

Recentering bias for temporal saccades only: Evidence from binocular recordings of eye movements

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It is well known that the saccadic system presents multiple asymmetries. Notably, temporal (as opposed to nasal) saccades, centripetal (as opposed to centrifugal) saccades (i.e., the recentering bias) and saccades from the abducting eye (as opposed to the concomitant saccades from the adducting eye) exhibit higher peak velocities. However, these naso-temporal and centripetal-centrifugal asymmetries have always been studied separately. It is thus unknown which asymmetry prevails when there is a conflict between both asymmetries, i.e., in case of centripetal nasal saccades or centrifugal temporal saccades. This study involved binocular recordings of eye movements to examine both the naso-temporal and centripetal-centrifugal asymmetries so as to determine how they work together. Twenty-eight participants had to make saccades toward stimuli presented either centrally or in the periphery in binocular conditions. We found that

temporal and abducting saccades always exhibit higher peak velocities than nasal and adducting saccades, irrespective of their centripetal or centrifugal nature. However, we showed that the velocity advantage for centripetal saccades is only found for temporal and not for nasal saccades. Such a result is of importance as it could provide new insights about the physiological origins of the asymmetries found in the saccadic system.

Introduction

Up to now, saccades are typically thought to be conjugated eye movements; thus saccades are generally recorded from one eye or data from the left and right eyes are averaged. However, during the 1980's (Colle-

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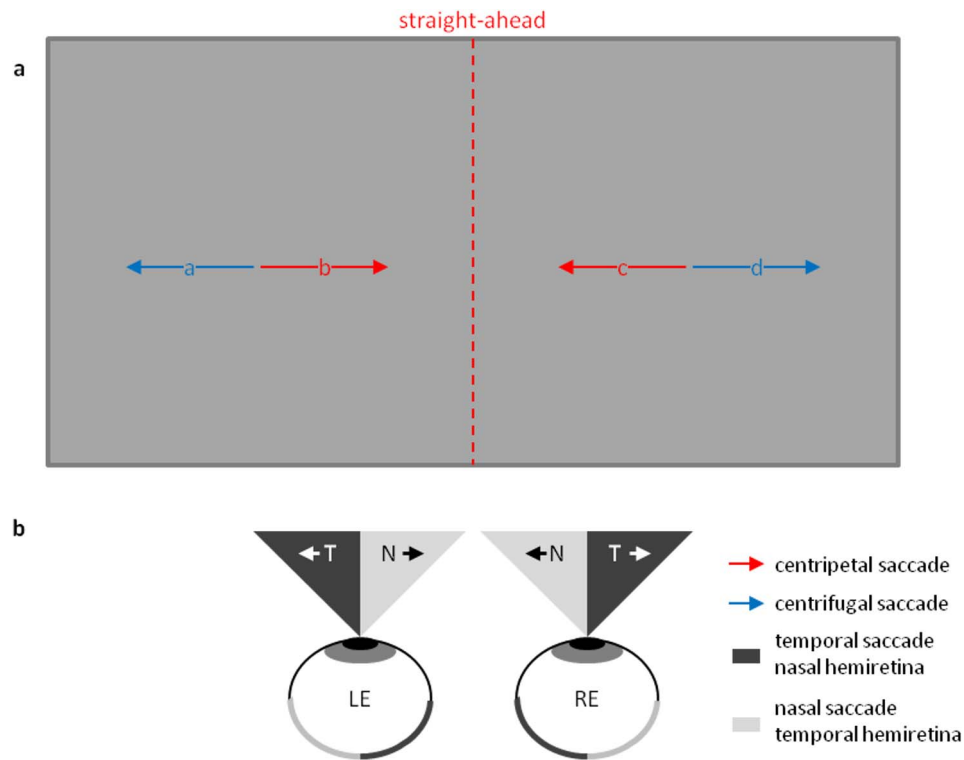


Figure 1. Illustration of the asymmetries of the saccadic system. (a) Illustration of centripetal saccades (in red) and centrifugal saccades (in blue). Centripetal saccades are saccades directed toward the straight-ahead direction (represented by the red dashed line) whereas centrifugal saccades are saccades directed away from the straight-ahead direction. (b) Illustration of the projections of the temporal and nasal hemifields on the nasal and temporal hemiretinas of each eye. For each eye, dark gray represents temporal saccades, directed toward the temporal hemifield and projected on the nasal hemiretina whereas light gray represents nasal saccades, directed toward the nasal hemifield and projected on the temporal hemiretina.

wijn, Erkelens, & Steinman, 1988; Miyoshi, Hiwatashi, Kishimoto, & Tamada, 1981), binocular recordings of eye movements have shown that traces of each eye present asynchronous and asymmetric profiles with the abducting eye (i.e., the eye moving toward the temple: the right eye for rightward saccades and the left eye for leftward saccades) starting a few milliseconds earlier than the adducting one (i.e., the eye moving toward the nose: the left eye for rightward saccades and the right eye for leftward saccades). Saccades of the abducting eye also have larger amplitudes, higher peak velocities, shorter durations as well as shorter acceleration phases than the concomitant adducting saccades of the fellow eye (Collewijn et al., 1988).

Such abducting/adducting differences are consistent with other studies reporting naso-temporal asymmetries (NTAs) on saccadic parameters by using monocular recordings. Note that, in this case, the asymmetries were not apprehended through the differences between the abducting eye and the adducting eye but between the saccades toward the temple (called temporal saccades) and saccades toward the nose (called nasal saccades) performed by one eye, the other eye being sometimes occluded. The temporal saccades are performed toward stimuli presented in the temporal

hemifield and therefore processed by the nasal hemiretina. Similarly, the nasal saccades are performed toward stimuli presented in the nasal hemifield and therefore processed by the temporal hemiretina (see Figure 1b). NTAs have been reported more or less consistently on different saccade parameters. Walker, Mannan, Maurer, Pambakian, and Kennard (2000) found shorter latencies for temporal than for nasal saccades only when a distractor was presented in the contralateral hemifield to the saccade target (no difference in the single target condition). Kristjánsson, Vandenbroucke, and Driver (2004) found shorter latencies for temporal prosaccades in one of their experiments whereas they found shorter latencies for nasal voluntary antisaccades. Finally, others argue for an absence of NTAs on saccade latency (Bompas, Sterling, Rafal, & Sumner, 2008; Honda, 2002; Rafal, Henik, & Smith, 1991). Studies examining NTAs on saccade amplitude also showed contradictory results (Collewijn et al., 1988; Jóhannesson, Ásgeirsson, & Kristjánsson, 2012; Kristjánsson et al., 2004; Walker et al., 2000). Concerning saccade duration, only few studies reported longer nasal than temporal saccades, with weak effects (from 2 to 5 ms) from small sets of participants (Collewijn et al., 1988; Robinson, 1964;

White, Eason, & Bartlett, 1962). Finally, the strongest NTAs were revealed for the saccadic velocity parameters such as the averaged velocity, the peak velocity (corresponding to the highest velocity attained during the saccade), and the skewness (which is a comparison between the acceleration and deceleration phase durations). The averaged velocity does not seem the best indicator of the NTA as it was found either lower (White et al., 1962) or higher (Fricker, 1971) for temporal than for nasal saccades. Only one study reported a NTA on skewness (Collewijn et al., 1988), the acceleration phase being shorter for temporal than for nasal saccades. More consistent are studies reporting higher peak velocities for temporal than for nasal saccades (Collewijn et al., 1988; Cook, Stark, & Zuber, 1966; Fricker, 1971; Hyde, 1959; Jóhannesson & Kristjánsson, 2013; Robinson, 1964), even if two studies reported a reversed NTA in a subset of their experiments or conditions (Boghen, Troost, Daroff, Dell'osso, & Birkett, 1974; Kristjánsson et al., 2004).

NTAs are generally explained by the visual system architecture. In each eye, information seen in the temporal visual hemifield is projected on the nasal hemiretina and information from the nasal hemifield is projected on the temporal hemiretina (see Figure 1b). Then, the ganglion cell axons from the nasal hemiretina cross at the optic chiasma to project on the contralateral hemisphere, whereas the ganglion cell axons from the temporal hemiretina do not cross and thus project in the ipsilateral hemisphere. At the level of the optic tract, 10% of the fibers join the superficial layers of superior colliculus (SC) to form the retinotectal pathway whereas the other part joins the lateral geniculate nucleus (LGN) and then the primary visual cortex (V1) to form the geniculostriate pathway. Anatomical asymmetries were shown as early as the retinal level with a higher density of cones and ganglion cells in the nasal hemiretina than in the temporal hemiretina (Curcio & Allen, 1990). First neurophysiological work on cats and monkeys (Hubel, LeVay, & Wiesel, 1975; Itaya & Van Hoesen, 1983; Sterling, 1973; Tigges & Tigges, 1981) have shown that these anatomical asymmetries are still present in the projections from the retina to the SC with larger and denser projections from the nasal hemiretina than the temporal one, arguing for a retinotectal origin of the NTA. In humans, a neuroimaging study revealed larger activation in the SC for temporal than for nasal visual stimuli and no such difference in the LGN and visual cortex (Sylvester, Josephs, Driver, & Rees, 2007). However, NTAs were also found in projections from the retina to the LGN (Connolly & Van Essen, 1984; Williams, Azzopardi, & Cowey, 1995) and in V1 (Tychsen & Burkhalter, 1997), suggesting multiple origins of the NTA, both in the retinotectal and in the geniculostriate pathways (see also Bompas et al., 2008). Jóhannesson

and Kristjánsson (2013) interpreted the presence of NTAs on saccadic peak velocity and their absence on latency by the larger projections from nasal than temporal retina that may transfer more signals, but with the same transfer time. Finally, the modulation of neural activity of the SC by direct projections from cortical brain areas (e.g., the frontal eye fields, FEF) during saccades (Segraves & Goldberg, 1987; Sommer & Wurtz, 2000) has been proposed to mitigate the NTA in visual pathways (Jóhannesson et al., 2012; Jóhannesson & Kristjánsson, 2013).

Besides NTAs, it is also known that saccades toward the straight-ahead direction (centripetal saccades) have different dynamics than saccades directed away from it (centrifugal saccades). Figure 1a gives some examples of centripetal and centrifugal saccades. As for the NTA, contradictory results were found for the possible presence of a centripetal-centrifugal asymmetry (CCA, also referred to as the recentering bias) on saccade latency. Some studies showed shorter latencies for centripetal than centrifugal saccades (Krebs, Boehler, Zhang, Schoenfeld, & Woldorff, 2012; Krebs, Schoenfeld, Boehler, Song, & Woldorff, 2010) whereas others did not find any CCA on saccade latency (Camors, Trotter, Pouget, Gilardeau, & Durand, 2016; Collewijn et al., 1988; Pelisson & Prablanc, 1988). Moreover, studies revealed no CCA on saccade amplitude (Camors et al., 2016; Collewijn et al., 1988; Pelisson & Prablanc, 1988), except one (Kapoula & Robinson, 1986) showing larger centripetal saccades than centrifugal saccades. CCAs on saccade duration have often been found, with longer centrifugal than centripetal saccades (Camors et al., 2016; Collewijn et al., 1988; Pelisson & Prablanc, 1988). However, Pelisson and Prablanc (1988) and Collewijn et al. (1988) both noted that this discrepancy on saccade duration was due to a longer deceleration phase, centrifugal saccades being more skewed than centripetal saccades. They thus suggest that the CCA found on saccade duration was the reflection of a CCA on saccadic skewness. Finally, there is a wide consensus for higher peak velocities for centripetal than centrifugal saccades (Abel, Dell'Osso, Daroff, & Parker, 1979; Camors et al., 2016; Collewijn et al., 1988; Frost & Pöppel, 1976; Inchingolo, Spanio, & Bianchi, 1987; Jürgens, Becker, & Kornhuber, 1981; Pelisson & Prablanc, 1988), indicating that peak velocity is the most sensible saccadic parameter to asymmetries.

At the muscular level, centripetal saccades seem driven by lower mechanical constraints than centrifugal saccades (Koene & Erkelens, 2002). Indeed, the connections between the paramedian pontine reticular formation (PPRF, pulse generator of horizontal saccades) and extraocular muscles suggest that agonist/antagonist pairs of muscles are organized in a push-pull arrangement (Fuchs, Kaneko, & Scudder, 1985; Ling,

Fuchs, Siebold, & Dean, 2007; Moschovakis & Highstein, 1994; Pelisson & Prablanc, 1988; Robinson, 1989; Van Gisbergen, Robinson, & Gielen, 1981). Therefore, in case of a centripetal saccade, orbital passive elastic forces pull the eyes toward their primary position (Robinson, 1981). Conversely, for a centrifugal saccade, much stronger active forces are involved to pull the eyes away from the straight-ahead direction. Besides these mechanical constraints, at the subcortical level centripetal saccades seem determined by more efficient neural signals than centrifugal saccades (Jürgens et al., 1981), in relation with different preparatory activity in the SC (Krebs et al., 2010; Paré & Munoz, 2001). Moreover, recent studies (Camors et al., 2016; Krebs et al., 2012, 2010) suggest that CCAs are also linked to cortical processes. In particular, an electroencephalography study (Krebs et al., 2012) reported a negative deflection in parieto-occipital regions contralateral to the future gaze location starting around 160 ms prior to saccade onset. Moreover, they show that this presaccadic negativity was shorter in duration and weaker prior to centripetal than to centrifugal saccades. These findings are consistent with the idea that the straight-ahead direction represents a default gaze direction in which the eye-centered and head-centered reference frames are aligned (Durand, Trotter, & Celebrini, 2010; Kardamakis & Moschovakis, 2009; Tatler, 2007) and suggest that the weaker presaccadic negativity for centripetal saccades reflects a diminished need for attentional guidance compared to centrifugal saccades (Krebs et al., 2012).

To sum up, NTAs and CCAs can be observed on saccadic parameters, mostly on peak velocity. However, these asymmetries have always been studied separately, and the relationship between them has never been investigated. Indeed, the large majority of the studies interested in the NTAs involved only centrifugal saccades (Bompas et al., 2008; Honda, 2002; Jóhannesson et al., 2012; Jóhannesson & Kristjánsson, 2013; Kristjánsson et al., 2004; Robinson, 1964) whereas studies examining the CCAs averaged leftward and rightward saccades using monocular recordings of eye movements (Krebs et al., 2012, 2010), or used binocular recordings but averaged the data from both eyes (Abel et al., 1979; Camors et al., 2016; Collewyn et al., 1988; Pelisson & Prablanc, 1988). To our knowledge, NTA and CCA have never been investigated together.

We therefore do not know which asymmetry prevails in case of a saccade leading to a conflict between the NTA and the CCA, i.e., a centripetal nasal saccade or a centrifugal temporal saccade. For example, the *saccade b* in Figure 1 is a centripetal nasal saccade for the left eye whereas it is a centripetal temporal saccade for the right eye. In the same manner, the *saccade a* is a centrifugal temporal saccade for the left eye and a centrifugal nasal

saccade for the right eye. Indeed, based on the known NTA and CCA we expect higher saccadic peak velocities for centripetal temporal saccades than for centrifugal nasal saccades. However, we don't know what will be going on for centripetal nasal saccades or centrifugal temporal saccades: Are they going to have higher/lower peak velocities because of the NTA or the CCA? Here, we present a study in which leftward and rightward saccades were initiated from five locations on the horizontal axis, thus involving centripetal and centrifugal saccades. Eye movements were binocularly recorded, allowing us to examine, in the same study, both NTAs and CCAs on different saccadic parameters. Moreover, because some contradictory results have been found concerning NTAs on reactive and voluntary saccades (Kristjánsson et al., 2004), we used Step and Overlap-600 procedures to systematically investigate NTAs and CCAs on both types of saccades.

Methods

Subjects

Twenty-eight people (21 females, seven male; mean age 26 ± 6.0 years) participated to this study. Twenty-three of them were naïve undergraduate students of the Institute of Psychology of Paris Descartes University and five of them were nonnaïve members of the Laboratory. All the participants reported normal or corrected to normal vision and no history of psychiatric or neurological disorders. Prior to their inclusion in the study, the procedure was clearly explained to the participants, who then gave their informed consent. The study has been approved by the ethics committee of Paris Descartes University (IRB number 20130500001072), and has therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Instruments and materials

Stimuli were presented on an Iiyama HM240DT monitor (Iiyama, Nagano, Japan) with a refresh rate of 170 Hz and a resolution of 800×600 pixels. The experimental sessions took place in a dimly lit room. The subjects were seated 57 cm away from the screen, and their heads were kept stable with a chin and forehead rest. Each participant's head was positioned so as to be centered on the screen center.

Binocular recordings of their eye movements were made using an EyeLink 1000® (SR Research, Ontario, Canada), with a temporal resolution of 500 Hz, a spatial resolution of 0.01° and an averaged spatial

accuracy of 0.25° . The online saccade detection corresponded to an above-threshold velocity ($30^\circ/\text{s}$) and acceleration ($8,000^\circ/\text{s}^2$).

Each trial involved a fixation cross and a saccade target, which both were a $0.5^\circ \times 0.5^\circ$ white “X” (luminance of 35 cd/m^2) displayed on a medium gray background of 4.5 cd/m^2 .

Procedure

Each session began with a 9-point calibration filling the screen. Before each trial, a small circle was presented at the starting position of the next saccade in order to compare the actual eye position with the previous calibration. The participants had to look at the circle and press a button on a pad. At this stage, the correspondence between the actual eye position on the circle and the position of the preceding calibration was checked. If the eye was outside a window of 0.75° around the position where the eye should be, a new calibration began. Otherwise, the trial began with the presentation of the fixation cross randomly displayed for 400 or 800 ms. During this time, each eye position was checked and if the distance between the eye position and the center of the cross was above 0.75° , the trial was cancelled and repeated later in the session. The fixation cross could randomly appear at five different locations on the horizontal axis: at the center (0°), 5° on the left (-5°), 10° on the left (-10°), 5° on the right ($+5^\circ$) or 10° on the right ($+10^\circ$). The saccade target was always displayed 5° away from the fixation cross, either on its left or on its right. It could thus appear at the following locations: -15° , -10° , -5° , 0° , $+5^\circ$, $+10^\circ$ and $+15^\circ$ (see Figure 2a). The participants were instructed to make a saccade toward the target as soon as the fixation cross disappeared, the saccade target remaining on the screen for 800 ms afterwards. A blank screen followed for 1,000 ms, and then a new trial began.

Each session consisted of one step block followed by one overlap block. In the step block, the fixation cross disappeared and the saccade target appeared simultaneously. In the overlap block, the saccade target appeared 600 ms before the fixation cross disappeared.

In total, each block included 40 trials for each of the ten experimental conditions (5 starting positions $\times 2$ saccade directions) which were randomly displayed inside each block. Each block of 40 trials was preceded by ten training supplementary trials, one per condition.

Data analysis

Saccade amplitude, duration, and peak velocity of both eyes were computed offline. Saccade latency was

defined as the time interval between the fixation cross disappearance and the saccade onset. We also calculated the saccade skewness, by dividing the time between the saccade onset and peak velocity (i.e., the acceleration period) by the total saccade duration. Thereby, a skewness of 0.5 indicates that the acceleration and deceleration phases have the same duration; a skewness inferior or superior to 0.5 indicates that the acceleration phase is shorter or longer than the deceleration phase, respectively. We discarded trials with saccade latency shorter than 80 ms (3.21%) or longer than 800 ms (0.08%), and outliers in latency (4.25%), amplitude (0.65%), duration (1.64%) and peak velocity (0.08%). Overall, 9.91% of the trials were discarded. For each block, the outliers were values that lied below ($Q1 - 2.3 \times IQR$) or above ($Q3 + 2.3 \times IQR$), $Q1$ and $Q3$ being the first and third quartiles respectively and IQR the interquartile range (Tukey box plot, Carling, 2000). This method deals with outliers with higher precision and resistance and is less affected by the sample size than the other more common methods (for example, those discarding trials with saccade performance below and above $2.5 SD$; see Carling, 2000).¹ Furthermore, this method is more and more used by researchers from different fields (e.g., Alahyane et al., 2016; Kulesz, Tian, Juranek, Fletcher, & Francis, 2015; Lemoine-Lardennois et al., 2016; Letham & Raij, 2011; Pernet et al., 2015; Tachibana, Namba, & Noguchi, 2014).

The Shapiro-Wilk test showed that all the measured variables were distributed normally (all $p > 0.05$) except the saccade latency ($p < 0.05$). However, the reciprocal of reaction time, called promptness, is known to follow a Gaussian distribution and is therefore more suitable for statistical analysis (Antoniades, Xu, Mason, Carpenter, & Barker, 2010; Camors et al., 2016). Saccadic reaction times have therefore been apprehended through the saccadic promptness (in s^{-1}) which corresponds to the inverse of the latencies. This way of normalization has the advantage of being easy to proceed and to understand as it is negatively related to the saccade latency (Camors et al., 2016). It is therefore easy to get the saccade latency from the saccade promptness and vice versa. All ANOVAs were run on Statistica 12 (Statsoft, Tulsa, USA) and posthoc analyses were done using Tukey's HSD. For each dependent variable, we tested the NTA and CCA.

NTAs were then analyzed by running a repeated-measures ANOVA with the following factors: paradigm (step/overlap), recorded eye (left/right), saccade direction (leftward/rightward), and starting position (-10° , -5° , 0° , $+5^\circ$, $+10^\circ$). This analysis allowed us to apprehend the NTA by comparing data from the abducting (temporal) and adducting (nasal) eyes for each of the ten possible saccades presented in Figure 2a (e.g., saccade s4 for the left/adducting eye and the right/

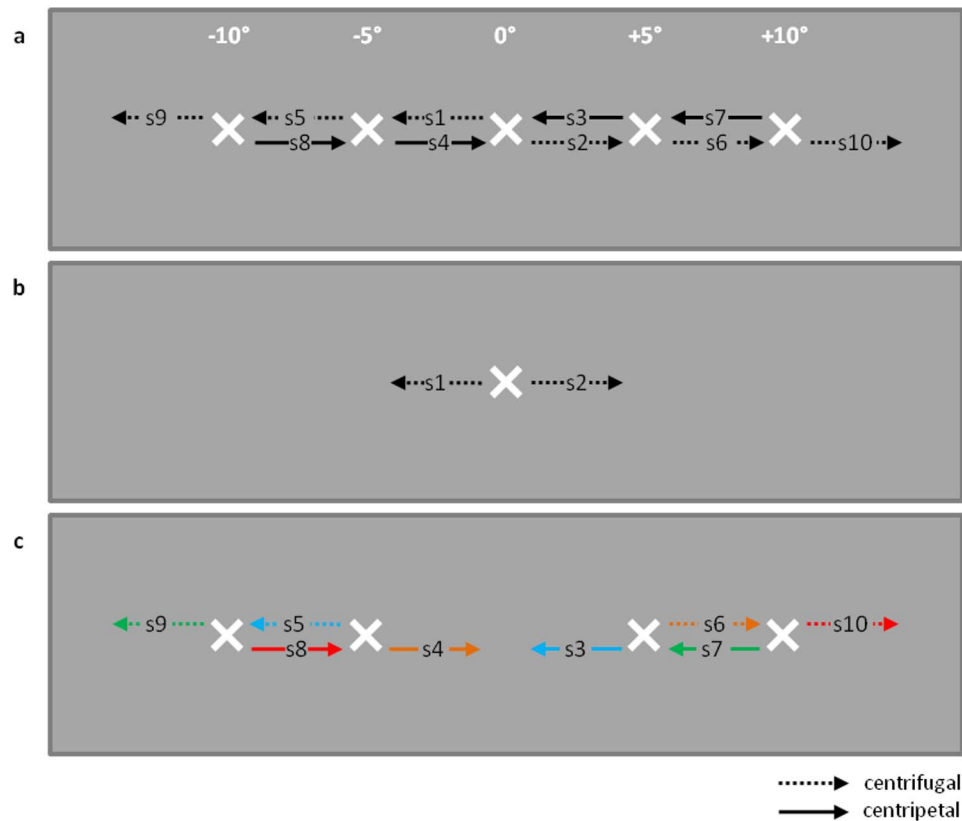


Figure 2. Illustration of the comparisons made to analyze the different asymmetries. Leftward and rightward 5° saccades were initiated from five locations on the horizontal axis. In panels (a) to (c), we present some illustrations of the comparisons made to analyze the different asymmetries. Dotted arrows represent centrifugal saccades. Full line arrows represent centripetal saccades. Even numbers represent rightward saccades whereas odd numbers represent leftward saccades. (a) Naso-temporal asymmetries were measured by comparing data from the left eye (abducting/temporal for leftward saccades, adducting/nasal for rightward saccades) and the right eye (adducting/nasal for leftward saccades, abducting/temporal for rightward saccades) for each of the ten possible saccades. (b) Naso-temporal asymmetries were also analyzed through the comparison of leftward and rightward saccades initiated from the center of the screen, separately for each eye. (c) Centripetal-centrifugal asymmetries were assessed by comparing centripetal saccades to centrifugal saccades executed from eccentric positions (-10° , -5° , $+5^\circ$, $+10^\circ$). Colors represent saccades compared with each other. More precisely, we opposed saccades s3 to s5, s7 to s9, s4 to s6, and s8 to s10, so as to have, in each comparison, only nasal or only temporal saccades, with centripetal and centrifugal saccades initiated from the same eccentricity with respect to the center of the screen. In this way, the naso-temporal asymmetry could not interfere in our measure of the centripetal-centrifugal asymmetry, and vice versa.

abducting eye). This was also done to have a look to complete data (the subsequent analyses were restricted to some of the conditions). The NTAs were also examined by restricting this analysis to the comparison of leftward and rightward saccades initiated from the center of the screen (see Figure 2b). This analysis was done for two reasons: (a) to compare our data with previous studies investigating the NTAs which mostly involved saccades from the center of the screen, and (b) to start from the only position from which leftward and rightward saccades are both centrifugal. Indeed, if we had compared leftward and rightward saccades of one of the eyes from eccentric positions, for instance from -5° (saccades s4 and s5 on Figure 2), we would have compared a temporal and a nasal saccade, but also a centripetal and a centrifugal saccade.

CCAs were analyzed by running a repeated-measures ANOVA with the following factors: paradigm (step/overlap), recorded eye (left/right), target hemifield (temporal/nasal), saccade direction relative to the straight-ahead direction (centrifugal/centripetal), and center proximity (starting position at 5° or 10° away from the central position). As illustrated in Figure 2c, CCAs were thus assessed by comparing centripetal saccades to centrifugal saccades for each eye initiated from a given center proximity. In details, we opposed saccades s3 to s5, s7 to s9, s4 to s6, and s8 to s10 of Figure 2c. Note that this analysis excluded saccades starting from the center of the screen as centripetal saccades cannot be initiated from this location. This analysis allowed us (a) for each eye, to compare centripetal and centrifugal saccades initiated from the

same center proximity (at 5° or 10°) and toward the same hemifield (temporal or nasal), and also (b) to study the relationship between the CCA and the NTA by examining directly the interaction between the direction relative to the straight-ahead direction (centrifugal/centripetal) and the target hemifield (temporal/nasal).

In the Results section, we present results with $M \pm SD$.

Results

Latency, amplitude, and duration as weak indicators of asymmetries in saccades

Because saccadic latencies were not distributed normally, we examined the initiation time of saccades through the promptness of the saccades (in s^{-1}), which corresponds to the inverse of the saccade latencies (Camors et al., 2016). Overall, we found a significant main effect of the paradigm, $F(1, 27) = 4.83$, $p < 0.05$, with promptness of $5.17 \pm 0.77 s^{-1}$ (i.e., latency of 198 ± 30 ms) in the step block and of $4.83 \pm 0.76 s^{-1}$ (i.e., latency of 213 ± 37 ms) in the overlap block. The step and overlap blocks therefore did involve respectively reactive and voluntary saccades. The analyses relative to the NTA, either by comparing temporal and nasal saccades made by the abducting and the adducting eyes (Figure 2a) or by focusing on leftward and rightward saccades initiated from the center of the screen for each eye (Figure 2b), both indicated a significant interaction between the recorded eye (left/right) and the saccade direction (leftward/rightward) respectively, $F(1, 27) = 6.71$, $p < 0.02$ and $F(1, 27) = 8.75$, $p < 0.01$, suggesting higher promptness (hence shorter latencies) for temporal than for nasal saccades. However, because all the observed effects corresponded to latency differences smaller than 2 ms, and thus under the refresh rate of the eye tracker, we concluded to an absence of any NTA on saccade promptness in our data. Similarly, when focusing on saccades initiated from eccentric locations (Figure 2c), centripetal saccades did not differ from centrifugal saccades, $F(1, 27) = 3.33$, $p > 0.05$, and this factor was not involved in any interaction (all $ps > 0.10$). Therefore, our data do not show either CCA on saccade promptness.

For saccade amplitudes, we found no effect of paradigm (step or overlap blocks) and no effect of saccade direction (leftward or rightward saccades), both $F < 1$. The examination of the NTA was done either by comparing temporal and nasal saccades made by the abducting and the adducting eyes (Figure 2a) or by focusing on leftward and rightward saccades initiated from the center of the screen for each eye

(Figure 2b). Both analyses indicated a significant interaction between the recorded eye and saccade direction, respectively $F(1, 27) = 29.1$, $p < 0.0001$ and $F(1, 27) = 12.8$, $p < 0.002$, suggesting larger amplitudes for temporal than for nasal saccades. However, the magnitude of the observed differences was too small (0.1° to 0.2°) to conclude to the existence of a NTA on this variable. Concerning the CCA, the analysis of saccades initiated from eccentric locations (Figure 2c) revealed a significant interaction between the direction relative to the straight-ahead direction (centripetal/centrifugal) and the target hemifield (temporal/nasal), $F(1, 27) = 8.13$, $p < 0.01$, with larger amplitude for centrifugal nasal saccades than for centripetal nasal saccades ($4.68 \pm 0.38^\circ$ vs. $4.55 \pm 0.32^\circ$, $p < 0.001$) but no difference on temporal saccades ($4.80 \pm 0.39^\circ$ vs. $4.79 \pm 0.33^\circ$, $p > 0.98$). Again, even if the reported differences reached the significance threshold and seem to suggest a first modulation of the CCA by the NTA, they have to be interpreted with caution because of their weak magnitude.

Finally, the analyses on saccade duration did not show any NTA. Indeed, no interaction was found between the recorded eye and saccade direction when we compared saccades made by the abducting and the adducting eyes or when we focused on saccades initiated from the center of the screen for each eye (both $F < 1$). However, the analysis on data from the abducting and adducting eyes (Figure 2a) showed a main effect of saccade starting position, $F(4, 108) = 6.32$, $p < 0.0002$, and a significant interaction between this latter factor and saccade direction, $F(4, 108) = 25.1$, $p < 0.0001$. Posthoc comparisons suggest that leftward saccades starting from positions -10° (39.8 ± 4.7 ms) and -5° (40.5 ± 4.3 ms) were longer than rightward saccades starting from the same positions (37.5 ± 3.4 ms and 37.8 ± 3.1 ms, respectively; both $ps < 0.0002$). Note that in this situation, leftward saccades were centrifugal whereas rightward saccades were centripetal. This pattern was reversed for saccades initiated from $+5^\circ$, with rightward saccades (40.0 ± 3.4 ms, centrifugal) longer than leftward saccades (39.0 ± 4.3 ms, centripetal; $p < 0.015$). However, when executed from position $+10^\circ$, leftward saccades were longer (39.4 ± 4.3 ms) than rightward saccades (38.2 ± 3.4 ms; $p < 0.003$), even if the former were centripetal. This interaction could thereby be the reflection of a CCA on saccade duration, but again, the small differences were very close to the temporal resolution of the eye tracker. This CCA has also been found during the analysis of saccades from eccentric locations (Figure 2c) with an effect of the direction of the saccade relative to the straight-ahead direction, $F(1, 27) = 27.1$, $p < 0.0001$. Actually, centrifugal saccades had longer duration (39.7 ± 4 ms) than centripetal saccades (38.5 ± 4 ms). This factor interacted with target hemifield, $F(1, 27) =$

23.7, $p < 0.0001$, showing that the difference between centrifugal and centripetal saccades was actually significant on nasal saccades (40.1 ± 4.2 ms vs. 38.1 ± 3.8 ms; $p < 0.0002$) but not on temporal saccades (39.2 ± 4 ms vs. 38.8 ± 4 ms; $p > 0.15$). Again, the small size of the reported effects recommends interpreting them with caution.

To conclude, the analyses performed on saccade duration did not reveal any clear NTA but showed a small CCA for nasal saccades. Remember that the CCA found on saccade duration by Collewyn et al. (1988) and Pelisson and Prablanc (1988) was actually due to a longer deceleration phase of centrifugal than centripetal saccades. To investigate whether the CCA found in our data was also due to an asymmetry on saccade velocity patterns, we ran an ANOVA on saccade skewness. This analysis did not reveal any difference in the shape of the velocity profiles between centripetal and centrifugal saccades. This suggests that the small differences in saccade duration we observed here were not due to differences in duration of the acceleration and deceleration phases.

Peak velocity as a great indicator of asymmetries in saccades

Overall, our analysis done on the complete set of data (Figure 2a) revealed a main effect of the paradigm, $F(1, 27) = 11.6$, $p < 0.003$, with higher peak velocities in the step block ($229 \pm 35^\circ/\text{s}$) than in the overlap block ($219 \pm 36^\circ/\text{s}$), as well as a main effect of the saccade starting position, $F(4, 108) = 5.02$, $p < 0.001$, but no effect of the recorded eye nor of saccade direction (both $F < 1$). We however found a significant interaction between saccade direction and the recorded eye, $F(1, 27) = 31.23$, $p < 0.0001$, which revealed higher peak velocity for leftward saccades from the left eye ($233 \pm 39^\circ/\text{s}$) than for leftward saccades from the right eye ($216 \pm 30^\circ/\text{s}$) and higher peak velocity for rightward saccades from the right eye ($233 \pm 39^\circ/\text{s}$) than for rightward saccades from the left eye ($215 \pm 31^\circ/\text{s}$, both $ps < 0.005$). In other words, this interaction showed higher peak velocity for saccades from the abducting eye than for saccades from the adducting eye. Importantly, the triple interaction with paradigm (step/overlap) was not significant ($p > 0.05$), suggesting that the velocity advantage for temporal saccades was observed similarly for both reactive and voluntary saccades. The triple interaction between saccade direction (leftward/rightward), recorded eye (left eye/right eye), and saccade starting position (-10° , -5° , 0° , $+5^\circ$, $+10^\circ$) was significant, $F(4, 108) = 3.66$, $p < 0.01$. This interaction is illustrated in Figure 3 and clearly shows that leftward saccades from the left eye and rightward saccades from the right eye (i.e., the temporal

saccades) have higher peak velocity than rightward saccades from the left eye and leftward saccades from the right eye (i.e., the nasal saccades), and this for all the starting positions. This interaction thus confirms that saccade peak velocity shows robust NTA. Note that this asymmetry found between abducting and adducting eyes is reinforced by the analysis restricted to saccades from the center of the screen (Figure 2b), which also exhibits a strongly significant interaction between saccade direction and recorded eye, $F(1, 27) = 26.9$, $p < 0.0001$. Posthoc comparisons showed higher peak velocity for leftward saccades from the left eye ($230 \pm 40^\circ/\text{s}$) than for rightward saccades from the left eye ($215 \pm 31^\circ/\text{s}$) and higher peak velocity for rightward saccades from the right eye ($232 \pm 38^\circ/\text{s}$) than for leftward saccades from the right eye ($216 \pm 31^\circ$), both $ps < 0.01$). In other words, this interaction showed that temporal saccades had consistently higher peak velocity than nasal saccades.

The analysis of the triple interaction between saccade direction (leftward/rightward), recorded eye (left eye/right eye), and saccade starting position, -10° , -5° , 0° , $+5^\circ$, $+10^\circ$ (see above) is particularly interesting as it reveals a modulation of the CCA by the NTA. Indeed, as illustrated in Figure 3, there is a strong CCA on temporal saccades (i.e., leftward saccades from the left eye and rightward saccades from the right eye) with higher peak velocity for centripetal (squares in Figure 3) than centrifugal (triangles in Figure 3) saccades. The CCA observed for temporal saccades seemed stronger when saccades started from a location 10° than 5° away from the center of the screen. The significance threshold was nevertheless reached for both starting locations (all $ps < 0.05$). A very different pattern was found for nasal saccades (i.e., rightward saccades from the left eye and leftward saccades from the right eye). When nasal saccades were initiated at 5° away from the center of the screen, peak velocity never differed between centrifugal and centripetal saccades, neither for the left eye ($p > 0.11$) or for the right eye ($p > 0.99$). Nonetheless, the centripetal nasal saccades initiated at 10° away from the center of the screen have significantly higher peak velocity than centrifugal nasal saccades, for both eyes (all $ps < 0.01$). This latter effect is however much weaker than for temporal saccades.

These results regarding the CCA are corroborated by the analysis restricted to saccades starting from eccentric locations (Figure 2c), which revealed a main effect of saccade direction relative to the straight-ahead direction, $F(1, 27) = 27.6$, $p < 0.0001$, with higher peak velocity for centripetal ($229 \pm 39^\circ/\text{s}$) than centrifugal ($220 \pm 33^\circ/\text{s}$) saccades. This factor interacted with target hemifield (temporal/nasal), $F(1, 27) = 42.8$, $p < 0.0001$, showing that the difference in peak velocity between centripetal and centrifugal saccades is significant for the temporal ($241 \pm 41^\circ/\text{s}$ vs. $225 \pm 35^\circ/\text{s}$; $p <$

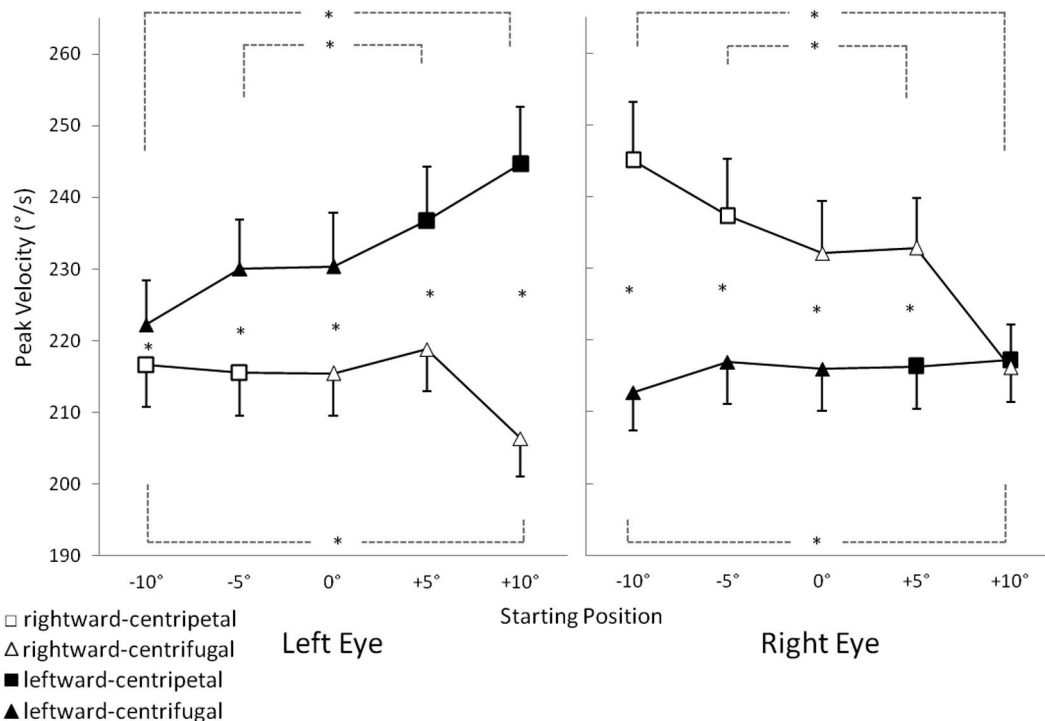


Figure 3. Saccadic peak velocity as a function of starting position, saccadic direction, and recorded eye. Left and right panels refer to data from the left and from the right eye, respectively. Black and white symbols refer to leftward and rightward saccades and squares and triangles refer to centripetal and centrifugal saccades, respectively. Error bars represent standard errors of the mean and asterisks indicate significant differences at $p < 0.05$.

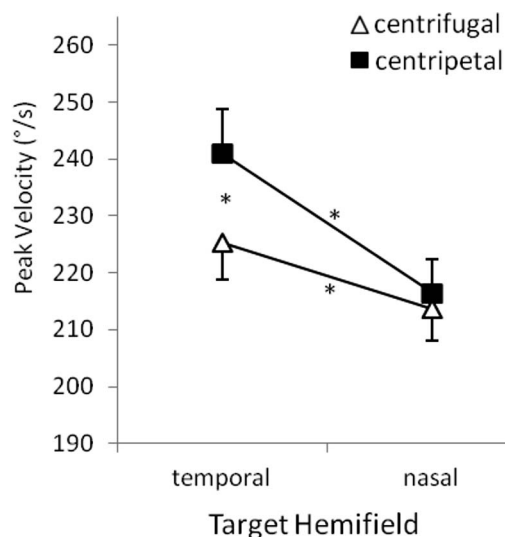


Figure 4. Saccadic peak velocity as a function of target hemifield and direction relative to the straight-ahead direction. For each target hemifield (temporal or nasal), centripetal saccades are indicated by black squares and centrifugal saccades by white triangles. Error bars represent standard errors of the mean, and asterisks indicate significant differences at $p < 0.05$.

0.0002) but not for the nasal saccades ($216 \pm 31^\circ/\text{s}$ vs. $214 \pm 30^\circ/\text{s}$; $p > 0.20$). This interaction, illustrated in Figure 4, confirmed that temporal saccades always have higher peak velocity than nasal saccades, but that the CCA exists only for temporal saccades and not for nasal saccades.

To sum up, our results on saccadic peak velocity indicate a strong NTA with higher peak velocity for temporal than for nasal saccades. We found a CCA with higher peak velocity for centripetal than for centrifugal saccades, but only when saccades were temporal. The CCA seems strongly attenuated when the saccade was made by the adducting eye (i.e., for nasal saccades). Note that the effects observed here were present independently of the saccade type (reactive/voluntary) as they were similar for the step block and for the overlap block.

Importantly, the effects described here at the population level are also observed on individual data. Figure 5 shows the averaged individual differences between peak velocity of centripetal and centrifugal saccades initiated from eccentric positions for each of the 28 participants, for temporal and nasal saccades separately. In order to test each centripetal-centrifugal difference at the individual level, we calculated Cohen's d for nasal and temporal saccades separately. Cohen's d tests were more informative than Student t tests because each comparison involved a very large number

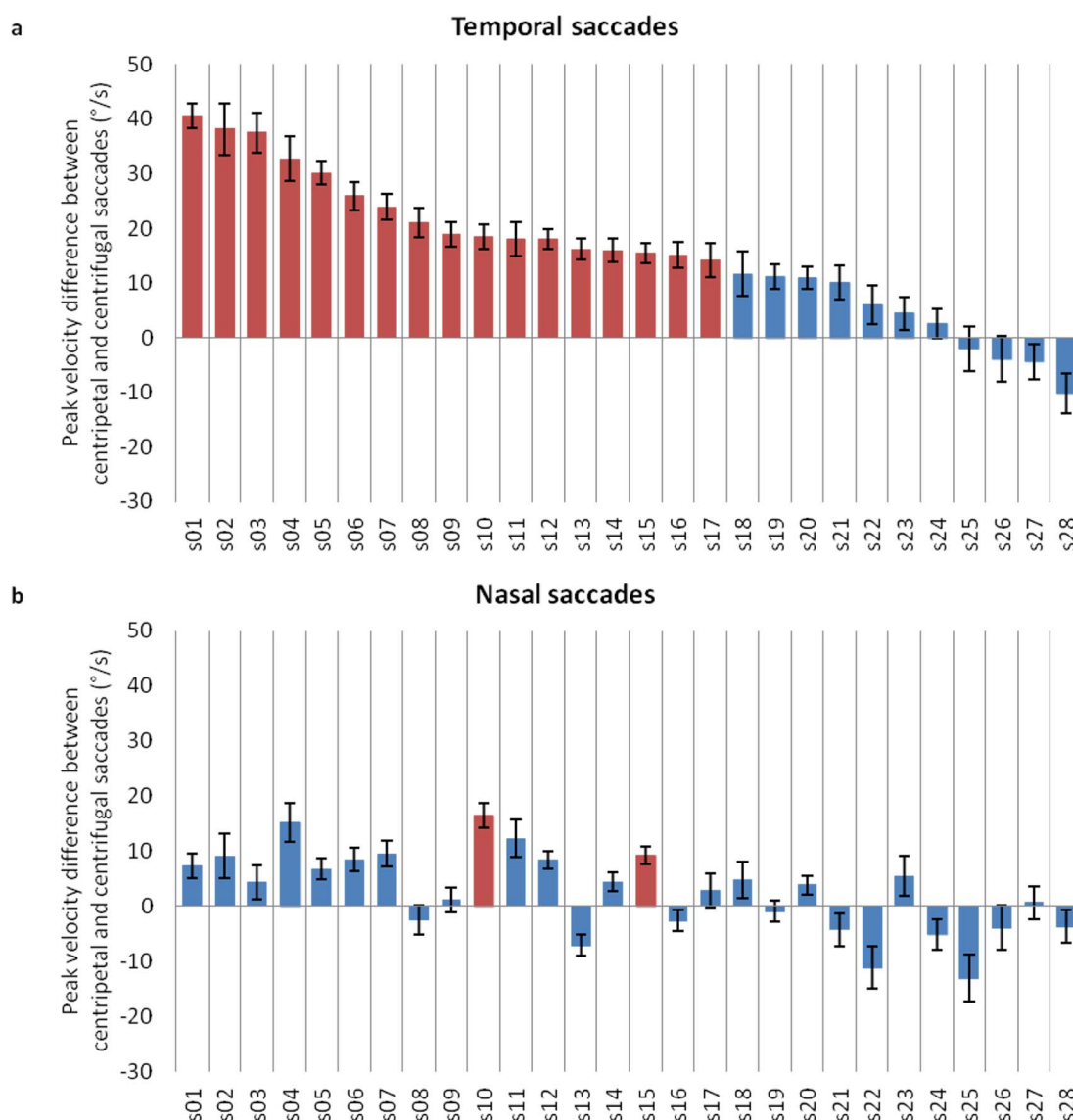


Figure 5. Individual results on peak velocity for the 28 participants. Each bar corresponds to one of the 28 participants and represents the saccadic peak velocity difference between centripetal and centrifugal saccades, separately for temporal (panel a) and nasal (panel b) saccades. Positive differences indicate higher peak velocity for centripetal than for centrifugal saccades whereas negative differences indicate the reverse. Red and blue bars represent differences with Cohen's $d \geq 0.5$ and < 0.5 , respectively.

of saccades (from 236 to 598) and thus the great majority of the comparisons led to significant differences. We considered as reliable the effects associated with a Cohen's $d \geq 0.5$ (indicated in red in Figure 5). This threshold has been chosen (a) because we used small saccades with amplitudes around 5° and the asymmetries of the saccadic system are known to be weakened on small saccades (Becker, 1989; Chen, Hung, Quinet, & Kosek, 2013; Collewyn et al., 1988; Pelisson & Prablanc, 1988), (b) because an effect of $d = 0.5$ means that the effect magnitude is at least of $1/2$ standard deviation which can be considered as reliable (Cohen, 1992). This analysis shows that on nasal saccades only 2/28 participants exhibit a reliable recentering bias on peak velocity. Conversely, on

temporal saccades 17/28 participants have a reliable velocity advantage for centripetal saccades. Importantly, a χ^2 test run on these proportions of participants was highly significant ($X^2 = 8.96$, $df = 1$, $p < 0.003$), showing that the CCA is present on temporal saccades but not on nasal saccades.

Discussion

The current study involved leftward and rightward saccades initiated from five different locations along the horizontal axis to induce centripetal and centrifugal saccades. Moreover, binocular recordings of eye

movements allowed us to compare saccades from the abducting and adducting eyes, and to compare temporal and nasal saccades initiated from the center of the screen. This procedure was used to systematically investigate the presence of CCA and NTA on saccadic parameters. CCA and NTA are two known asymmetries, usually studied separately in the literature. In other words, previous papers focused either on the CCA or on the NTA. Here, we tested them together. More precisely, our study was aimed at examining which of the two asymmetries takes over the other in case of a contentious situation (i.e., when a saccade is both centripetal and nasal or both centrifugal and temporal). Moreover, we investigated whether NTA and CCA differ between reactive and voluntary saccades by using step and overlap paradigms.

At first sight our results could suggest the presence of NTAs on saccade promptness and amplitude. However, the magnitudes of the effects that we found are too small (2 ms and 0.2° , both under the resolutions of our eye tracker) to conclude to NTAs. This is consistent with studies reporting no NTA on saccade latency (Bompas et al., 2008; Honda, 2002; Rafal et al., 1991) and amplitude (Kristjánsson et al., 2004; Walker et al., 2000). The few studies reporting NTAs on saccadic latency (Walker et al., 2000) or amplitude (Collewijn et al., 1988) also found very small differences close to the resolution limits of the measurements. Similarly, we observed very weak CCAs on saccade amplitude and duration, with centripetal saccades exhibiting higher amplitude and shorter duration than centrifugal saccades. Again, the effects were very small (0.13° and 2 ms) but nonetheless comparable to the ones found in the literature, including studies using the same eye tracker (Camors et al., 2016).

The saccadic parameter on which both the literature and our results exhibit clear and strong asymmetries is peak velocity. Saccadic peak velocity is higher for temporal than for nasal saccades (Collewijn et al., 1988; Cook et al., 1966; Fricker, 1971; Hyde, 1959; Jóhannesson & Kristjánsson, 2013; Robinson, 1964), and higher for centripetal than for centrifugal saccades (Abel et al., 1979; Camors et al., 2016; Collewijn et al., 1988; Frost & Pöppel, 1976; Inchingolo et al., 1987; Jürgens et al., 1981; Pelisson & Prablanc, 1988). Importantly, the magnitude of about $20^\circ/\text{s}$ we found for both the NTA and the CCA is well above the resolution of our eye tracker (about $4^\circ/\text{s}$). Moreover, we observed these asymmetries on peak velocities for both reactive and voluntary saccades, elicited respectively by step and overlap paradigms in separate blocks. This finding confirms that our experimental procedure leads to robust NTA and CCA on peak velocity, whether the saccade is reactive or voluntary. This is consistent with the study of Kristjánsson et al. (2004) reporting NTA on peak velocities both for reactive prosaccades and

voluntary antisaccades. The NTA and CCA therefore seem very robust on saccadic peak velocity whereas they are sometimes found and sometimes not on saccade latency and amplitude (Bompas et al., 2008; Collewijn et al., 1988; Honda, 2002; Kristjánsson et al., 2004; Rafal et al., 1991; Walker et al., 2000). This could be explained by the fact that saccade velocity is less sensitive to top-down influences (attention, decision-making...) than the other saccadic parameters (Galley, 1989; see also Di Stasi, Catena, Canas, Macknik, & Martinez-Conde, 2013; Leigh & Zee, 2006). Indeed, the NTA and CCA may be present on saccade latency and amplitude, but the top-down influences on these parameters may counteract with their observation.

Our results on saccadic peak velocity show that the CCA can be modulated according to the temporal or nasal characteristic of the saccade. Indeed, while we found a quite robust NTA whatever the saccade starting position or the recorded eye (see Figures 3 and 4), the CCA was much weaker for nasal than for temporal saccades (see Figure 4). Therefore, our results show that the velocity advantage of centripetal saccades is only present for temporal (abducting) saccades and not for nasal (adducting) saccades. Note, however, that individual data presented on Figure 5a show that 39% of the participants (11/28) do not show a reliable CCA on temporal saccades. This can be related to the small saccade amplitude tested here (5°). Indeed, the advantage for centripetal saccades has been found higher for large than for small saccades (Becker, 1989; Chen et al., 2013; Collewijn et al., 1988; Pelisson & Prablanc, 1988). It is thus possible that larger saccades would have led to larger asymmetries between centripetal and centrifugal saccades. Moreover, we know that there is some variability in the asymmetries of the saccadic system (e.g., Boghen et al., 1974; Camors et al., 2016; Collewijn et al., 1988). For instance, the proportion of participants who do not show a CCA on peak velocities is similar in the Camors et al.'s (2016) study involving 8° centripetal and centrifugal saccades (40% of the participants, 8/20). This individual variability on saccadic peak velocities is still to be explained, and further research should be carried out to investigate its origins. Nonetheless, our individual data still show that the majority of the participants exhibit no CCA on peak velocities of nasal saccades while they show a reliable velocity advantage for centripetal compared to centrifugal saccades when the target is presented in the temporal hemifield. Thus, when present, the CCA is only found on temporal saccades.

Our results suggest that the recentering bias (i.e., the CCA) exists only for saccades of the abducting eye, which is the eye closest to the straight-ahead direction before the saccade. This finding is of great importance as research is currently being carried on to understand

the nature and the role of the straight-ahead preference (Camors et al., 2016; Durand et al., 2010; Przybyszewski, Kagan, & Snodderly, 2014; Strappini et al., 2015). Indeed, the straight-ahead direction represents a default gaze location in which the eye-centered and head-centered reference frames are aligned (Durand et al., 2010; Kardamakis & Moschovakis, 2009; Tatler, 2007). The advantage for centripetal saccades has therefore been explained by a return of the gaze to the default coordinate of the eye-centered and head-centered spaces (Krebs et al., 2012, 2010). Another interpretation proposes that the advantage for centripetal saccades is behaviorally driven, to quickly keep one's attention on the stimuli presented straight-ahead, which are potential obstacles for locomotion (Camors et al., 2016; Durand et al., 2010). Indeed, these studies suggest that stimuli presented straight-ahead benefit from a privileged visual processing in V1 compared to stimuli presented at other locations. Note that in the study of Durand et al. (2010), the authors recorded the activity of neurons of V1 in monkeys while they were exposed either to central or eccentric stimuli. The monkeys therefore did not have to make saccades toward the visual stimuli. In a more recent behavioral study, Camors et al. (2016) asked human participants to perform saccades toward (prosaccade task) or away from (antisaccade task) a stimulus either presented straight-ahead or in the periphery. The stimuli presented centrally triggered saccades with shorter latencies than stimuli presented elsewhere (whichever the centripetal or centrifugal nature of the saccade) and centripetal saccades had higher peak velocities and shorter durations than centrifugal saccades (whichever the central or peripheral position of the stimulus triggering the saccade). As their analyses relied on averaged data from the left and right eyes, the CCA could not be investigated separately for the nasal and temporal hemiretinas. Overall, they concluded to a behavioral advantage for stimuli presented straight-ahead on saccade initiation and for centripetal saccades on saccade execution. Our present results suggest that this velocity advantage for centripetal saccades is present only for the execution of temporal saccades. This precision of the CCA can be explained physiologically with two possible hypotheses.

Firstly, based on the known physiological origins of the NTA and the CCA, we could consider that the NTA originates at the level of the visual pathways (Hubel et al., 1975; Itaya & Van Hoesen, 1983; Sterling, 1973; Tigges & Tigges, 1981; Williams et al., 1995) and the CCA at the level of the extraocular muscles (Koene & Erkelens, 2002; Pelisson & Prablanc, 1988). This would mean that the NTA and the CCA are underpinned by independent physiological asymmetries. According to this assumption, the NTA on saccadic peak velocity could be a result from the

anatomical and functional asymmetries found in the retinotectal and geniculostriate pathways between fibers from the nasal hemiretina and the temporal hemiretina while the CCA could be due to lower mechanical constraints for executing centripetal saccades compared to centrifugal ones. The execution of a centripetal temporal saccade would require the lateral rectus contraction and the medial rectus stretching, and vice versa when a centripetal nasal saccade is executed. Similarly, the execution of a centrifugal temporal saccade would require the lateral rectus contraction while a centrifugal saccade the medial rectus contraction. The fact that we found a CCA restricted to temporal saccades could then suggest that when the medial rectus relaxes (and the lateral rectus contracts), saccades are faster than when the lateral rectus relaxes (and the medial rectus contracts). Note that this is consistent with the interpretation of the NTA found on saccadic peak velocity by Jóhannesson & Kristjánsson (2013) who suggest that the stronger signals from the nasal hemiretina than from the temporal hemiretina may lead to faster contraction of the lateral rectus than of the medial rectus.

Secondly, the modulation of the CCA by the NTA could be seen as resulting from the sharing of structures in the physiological origins of these two asymmetries. The NTA has been shown to have a mixed origin, both in the retinotectal (Hubel et al., 1975; Itaya & Van Hoesen, 1983; Sylvester et al., 2007; Tigges & Tigges, 1981) and in the geniculostriate (Bompas et al., 2008; Tychsen & Burkhalter, 1997; Williams et al., 1995) pathways. Indeed, the NTA is present at all the steps of the geniculostriate pathway: from the retina (Curcio & Allen, 1990) to the LGN (Connolly & Van Essen, 1984; Williams et al., 1995) until V1. In V1, ocular dominance columns made from the inputs of the nasal hemiretina are larger and occupy more area compared to the ocular dominance columns made from the inputs of the temporal hemiretina (Tychsen & Burkhalter, 1997). Similarly, the CCA has been linked to cortical processes (Camors et al., 2016; Krebs et al., 2012, 2010). Saccades toward the straight-ahead direction are proposed to be faster because they realign the head-centered and eye-centered reference frames (Krebs et al., 2012, 2010). This results in a negative deflection in parieto-occipital regions contralateral to the future gaze location shorter in duration and weaker prior to centripetal than centrifugal saccades (Krebs et al., 2012, 2010). Moreover, the study of Rieger, Schoenfeld, Heinze, and Bodis-Wollner (2008) shows that the earliest cortical structure coding saccades in a head/body centered egocentric reference frame is V1. Therefore, in agreement with previous studies (Durand et al., 2010; Krebs et al., 2012, 2010; Rieger et al., 2008), we suggest that the recentering bias could be linked to V1. In this case, stimuli presented straight-

ahead induce an enhanced neural activity in V1 (Durand et al., 2010; Przybyszewski et al., 2014; Strappini et al., 2015). Thereby, we speculate that the potential common structure to the proposed origins of both NTA and CCA could be V1 and that the CCA restricted to temporal saccades could be physiologically driven by asymmetries in V1. More precisely, the advantage of centripetal saccades could be present only when saccades are driven by stimuli presented in the temporal hemifield, and thus projected on the nasal hemiretina. So, in V1, the CCA might then be present only for columns receiving inputs from the nasal hemiretina but not for columns receiving inputs from the temporal hemiretina.

One question, however, remains: how asymmetries in V1 can lead to asymmetries on saccadic peak velocities? At the neurophysiological level, saccadic peak velocity corresponds to the peak burst firing frequency of the excitatory burst neurons (EBN) of the PPRF (see Corneil & Munoz, 2014; Galley, 1989; Leigh & Zee, 2006; Sparks, 2002). To trigger a saccade toward a visual target, these premotor neurons receive signals from the intermediate and deeper layers of the SC (SCi) in which an oculocentrically coded motor map codes the amplitude and direction of the saccade in polar coordinates. Importantly, the SCi receive signals from the parietal and frontal eye fields (PEF and FEF, respectively), two cortical structures involved in the generation of reactive and voluntary saccades (Corneil & Munoz, 2014; Leigh & Zee, 2006; Sparks, 2002; White & Munoz, 2011). The FEF also receives signals from the PEF, which directly receives the visual information from V1. Overall, the generation of reactive saccades is controlled by the V1-PEF-SCi pathway, and the generation of voluntary saccades by the V1-PEF-FEF-SCi pathway. The SCi then send the motor command to the brainstem saccadic generator. We propose that the asymmetries found in the geniculostriate pathway, from the retina to V1, might also be present in the projections from V1 to the PEF, FEF, and SCi, and therefore reflected on the peak velocity of the upcoming saccade. Note that Jóhannesson and Kristjánsson (2013) have already proposed that the NTA could be present in the projections from the FEF to the SC. Moreover, Bompas et al. (2008) suggested that NTA found in the geniculostriate pathway could also be present after V1, in the cortical pathway involved in the saccade target selection. However, as the authors pointed out in their discussion, there is no evidence that information from the left and the right eyes are dissociated in signals reaching the target selection level. This is why the presence of NTA and CCA after V1 still has to be demonstrated.

Further research is needed to test the different physiological interpretations we proposed here to

account for the modulation of CCA by the NTA. Physiological recordings of extraocular muscles activity or/and of V1 activity during centripetal temporal saccades and centripetal nasal saccades could clarify the physiological explanations of the CCA restricted to temporal saccades we revealed here.

Keywords: saccadic eye movements, asymmetries, naso-temporal, centripetal-centrifugal, binocular

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Footnote

¹ Note that we reanalyzed our data by filtering outliers (1) with a more conventional method (discarding trials above and below 2.5 *SD*, for a total of 8.64% of the trials) and (2) without applying any filter of the outliers (discarding only anticipatory trials with latency <80 ms and trials with latency >800 ms, for a total of 3.29% of the trials). The results were similar whichever the filtering method. Overall, these follow-up analyses show that our main results on peak velocity showing that the CCA is found for temporal saccades only is very robust because it is observed whichever the filtering method.

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