu et al. (2018) we found that NTA and CCA interacted. Indeed, the significant interaction between recorded eye, saccade direction, and starting position ($F[4,212]=3.98$, $p < .004$; see Figure 3a) confirmed that CCA only appears in temporal saccades. Specifically, Figure 3a shows that temporal saccades (leftward for the left eye and rightward for the right eye) show higher peak velocity when they are centripetal rather than centrifugal; both when starting at 5° (left eye: $230 \pm 39^\circ/\text{s}$ vs. $226 \pm 37^\circ/\text{s}$, $p < .0005$; right eye: $234 \pm 40^\circ/\text{s}$ vs. $231 \pm 38^\circ/\text{s}$, $p < .001$) and at 10° (left eye: $238 \pm 42^\circ/\text{s}$ vs. $219 \pm 36^\circ/\text{s}$; right eye: $241 \pm 40^\circ/\text{s}$ vs. $214 \pm 33^\circ/\text{s}$; both $p < .0005$) away from the straight-ahead. However, in nasal saccades (rightward for the left eye and leftward for the right eye) CCA is not as clear-cut. Indeed, centripetal saccades reach higher peak velocity than centrifugal saccades when their starting point is 10° away from the straight-ahead (left eye: $217 \pm 34^\circ/\text{s}$ vs. $207 \pm 33^\circ/\text{s}$, $p < .0005$; right eye: $216 \pm 33^\circ/\text{s}$ vs. $213 \pm 32^\circ/\text{s}$, $p < .002$); but the effect is reversed for a 5° eccentricity (left eye: $215 \pm 34^\circ/\text{s}$ vs. $219 \pm 36^\circ/\text{s}$, $p < .0005$; right eye: $214 \pm 32^\circ/\text{s}$ vs. $217 \pm 33^\circ/\text{s}$, $p < .02$).

Interestingly, when strong and weak ED groups are examined separately, it turns out that this interaction between recorded eye, saccade direction, and starting position is significant for the weak ED group ($F[4,116]=3.20$, $p < .01$, Figure 3b) but not for the strong ED one ($F[4,96]=2.33$, $p = .06$; Figure 3c). These results therefore suggest that all of the saccadic system asymmetries are strongly linked to weak ED.

A second analysis, restricted to saccades starting from peripheral positions, allowed to directly assess the effect of NTA [target hemifield (temporal vs. nasal) factor] and CCA [saccade direction relative to the straight-ahead (centripetal vs. centrifugal) factor]. It confirmed the presence of NTA ($F[1,53]=56.54$, $p < .0001$) and CCA ($F[1,53]=26.02$, $p < .0001$)

and their modulation by ED strength ($F[1,53]=7.02$, $p<.01$), as both these asymmetries co-occur with weak ED ($p<.0001$), not with strong ED ($p=.29$). Again, ED did not modulate NTA ($F<1$) nor CCA ($F[1,53]=3.31$, $p>.07$).

The significant interaction between target hemifield and saccade direction relative to the straight-ahead ($F[1,53]=69.92$, $p<.0001$, Figure 4a) confirms that among temporal saccades, peak velocity is higher for centripetal saccades than for centrifugal ones ($236\pm 40^\circ/\text{s}$ vs. $223\pm 40^\circ/\text{s}$, $p<.0002$), while nasal saccades do not exhibit this CCA ($216\pm 33^\circ/\text{s}$ vs. $214\pm 34^\circ/\text{s}$, $p>.63$). It is worth noting that although this interaction is significant in both weak and strong ED groups (both $p<.0001$, Figures 4b and 4c respectively), the magnitude of the CCA observed in temporal saccades is much higher for the weak ED group (difference of $17^\circ/\text{s}$, Cohen's $d=.51$, Figure 4b) than for the strong ED one (difference of $8^\circ/\text{s}$, Cohen's $d=.2$, Figure 4c).

Altogether, group analyses have shown that both NTA and CCA are found only with weak ED, while strong ED seems to “immunize against” the saccadic system asymmetries. Such a result suggests a relationship between the two saccadic asymmetries, a relationship that we investigated by analyzing the correlation between the magnitude of NTA (averaged temporal-nasal peak velocity difference) and the magnitude of CCA (averaged centripetal-centrifugal peak velocity difference) of each participant. As shown in Figure 5, the significant positive correlation ($r=.42$, $p<.0006$) confirms that the higher the NTA, the higher the CCA.

Interestingly, Figure 5 shows that some participants exhibiting no NTA however show CCA. This may be related to the findings (Figure 4b-c) that participants with strong ED (who show no NTA) still display CCA in temporal saccades, although the magnitude of this asymmetry is weaker than that of participants with weak ED (who show NTA). The variability in CCA between participants with the same NTA profile may help refine the quantification of

ED strength. While ED strength has previously been known to modulate NTA (Chaumillon et al., 2017; Tagu et al., 2016; Vergilino-Perez et al., 2012), the present study shows, for the first time, that it also modulates CCA. We contend that studying NTA and CCA jointly should help compute a more precise measure of ED strength.

3.2. Individual analyses: Toward a continuum of eye dominance strength

To compute a continuous measure of ED strength and assign each individual a percentage of ED strength, we computed a precise NTA and CCA profile for each of the 63 participants. To do so, participants were individually tested for rightward-leftward difference in peak velocity for each eye and each starting-position eccentricity relative to the straight-ahead. This was meant to determine the number of conditions¹ in which NTA was higher than the resolution limits of the eyetracker we used (examples are given in Figure 6). Such an analysis revealed that the 63 participants could be divided into three ED profiles. (1) The weak ED profile includes twenty-five participants displaying NTA in almost all the conditions (a representative subject is presented in Figure 6a). (2) The strong ED profile includes seventeen participants displaying no NTA in almost all the conditions; instead, both their eyes showed higher peak velocities for saccades toward the same visual hemifield (Figure 6b). (3) The intermediate ED profile includes twenty-one participants displaying NTA in a few conditions (Figure 6c).

In order to rank participants according to their ED strength, we propose to compute a percentage of ED strength based on NTA ($\%EDS_{NTA}$), (1) by subtracting the number of conditions in which a participant exhibits NTA (Figure 6a), reflecting weak ED (Nb_{Weak}) from the number of conditions in which she/he exhibits higher peak velocity toward a same visual hemifield with both eyes (Figure 6b), reflecting strong ED (Nb_{Strong}); and (2) by dividing the previous result by the total number of conditions in which NTA is tested ($Total_{NTA}$, here equal to ten):

$$\%EDS_{NTA} = \frac{Nb_{Strong} - Nb_{Weak}}{Total_{NTA}} \times 100$$

Based on this formula, a value of +100% corresponds to very strong ED, -100% corresponds to very weak ED, and values around 0% correspond to intermediate ED. The key point is that, as shown in Figure 7, the 63 participants are consistently distributed along the possible values of %EDS_{NTA}.

However, this measure is only based on NTA, and as group analyses have revealed that ED strength modulated both NTA and CCA, we propose to refine the %EDS_{NTA} by taking the CCA profile of participants into account. We quantified individual CCA by counting the number of conditions (Nb_{CCA}) in which CCA was found above the resolution limits of the eyetracker we used. Note however that this does not involve the same number of conditions than for NTA, because (1) unlike NTA, CCA can be assessed for each eye separately, and (2) CCA cannot be assessed in saccades starting from position 0°. In the current study, we tested NTA over ten conditions (5 starting positions x 2 block types) while CCA was tested over sixteen conditions (4 starting positions x 2 block types x 2 recorded eyes). This Nb_{CCA} should be used to modulate ED strength between two successive graduations of %EDS_{NTA}. Therefore, Nb_{CCA} has to be weighted by $100/(Total_{NTA} \times Total_{CCA})$ where $Total_{NTA}$ and $Total_{CCA}$ correspond to the number of conditions in which NTA and CCA are respectively tested. Then, the final measure of ED strength, integrating both NTA and CCA (%EDS), is obtained by adding or subtracting the weighted Nb_{CCA} to/from the participant's %EDS_{NTA}. The formula depends on the sign of the %EDS_{NTA}, which has a negative lower bound and a positive upper bound. Consequently, the weighted Nb_{CCA} decreases positive %EDS_{NTA} and increases negative %EDS_{NTA}. An adjustment of the formula is also necessary to deal with the central value of the scale (%EDS_{NTA} = 0%) because in this case, the %EDS values can be either negative or positive. Ultimately, if %EDS_{NTA} is (1) > 0%, (2) < 0%, or (3) equal to 0%, then %EDS equals:

- (1) $\%EDS = \%EDS_{NTA} - \left[Nb_{CCA} \times \left(\frac{100}{Total_{NTA} \times Total_{CCA}} \right) \right]$
- (2) $\%EDS = \%EDS_{NTA} + \left[(Total_{CCA} - Nb_{CCA}) \times \left(\frac{100}{Total_{NTA} \times Total_{CCA}} \right) \right]$
- (3) $\%EDS = \frac{100}{2 \times Total_{NTA}} - \left[Nb_{CCA} \times \left(\frac{100}{Total_{NTA} \times Total_{CCA}} \right) \right]$

For example, the participant presented in Figure 6a shows a $\%EDS_{NTA}$ of -100%. By integrating his Nb_{CCA} (13 out of 16), we obtain his precise $\%EDS$ between -100% and -90%: $-100 + [(16-13) \times (100 / (10 \times 16))] = -98.125\%$. Likewise, participants in Figure 6b ($\%EDS_{NTA}$: +100%; Nb_{CCA} : 3/16) and Figure 6c ($\%EDS_{NTA}$: 10%; Nb_{CCA} : 8/16) have $\%EDS$ of 98.125% and 5%, respectively. In conclusion, what we propose here is a new way to measure ED strength based on oculomotor performance.

4. Discussion

In the present study, we confirmed that participants with weak ED show NTA in saccadic peak velocity whereas no NTA is observed in participants with strong ED (Chaumillon et al., 2017; Tagu et al., 2016; Vergilino-Perez et al., 2012). Moreover, our data indicate that ED strength also affects another asymmetry in saccadic peak velocity: indeed, while CCA was observed in participants with weak ED, all the asymmetries of the saccadic system are reduced - if not suppressed - in participants with strong ED. These results suggest that ED strength, NTA and CCA are all related, but the nature of physiological mechanisms underlying this relationship remains an open issue.

4.1. On the links between eye dominance strength and saccadic asymmetries

On the one hand, neuroimaging studies have uncovered the existence of a special relationship between the dominant eye and its ipsilateral V1, the latter being both larger (Erdogan et al., 2002) and more strongly activated than the contralateral V1 when the dominant eye is stimulated (Shima et al., 2010). Importantly, Shima et al. (2010) observed this asymmetry in V1 after stimulating the temporal hemiretina (i.e., the nasal hemifield) of the dominant eye; but stimulating the nasal hemiretina (i.e., the temporal hemifield) of the

dominant eye produced no difference in the activation levels of the ipsi- and the contralateral V1. Thus, it seems that the special relationship between the dominant eye and its ipsilateral V1 is closely linked to the temporal hemiretina.

On the other hand, NTA is generally explained with reference to the architecture of the visual pathways. For each eye, the information presented in the temporal hemifield is projected on the nasal hemiretina and the information presented in the nasal hemifield is projected on the temporal hemiretina. Then, at the optic chiasm, the axons from the nasal hemiretina (i.e., temporal hemifield) cross to project onto the contralateral hemisphere whereas the axons from the temporal hemiretina (i.e., nasal hemifield) do not cross and project onto the ipsilateral hemisphere. It has been shown that there is greater retinal density of cones and ganglion cells in the nasal hemiretina than in the temporal hemiretina (Curcio & Allen, 1990). Importantly, this retinal asymmetry - present at every step of the geniculostriate pathway - leads to NTAs in the projections from the retina to the lateral geniculate nucleus (Connolly & Van Essen, 1984; Williams et al., 1995) and in V1 (Toosy et al., 2001; Tychsen & Burkhalter, 1997). Tychsen & Burkhalter (1997) have shown that in V1, ocular dominance columns formed by the inputs of the nasal hemiretina are larger, and occupy more space than the ocular dominance columns made from the inputs of the temporal hemiretina.

NTA in saccadic parameters has therefore been attributed to asymmetries in the geniculostriate pathway, from the retina to V1 (Tagu et al., 2018; see also Bompas et al., 2008). This might account for the pattern we found in weak ED. We propose that for strong ED, the relationship between the temporal hemiretina of the dominant eye and the ipsilateral V1 strengthens the signals from the temporal hemiretina, possibly mitigating the advantage of inputs from the nasal hemiretina in V1 (i.e., counteract the NTA). Therefore, for strong ED, the absence of NTA in saccadic peak velocity could result from the fact that in V1, the advantage of ocular dominance columns receiving inputs from the nasal hemiretina is masked by the relationship between inputs from the temporal hemiretina of the dominant eye and the ipsilateral V1. This assumption predicts that the stronger the relationship between

the dominant eye and the ipsilateral V1 (and thus ED strength), the weaker the NTA. This physiological interpretation would be congruent with the ED strength index we have computed here; but of course, it should be tested using neuroimaging techniques.

The saccadic peak velocity corresponds to the peak burst firing frequency of the premotor neurons of the brainstem saccadic generator (Corneil & Munoz, 2014; Sparks, 2002). When triggering a saccade, V1 sends the visual information to the parietal and frontal eye fields, which both project onto the superior colliculus. The latter then transmits the motor command to the brainstem saccadic generator (Corneil & Munoz, 2014; Leigh & Zee, 2006; Sparks, 2002; White & Munoz, 2011). Our assumption is that asymmetries in V1 probably spread across the upcoming saccade generation network, and *in fine*, lead to asymmetries in peak velocity. One could however expect that asymmetries in V1 should more directly affect saccade latency. However, as saccade latency is more sensitive to cortical influences than peak velocity (Pierrot-Deseilligny et al., 1995; Sommer & Wurtz, 2000; Leigh & Zee, 2006), it is accordingly strongly modulated by top-down influences such as decision making or visual attention which may compete with NTAs and CCAs (see also Bompas et al., 2008; Tagu et al., 2018 for similar arguments). In contrast with saccade latency, peak velocity is not affected by top-down influences (Galley, 1989; see also Di Stasi et al., 2013; Leigh & Zee, 2006), which explains why saccadic asymmetries are observed in this parameter.

In the present study, we also found that NTA (and therefore ED strength) modulates CCA, and that the higher the NTA (i.e., the weaker the ED strength), the higher the CCA. As evidenced in previous studies (Krebs, Boehler, Zhang, Schoenfeld, & Woldorff, 2012; Krebs, Schoenfeld, Boehler, Song, & Woldorff, 2010), centripetal saccades directed toward the straight-ahead direction are faster than centrifugal ones because they re-align the head-centered and the eye-centered reference frames. Moreover, the speed advantage of centripetal saccades is supposed to be behaviorally driven by the necessity to quickly focus one's attention on stimuli appearing straight-ahead, as they may be obstacles during locomotion (Camors et al., 2016; Durand, Camors, Trotter, & Celebrini, 2012). Using

electroencephalography, Krebs et al. (2012) have shown a negative deflection in parieto-occipital regions contralateral to the future gaze location. The deflection is weaker and its duration is shorter before centripetal saccades than before centrifugal saccades. As V1 is the earliest structure in which saccades are coded in a head/body-centered reference frame (Rieger, Schoenfeld, Heinze, & Bodis-Wollner, 2008), it seems that the CCA is driven by asymmetries in V1. This is consistent with the findings of Durand et al. (2010). Using single- and multiunit recordings in macaques, they have shown that stimuli presented straight-ahead benefit from privileged processing in V1 compared to stimuli presented from other locations.

Having recently shown that CCA in peak velocity is only present in temporal saccades (not in nasal ones), Tagu et al. (2018) proposed two physiological explanations to this result. First, NTA and CCA have different neurophysiological origins - NTA would originate from asymmetries in the visual pathways while CCA would originate from asymmetries in the extra-ocular muscles. Second, the two asymmetries have a common structure in their physiological origin, which could explain their relationship. As discussed above, we assume that this common structure might well be V1. Here, we have shown (1) that NTA and CCA are closely linked and (2) that this relationship could be modulated by ED strength. The data from our weak ED group replicated the results of Tagu et al. (2018), with the presence of CCA in temporal saccades only, a restriction probably driven by asymmetries in the visual pathways up to V1. However, no consistent NTA and CCA in peak velocity could be found among individuals with strong ED, reinforcing the assumption that ED, NTA and CCA share the same common structure V1. In previous research, we have shown that the relationship between the dominant eye and ipsilateral V1 led to better perceptual (Chaumillon et al., 2017) and visuo-motor (Tagu et al., 2016) processing in its contralateral than in its ipsilateral hemifield. This dissimilar processing of the visual fields might conceal the privileged processing of the straight-ahead direction. Indeed, before centripetal saccades, as the eyes are not aligned on the straight-ahead direction, the latter coincides with one of the visual hemifields. Presenting the straight-ahead direction in the hemifield ipsilateral to the dominant

eye may create a conflict between the privileged processing of the straight-ahead direction and the privileged processing of the hemifield contralateral to the dominant eye. This conflict could possibly result in weaker CCA or no CCA in participants with strong ED. Note, however, that our data cannot provide evidence for such a conflict. Indeed, the two participants with the highest ED strength do not present any asymmetry in CCA between contralateral and ipsilateral hemifields. Still, it should be emphasized that (1) this observation is based on two participants only, and that (2) our paradigm was not designed to explore this conflict. Indeed, we only included small 5° saccades, and there is evidence that for small saccades, saccadic asymmetries are reduced (Becker, 1989; Chen, Hung, Quinet, & Kosek, 2013; Collewijn et al., 1988; Pelisson & Prablanc, 1988). We therefore believe that additional studies are needed to test the hypothesis of a conflict in V1 (between the processing of the hemifield contralateral to the dominant eye and the processing of the straight-ahead direction) among strong ED individuals, and that these studies should use a paradigm including larger leftward and rightward centripetal and centrifugal saccades.

It should be noted that from an evolutionary perspective, having strong rather than weak ED might appear to be a disadvantage. Indeed, CCA - which enables better processing of potential obstacles during locomotion in the straight-ahead direction - is not detected among strong ED individuals, while it is exacerbated among weak ED ones. Nevertheless, this is consistent with the number of participants with either weak or strong ED. In all our studies focused on the quantification of ED strength, participants with strong ED have always been less numerous than participants with weak ED. 6 out of 18 participants, 32 out of 92 participants, and 15 out of 50 participants elicited strong ED in Vergilino-Perez et al. (2012), Tagu et al. (2016), and Chaumillon et al. (2017), respectively. Thus, it seems that the proportion of strong ED in the population is around 33%.

It is worth noting that contrary to ED strength (strong vs. weak ED); ED laterality (left vs. right ED) does not impact saccadic asymmetries. This result is not surprising given that participants with weak ED are unlikely to present a dominant eye. Thus, ED strength and ED

laterality should not be measured in the same way. First, a test of ED strength should be administered to identify participants who actually have a dominant eye, and only then, ED laterality of these participants should be assessed.

4.2. Toward a continuum of eye dominance strength

In the current study, individual analyses have confirmed that the measurement of ED strength based on NTA in peak velocity proposed in Vergilino-Perez et al. (2012) was quite robust. Moreover, we have shown that the joint study of several asymmetries in the saccadic system made it possible to compute a continuous numerical index of ED strength. By using binocular recordings of eye movements during leftward and rightward saccades from different starting positions, we could jointly assess NTA and CCA. Moreover, the potential variability of saccadic asymmetries between reactive and voluntary saccades was tested using step- and overlap paradigms. Based on their NTA and CCA profiles, each participant was assigned his specific percentage of ED strength, from -100% (very weak ED) to +100% (very strong ED). Moreover, in previous measures of sighting ED strength (e.g., Carey & Hutchinson, 2013; Dalton et al., 2015; Ho et al., 2017) experimenters often have no direct access to the percept experienced by participants, and ED strength measures are often based on oral responses impossible to substantiate objectively. For the first time, we propose an objective continuous ED scale, based on oculomotor performance. The availability of an accurate measure of ED strength is of particular importance with regards to clinical ophthalmology. Indeed, the precise measurement of ED strength being extremely difficult, it is hard for physicians to make clinical decision to correct differently the dominant and non-dominant eyes - e.g., monovision correction in presbyopic patients (Evans, 2007; Greenbaum, 2002; Handa et al., 2004; Jain, Arora, & Azar, 1996; Papas, Young, & Hearn, 1990; Wright, Guemes, Kapadia, & Wilson, 1999). The monovision technique, frequently used to correct presbyopia, consists in jointly correcting distal and proximal visions in the dominant and in the non-dominant eye respectively. Monovision can be carried out with contact lenses, glasses, refractive surgery, or intraocular lens implantation (typically

performed during cataract surgery), but patient satisfaction after monovision is only about 70-80% (Finkelman, Ng, & Barrett, 2009; Jain et al., 1996; Zhang, Sugar, Jacobsen, & Collins, 2011). Today, more than one billion people in the world suffer from presbyopia, including more than 500 million with no appropriate optical correction (Holden et al., 2008). Thus, identifying the factors leading to patients' tolerance of monovision is critical to prevent surgery failures. It seems that one of the factors leading to successful monovision is weak ED strength (Handa et al., 2004; Seijas et al., 2007). Indeed, in their 2004 study, Handa et al. asked twenty formerly presbyopic patients having benefited from monovision intraocular lens implantation during cataract surgery to give some feedback on monovision. They found that sixteen patients were satisfied with monovision, while four were dissatisfied. Moreover, the authors measured participants' ED using the hole-in-card test (Durand & Gould, 1910; Miles, 1930) and assessed "ED strength" with a binocular rivalry paradigm, in other words with a measure of *sensory* ED strength (not of *sighting* ED strength). They found that the four patients dissatisfied with monovision had very high sensory ED compared to the other patients. The authors concluded that weak sensory ED predicted successful monovision, whereas strong sensory ED should contraindicate monovision. Indeed, monovision requires constant switching between the inputs from each eye to explore distal and proximal visual environments. But individuals with strong ED may possibly be unable to suppress the input from their dominant eye and explore their proximal environment with their non-dominant one. To our knowledge, the impact of sighting ED strength on the success of monovision has not yet been tested (maybe due to the lack of testing methods). This is all the more surprising since in monovision, the eye chosen to correct distal vision is the sighting dominant eye, not the sensory one. We are convinced that an accurate measurement of sighting ED strength is necessary to improve the success of monovision, and the percentage-based continuous scale we propose is a significant step toward the achievement of this project. However, we acknowledge that in its current form the quantification we developed here is hardly accessible to physicians and ophthalmologists. Although our measure takes into account the resolution limits of the eyetracker we used, it still has to be tested with more accessible (but

less accurate) eyetrackers. Moreover, the very large number of conditions and of trials per condition included in the current study made it highly time-consuming. It allowed us identifying the main factors impacting the ED strength measure. Further studies might use a less time-consuming procedure, so that physicians and ophthalmologists could easily use our ED-strength scale in their practice. As a matter of fact, we have shown that ED strength value was not affected by block type (step vs. overlap). Besides, analyses have shown that CCA was more consistently present at starting position 10° away than 5° away from the straight-ahead direction. Involving only one block type and one eccentricity would considerably reduce the test duration. Note however that as our ED strength index includes the number of trials in which NTA and CCA are tested ($Total_{NTA}$ and $Total_{CCA}$), reducing the number of tested conditions would lessen the accuracy of the obtained ED quantification.

4.3. Conclusions and Future directions

Altogether, the present study reveals that NTA and CCA were strongly related, suggesting that they may share common neurophysiological origins. Moreover, it shows that ED strength modulates both NTA and CCA, and that observing how these asymmetries are organized in an individual provides a means to measure his ED strength. Our assumption is that V1 is probably the key structure for the relationship between ED strength, NTA and CCA, but research is needed to support this hypothesis using neuroimaging techniques. Moreover, by analyzing how NTA and CCA varied within and between individuals, we were able to propose a precise evaluation of ED strength, on a continuum from -100% to +100%. We are convinced that future studies may adapt this ED test, allowing physicians and ophthalmologists to include this tool in their clinical practice. Lastly, the calculation formula we propose here is designed to measure ED strength (i.e., from weak to strong ED), but it provides no information about ED laterality (i.e., dominant left or right eye); but after all, ED laterality information only makes sense for participants with strong ED. Therefore, our study represents the first but necessary step toward an objective measurement of ED based on

oculomotor performance, the second step being the measurement of ED laterality, based on the oculomotor performance of individuals with very high ED strength scores.

Footnotes

(I.424 p.17) 1. We chose the number of conditions showing NTA rather than the magnitude of the NTA in peak velocity as an indicator of ED strength because the primary factor leading to strong ED is the consistency of the peak velocity pattern between the left eye and the right eye. We argue that a participant with small but consistent NTA across all conditions exhibits weaker ED than a participant exhibiting high NTA in one condition only but consistently showing higher peak velocity toward a same visual hemifield with both eyes in all other conditions.

Declaration of interest

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Figure Captions:

Caption for Figure 1: Illustration of temporal, nasal, centripetal and centrifugal saccades. Panel (a) presents centrifugal saccades, directed away from the straight-ahead direction (location 0°), and panel (b) presents centripetal saccades, directed toward the

straight-ahead direction. Red arrows are saccades from the left eye and black arrows are saccades from the right eye. Solid arrows are temporal saccades whereas dotted arrows are temporal saccades. Thereby, in panel (a) solid arrows are centrifugal-temporal saccades and dotted arrows are centrifugal-nasal saccades; and in panel (b) solid arrows are centripetal-temporal saccades and dotted arrows are centripetal-nasal saccades. The five showed starting positions (-10° , -5° , 0° , $+5^\circ$, $+10^\circ$) are the one used in Tagu et al. (2018) and in the current study.

Caption for Figure 2: Time course of a trial in each block type. (a) In the step block, each trial started with the presentation of a fixation-cross for 400 or 800 ms. It was immediately followed by the presentation of the saccade target. The target remained on the screen for 800 ms, and was followed by an inter-trial 1000 ms blank screen. (b) In the overlap block, the fixation was followed by a 600 ms overlap during which participants were asked to go on fixating. Then, the fixation-cross disappeared and participants had to make a saccade toward the target. The latter remained 800 ms on the screen, and was followed by a 1000 ms inter-trial blank screen.

Caption for Figure 3: Saccadic peak velocity as a function of starting position, saccadic direction, and recorded eye. Panel (a) presents the interaction for the 57 participants who completed both step- and overlap blocks. Panel (b) presents the same interaction for the 31 participants with weak ED and panel (c) for the 26 participants with strong ED. Error bars represent standard errors of the mean and asterisks indicate significant differences at $p < .05$.

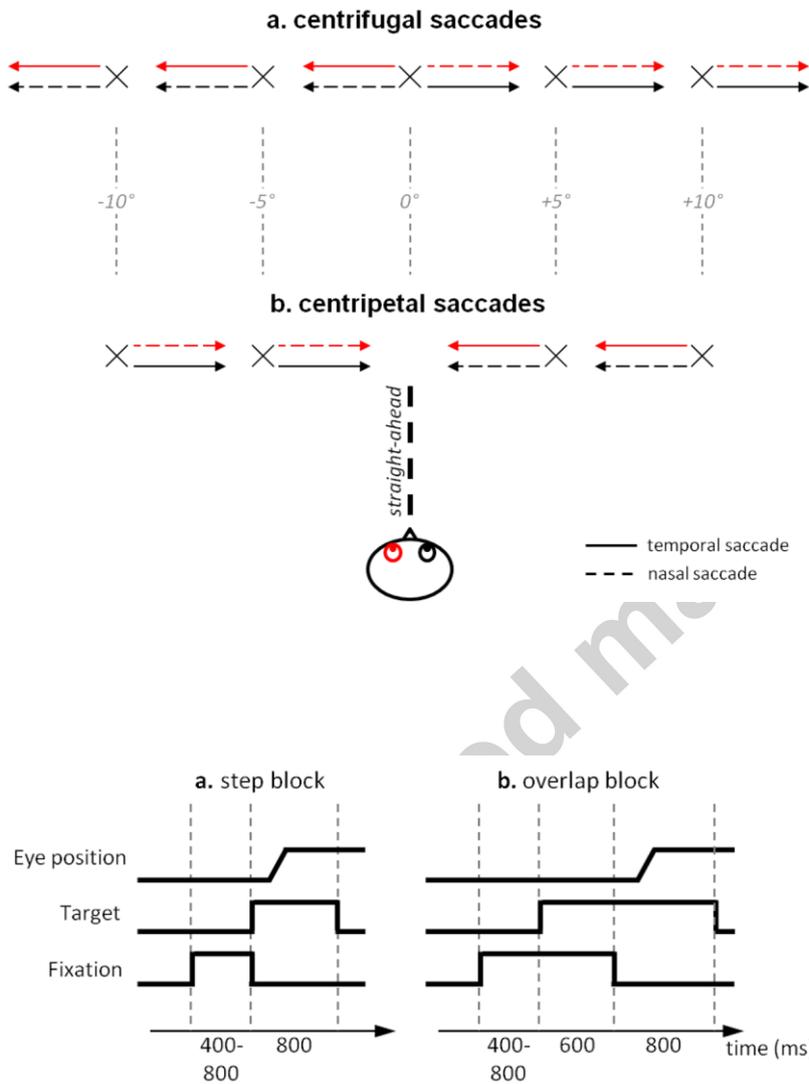
Caption for Figure 4: Saccadic peak velocity as a function of target hemifield and direction relative to the straight-ahead. Black squares represent centripetal saccades and

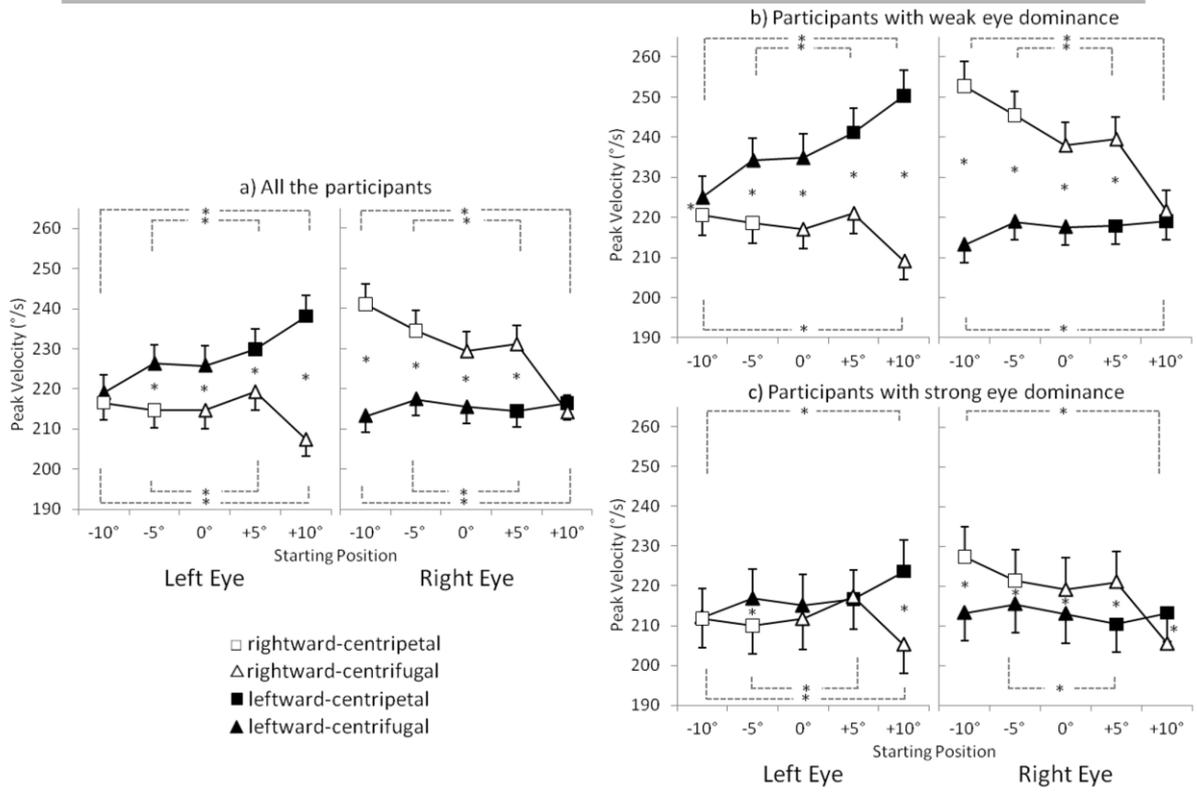
white triangles represent centrifugal saccades for each target hemifield (temporal or nasal). Panel (a) presents data from all the 57 participants. Panel (b) presents the data from the 31 weak ED participants, and panel (c) presents the data from the 26 strong ED participants. In each panel, error bars represent standard errors of the mean and asterisks indicate significant differences at $p < .05$.

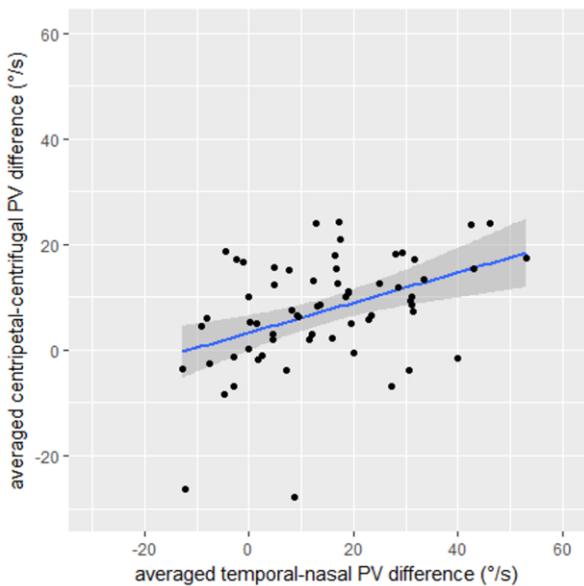
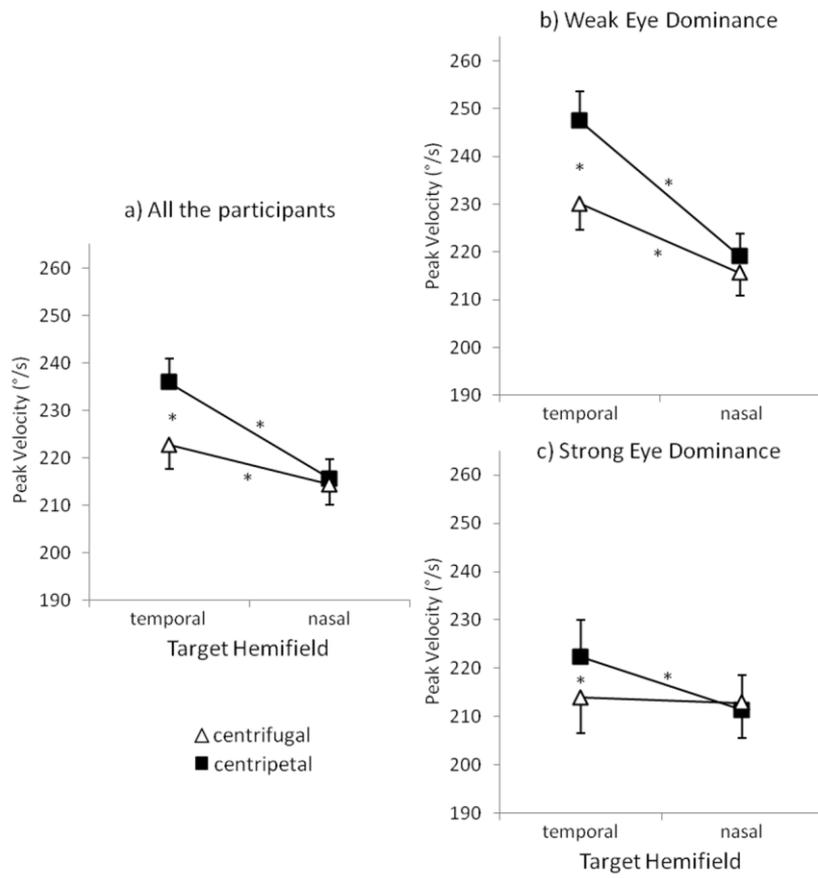
Caption for Figure 5: Correlation between NTA magnitude and CCA magnitude. Each point represents one of the 63 participants. Participants are plotted according to their averaged temporal-nasal peak velocity (PV) difference, and their averaged centripetal-centrifugal peak velocity (PV) difference. The blue line corresponds to the linear regression slope, and the shaded area delimits the 95% confidence interval.

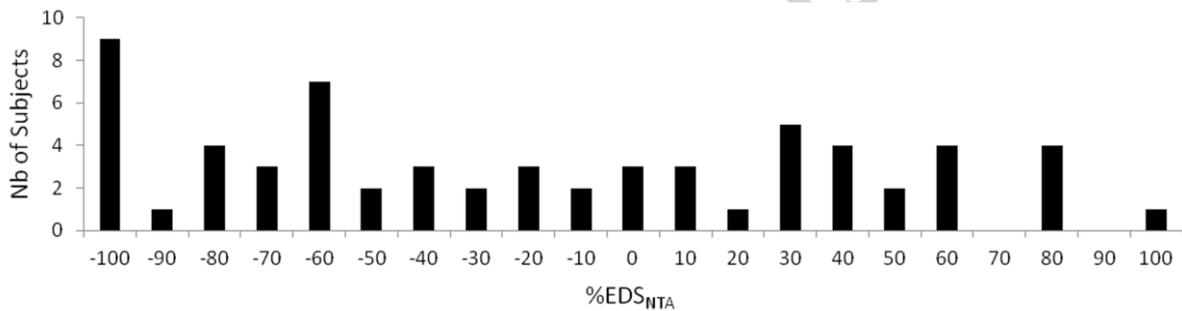
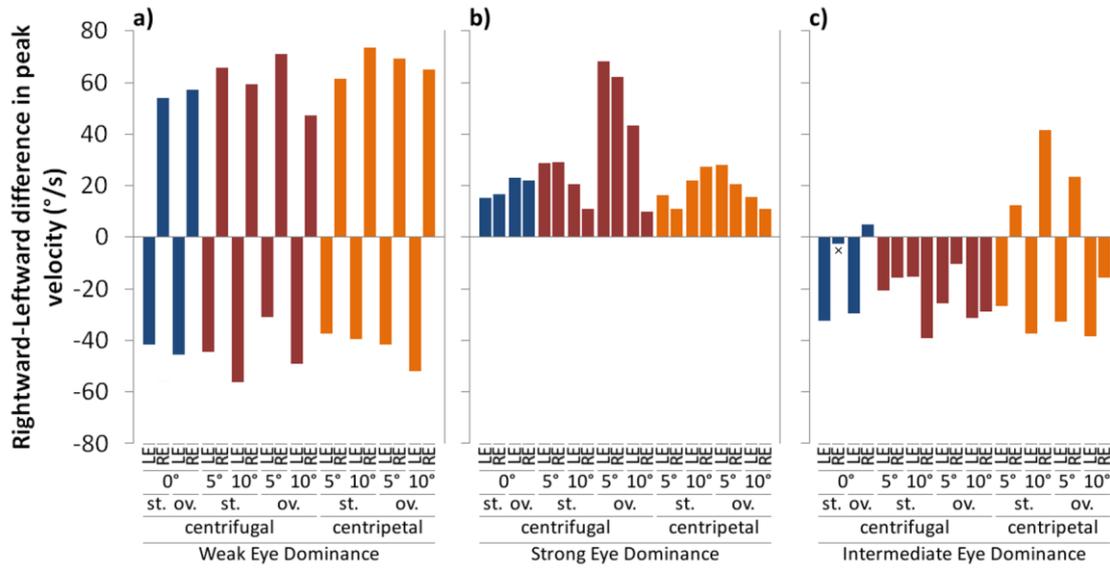
Caption for Figure 6: Rightward-Leftward differences in peak velocity showing weak, strong, and intermediate eye dominance. (a), (b) and (c) correspond to representative participants with weak, strong, and intermediate ED profiles, respectively. Colored bars represent the difference in peak velocity between rightward and leftward saccades. Positive differences indicate higher peak velocity in rightward than in leftward saccades whereas negative differences indicate the reverse. Therefore, standard naso-temporal asymmetry corresponds to a negative difference for the left eye and a positive difference for the right eye. Blue bars correspond to (centrifugal) saccades starting from the central position, red bars to centrifugal saccades starting from peripheral positions, and orange bars to centripetal saccades. In (a), the representative participant with weak ED exhibits NTA for all the saccades. In (b), the representative participant with strong ED exhibits no NTA at all. In (c), the representative participant with intermediate ED exhibits NTA in centripetal saccades only. For all panels: LE = Left Eye, RE = Right Eye; 0°, 5° and 10° correspond to starting positions; st. = Step block, ov. = Overlap block. x indicate differences below the resolution limits of the used eyetracker ($< 4^\circ/s$).

Caption for Figure 7: Distribution of the 63 participants over the different values of %EDS_{NTA}. Each bar represents the number of subjects showing the corresponding percentage of eye dominance strength based on naso-temporal asymmetry in saccadic peak velocity (%EDS_{NTA}).









Highlights:

- Naso-temporal asymmetry distinguishes between weak and strong eye dominance.
- Eye dominance strength also modulates centripetal-centrifugal asymmetry.
- Combined saccadic asymmetries enable continuous measure of eye dominance strength.
- The influence of eye dominance on both asymmetries indicates the implication of V1.