Exp Brain Res (2013) 227:101–110
DOI 10.1007/s00221-013-3490-8

RESEARCH ARTICLE

# Violating the main sequence: asymmetries in saccadic peak velocities for saccades into the temporal versus nasal hemifields

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Received: 12 December 2012 / Accepted: 14 March 2013 / Published online: 30 March 2013
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**Abstract** Saccadic peak velocities during monocular and binocular presentation were tested. While the main sequence linear increase in peak velocities as a function of saccade amplitude is well documented, our results provide demonstrations of violations of the main sequence. Peak velocities during monocular presentation were considerably higher toward temporal than nasal stimuli. This nasal–temporal asymmetry (NTA) was not explained by amplitude differences and was most pronounced for the lowest amplitudes tested, decreasing with increased amplitude. Under binocular presentation, this NTA was much smaller. While the exact reasons for this difference in peak velocities between hemifields are unclear at present, we propose that anatomical NTAs result in stronger signals from the nasal, than temporal retina leading to higher peak velocities into the temporal visual hemifield. NTAs in peak velocity are consistent with NTAs in attentional choice and in attentional function, which might also be explained by anatomical NTA.

**Keywords** Eye movements · Saccades · Peak velocity · Main sequence · Naso-temporal asymmetry

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## Introduction

Visual acuity is by far the best at the fovea at the center of the retina and declines rather abruptly outside it and faster in the temporal than the nasal hemiretina (Fahle and Schmid 1988). This corresponds well with retinal physiology (Curcio and Allen 1990) and has generated interest in nasal–temporal asymmetries (NTAs) for attentional function and saccadic performance. Such experiments typically involve blocking the view of one eye so that the nasal visual field projects only to the temporal hemiretina of the open eye and the temporal visual field projects to its' nasal hemiretina. There is indeed considerable evidence in the literature for NTAs in attentional function (Dodds et al. 2002; Rafal et al. 1991; Walker et al. 2000). The benefits of valid cues are greater when they appear in the temporal hemifield than in the nasal hemifield and the cost of invalid cues is greater when they appear in the temporal than nasal hemifield (Rafal et al. 1991). In free saccadic choice tasks, observers prefer to make saccades to the temporal than nasal hemifield (Bompas et al. 2008; Posner and Cohen 1980) and some authors have found evidence for NTAs in saccade latency (Kristjansson et al. 2004; Walker et al. 2000) while others have not (Bompas et al. 2008; Honda 2002; Jóhannesson et al. 2012). Tomalski et al. (2009) reported that observers respond faster to upright face-like stimuli presented in the temporal than nasal hemifield, an effect not observed for inverted face-like stimuli, showing how such asymmetry can translate into higher level perceptual effects. Evidence for attentional and saccadic NTAs has sometimes been connected with greater density in retinotectal projection from the nasal than temporal hemiretina (Rafal et al. 1989, 1991) although whether such asymmetries are indeed larger for retinotectal than retinostriate connections has been questioned (Williams et al. 1995).

In a recent study, Jóhannesson et al. (2012) comprehensively tested for nasal–temporal asymmetries in saccadic latency and landing point accuracy. In other studies containing data speaking to this question, the question of NTAs in latency was a secondary aim, while Jóhannesson et al. reported seven experiments with the sole aim of investigating NTAs. Little evidence of any NTAs was found for latency, while there were non-significant trends toward more hypometry for saccades to nasal than temporal targets (nasal targets projecting to the temporal hemiretina). This absence of any NTA in latency was consistent with some results (Bompas et al. 2008; Honda 2002) but inconsistent with others (Kristjansson et al. 2004; Walker et al. 2000). The absence of latency NTAs was especially surprising in light of findings of strong attentional and choice NTAs (Posner and Cohen 1980; Rafal et al. 1991; see also Bompas et al. 2008), and the well-known relationship between attention and saccades (Deubel and Schneider 1996; Hoffman and Subramaniam 1995; Kowler et al. 1995; Kristjansson et al. 2001; Kustov and Robinson 1996; see e.g. Kristjánsson 2007, 2011 for review). In light of what is known about anatomical NTAs, this result was also surprising (see general discussion). Jóhannesson et al. speculated that this could reflect that saccadic choice may be disconnected from saccade execution.

While Jóhannesson et al. (2012) did not find evidence of NTAs in latency and landing point accuracy, here we present the results of further analyses of their data. More specifically, we report, for the first time, unequivocal evidence of nasal–temporal asymmetries in saccadic peak velocities under monocular viewing. Peak velocities denote the highest velocity that the eye reaches during a saccade and can be found with numerical differentiation of amplitude with respect to time in the duration of the saccade. Peak velocities vary with amplitude and have, for example, been measured to be 307°/s for amplitudes of 10° and 395°/s for saccades of 15° amplitude in a representative study (Beydagi et al. 1999). Neurophysiological findings provide some plausible reasons why such asymmetries might exist (see general discussion).

A common assumption in the literature is that there is a linear relationship (*the main sequence*) between saccadic amplitude and peak velocity up to 20° amplitude where PVs reach asymptote at about 500°/s (Bahill et al. 1975; Collewijn et al. 1988; Leigh and Zee 2006). A distinct possibility is therefore that if higher PVs toward targets in the temporal than nasal hemifield are found, this might simply reflect less hypometric saccades into the temporal than the nasal hemifield (Jóhannesson et al. 2012). This question will be addressed in detail in the following analyses. For binocular saccades, Collewijn et al. (1988) found that the peak velocity of the abducting eye (saccades toward the temporal hemifield) was higher than of the adducting eye (see also Vergilino-Perez et al. 2012). Whether this holds for monocular saccades is, however, unclear. Since under monocular viewing, anatomical differences between the nasal and temporal hemiretina are more likely to have an effect, larger effects upon peak velocity might therefore be expected.

Here, we present analyses of the velocity data from the monocular saccades measured in Jóhannesson et al. (2012), focusing on peak velocity (PV) while taking into account any modulatory effects of amplitude and latency. To preview the results, we found a clear pattern of asymmetries in PVs between the hemifields, such that the PVs were higher when saccades were made to temporal than nasal stimuli (see Fig. 1). This pattern held even when amplitude and latency were controlled for. In an additional experiment, run especially for this project, we tested NTAs in peak velocity during binocular viewing, to better characterize the asymmetry.

## Saccadic peak velocities during monocular presentation

### Brief overview of experimental methods in Jóhannesson et al. (2012)

To examine peak velocities under monocular presentation, we used the data collected in experiments 3–7 in Jóhannesson et al. (2012).[1] We therefore only provide an overview of the experimental procedures and refer to Jóhannesson et al. (2012) for further details. Experiments 3 through 7 involved only centrifugal saccades. Each trial started with central fixation and observers then made a saccade to the left or right. All experiments involved horizontal saccades made from central fixation toward suddenly appearing peripheral stimuli. The required saccadic amplitude in experiment 3 (10 observers) was 8°, in experiment 6 (5 observers), it was 20°, and in experiment 7, (12 observers, 3 excluded because of high error rates) three different amplitudes (5°, 10° and 20°) were interleaved within blocks. In experiment 4 (14 observers, 5 excluded because of high error rates), the amplitude was 8° and peripheral valid (we only used data from the valid cue condition) or invalid cues appeared (to test the involvement of exogenous attention; see e.g. Kristjánsson 2009; Kristjansson and Nakayama 2003; Posner and Cohen 1980). In experiment 5 (amplitude 8°; 14 observers, 5 excluded because of high error rates), a concurrent discrimination task was presented.[2] Note that the optic disk is located 15.5° ± 1.1° nasal to the fovea (Rohrschneider 2004),

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[1] In experiments 1 and 2 in Jóhannesson et al. (2012), a very different task involving interleaved centripetal, centrifugal, abducting, and adducting saccades was used, so data from those experiments are not included here.

[2] Exogenous attention and discrimination tasks will not be further discussed here since they are irrelevant to the current topic.

so none of the chosen target locations were in the observers' blind-spot.

In all experiments, the movement of one eye at a time was recorded while the other eye's view was blocked with an eye patch. In experiment 7, only the movement of the dominant eye (determined by the pointing method introduced by Greenberg 1960) of each participant was recorded while in experiments 3 through 6, the movement of both eyes of each observer was recorded (on separate instances). When both eyes were recorded, the data from each eye were compared (left vs. right; dominant vs. non-dominant; interaction of those two factors), but no differences in performance were found (all $p$'s > .1), so the data were combined. Saccades with latencies shorter than 80 ms are most likely anticipatory (Becker 1991; Rolfs and Vitu 2007) and were therefore excluded from all analyses. Furthermore, trials with latencies, peak velocities and/or amplitude that deviated more than 3 SD from their mean were removed from each observer's data before analysis. The 55 participants (32 females, aged from 19 to 55, $M = 28.6$ years) were all students at the University of Iceland and received course credit for participating. Of the 55, 43 had a right dominant eye. Thirteen were excluded because their total error rate exceeded our criteria. A high-speed monocular eyetracker (250 Hz) from Cambridge Research Systems was used in all experiments. The eyetracker is based on infrared reflection technology and uses the pupil and dual first Purkinje reflection to record gaze. The spatial accuracy of the eyetracker is 0.125° to 0.25° and its' horizontal range is ±40° (Cambridge Research Systems 2006). The only illumination in the soundproof booth, where the experiments were run, came from the experimenter's LCD monitor and the CRT monitor used to display the stimuli. The observer's head was stabilized with a head- and chinrest with a viewing distance of 53 cm in all experiments. The observers were told they could rest between blocks as needed.

## Data preparation

In the following analyses, data from different experiments with the same amplitude requirement were combined (experiment 7, amplitude = 5°; experiments 3, 4, and 5, amplitude = 8°; experiment 7, amplitude = 10°; experiments 6 and 7, amplitude = 20°). No inter-experiment differences in latency, peak velocity, or amplitude were found for experiments with the same amplitude requirement, justifying the combination of the data for the purposes of the current analyses. Table 1 shows an overview of combined peak velocities from the 5 experiments. The differences in peak velocity between saccades toward nasal versus temporal stimuli were significant for the 5°, 8°, and 10° conditions (all $F$'s > 8 and all $p$'s < .02) but not for the 20° condition ($F(1,14) = 2.45$; $p = .14$), and numerically, the difference was smallest for this highest amplitude (see Table 1). The difference is always in the direction that PVs are higher toward temporal than nasal stimuli. For 5° eccentricity, the average amplitude for saccades toward temporal stimuli was 5.3°, and toward nasal stimuli, it was 4.1°, for 8° eccentricity, it was 7.5° and 7.0°, for 10° eccentricity, it was 9.7° and 8.3°, and for 20° eccentricity, it was 17.8° and 17.0° for saccades toward temporal and nasal targets, respectively. NTAs in latency and landing point accuracy never reached significance (see Jóhannesson et al. 2012).

## Analyses of peak velocities and amplitude in Jóhannesson et al. (2012)

As an introduction to the peak velocity results, we present a scatterplot (Fig. 1) with symbols for each individual observer from experiments 3 through 7 in Jóhannesson et al. (2012), as a function of difference scores for peak velocity (temporal − nasal) on the ordinate and amplitude (temporal − nasal) on the abscissa. Different symbols denote different amplitudes tested in experiments 3 through 7.

Temporal peak velocities minus nasal peak velocities are plotted on the ordinate so that if the score for each individual is above the 0 line, peak velocities of saccades toward temporal stimuli were higher than toward nasal stimuli for this observer. The horizontal dotted line shows the mean difference score for peak velocity. The abscissa denotes the difference in amplitude (temporal amplitude − nasal amplitude). If the score for an individual is to the right of 0, the amplitude was higher toward temporal than nasal stimuli, and the vertical dotted line denotes the mean difference score for amplitude.

There are several notable features to the scatterplot in Fig. 1a. Firstly, a large majority of the observers show higher saccadic peak velocities toward temporal stimuli (which project to the nasal hemiretina) than to nasal stimuli (the average difference score denoted by the dashed horizontal line). Secondly, the graph shows a similar difference score for amplitude (abscissa) indicating that the saccades toward nasal hemifield targets are more hypometric than those toward temporal stimuli. Most importantly, however, this graph clearly suggests that the faster peak velocities are *not* explained by differences in amplitude. The *main sequence* relationship between saccadic amplitude and velocity does, in other words, not explain the pattern. If the difference in peak velocities was completely explained by larger hypometry for saccades toward nasal stimuli, we should not expect to see the large majority of the points in the upper part of the graph. For saccades where amplitude is higher into the temporal hemifield, they should be above the 0 line for peak velocity differences, but when nasal amplitude is higher, they should be below the 0 line. But this is not the case. The majority of points is above the no difference line for PV.

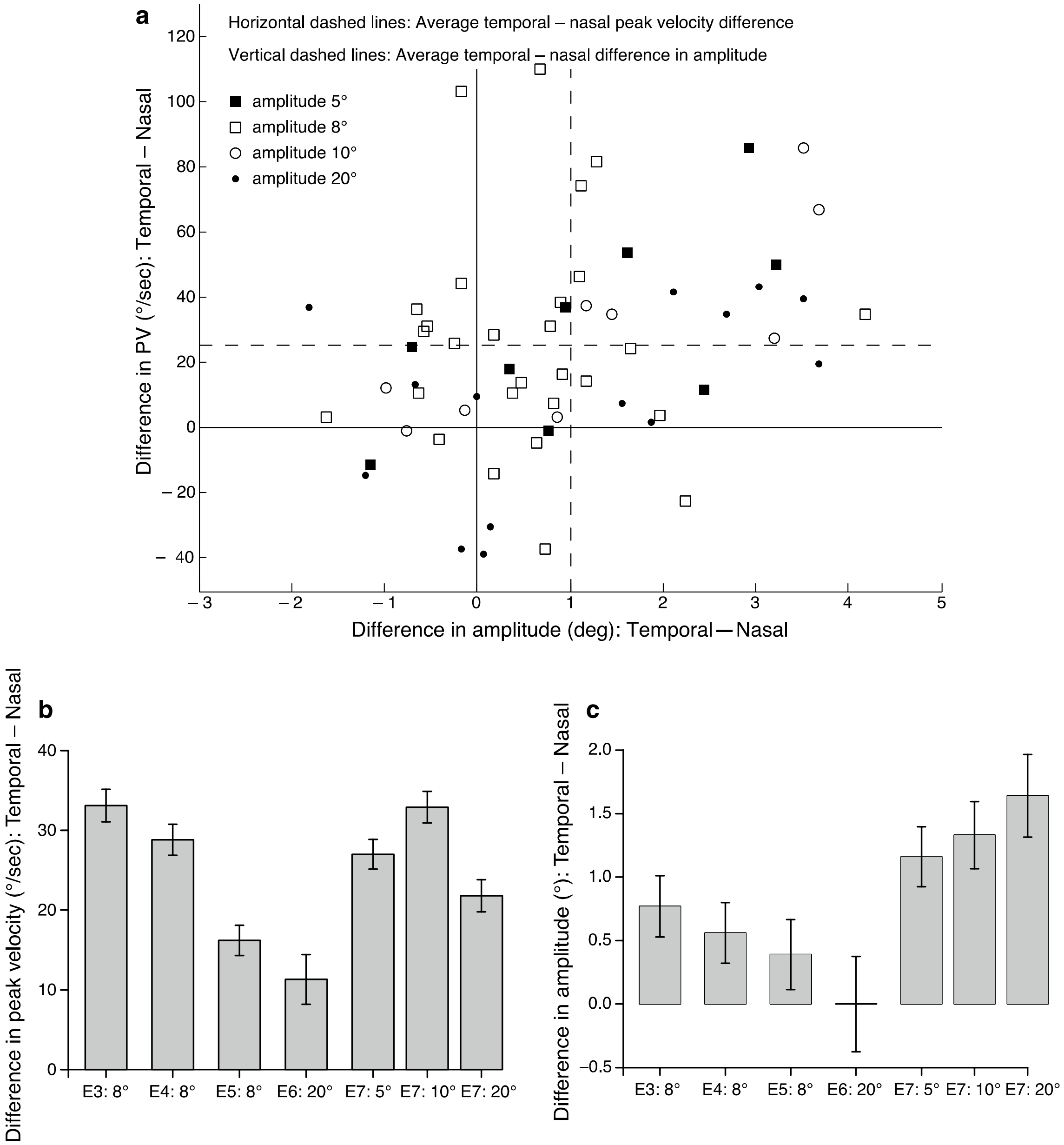

**Fig. 1** Differences in average peak velocity and amplitude toward temporal versus nasal stimuli shown individually for 42 observers (13 of 55 were excluded because of high error rates). **a** The difference in peak velocity ($PV_{temporal} - PV_{nasal}$) is plotted on the ordinate as a function of amplitude difference ($amplitude_{temporal} - amplitude_{nasal}$) on the abscissa. The *vertical* and *horizontal solid lines* denote no difference between temporal and nasal hemifields. The *dashed vertical line* denotes the actual average difference between temporal and nasal amplitude, and the *horizontal dashed line* denotes the actual average difference in peak velocity between the temporal and nasal hemifields. *Different symbols* denote different saccade amplitudes as required in the different experimental instructions. **b** Naso-temporal asymmetry in peak velocity showing how peak velocities of saccades toward stimuli in the temporal hemifield are higher than toward nasal stimuli for the different experiments. **c** Naso-temporal asymmetry in amplitude showing how amplitude is higher for saccades toward stimuli in the temporal than in the nasal hemifield. The *error bars* denote the standard error of the difference score

Note also that the graph implies that the larger the amplitude the higher the peak velocity, but our point is simply that this is far from being the whole story. If the pattern truly followed the main sequence, when the saccades to the temporal hemifield have higher amplitude, the peak velocities should be higher for saccades to the temporal hemifield (upper right quadrant relative to 0 lines) while if they have higher amplitude to the nasal hemifield, the peak velocities should also be higher for the nasal hemifield (lower left quadrant). But importantly, for the large majority of observers, the peak velocities toward the temporal hemifield are higher irrespective of amplitude. In what follows, we further analyze

**Table 1** Overview of the peak velocities from Jóhannesson et al. (2012) for the four different amplitudes. In the table, "Temporal" and "Nasal" refer to locations of target stimuli

| | Temporal | | Nasal | | Diff | *df* | *F* value | *p* value |
|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | | | | |
| PV (5° amp) | 299.5 | 65.6 | 269.0 | 58.4 | 30.5 | 1.8 | 8.18 | .021 |
| PV (8° amp) | 364.2 | 74.3 | 341.1 | 67.1 | 23.1 | 1.27 | 13.53 | .001 |
| PV (10° amp) | 412.2 | 72.6 | 379.9 | 68.6 | 32.3 | 1.8 | 10.47 | .012 |
| PV (20° amp) | 502.6 | 89.5 | 485.5 | 105.7 | 17.1 | 1.14 | 2.45 | .140 |

these relationships incorporating peak velocity, latency, and amplitude as a function of hemifield.

Figure 1, panel b, shows, for completeness, the differences in peak velocity between saccades made to stimuli in the temporal hemifield versus toward stimuli in the nasal hemifield for the 5 experiments (3 different amplitudes for experiment 7). If the difference score lands above the horizontal solid line, which denotes no difference, the peak velocities of saccades toward temporal hemifield stimuli are higher, while if it lands below it, the peak velocities were lower. Figure 1c shows similar results for amplitude.

### Regression analyses of peak velocities, latencies, and amplitude

We used the *lmer* function (Bates 2010) in R to fit regression models with both fixed and random effects (mixed-effects model) to the results. The dependent variable was peak velocity, while the independent variables were saccadic amplitude, latency, and hemifield. The aim was to investigate the relationship between those variables and peak velocity. In all experiments, there was some variation between observers and between hemifields both in the intercept and the slope of amplitude. Because of this, the random effect was considered to be the effect of observer, of amplitude and observer, and of hemifield and observer (Baayen et al. 2008; Dixon 2008). To find the model that best fits the data, we compared multiple mixed-effects regression models: (1) a base model where amplitude was the only independent variable with the random effect of observer on the intercept, (2) a model with amplitude and hemifield as independent variables and (3) a model with amplitude, hemifield, and latency as independent variables. The model with the lowest AIC (Akaike information criterion; Akaike 1974) is considered to be the best fit to the data of the models being compared (Akaike 1974; Burnham and Anderson 2004). We used the *anova* function in R to test if there was a significant difference between the chosen model and the rejected models. We only report the statistics for the base model and the chosen model. For all amplitudes, a model with amplitude and hemifield main effects was chosen as the best one from the results of the AIC tests (indicating that latency did not have a modulatory effect on the peak velocities).

The statistics for the base model and the chosen model for the different experiments are shown in Table 2. The *t*-values for intercepts and slopes of amplitude are high, suggesting that the intercepts and the slopes of amplitude are always significant both in the base model and the chosen model. In the chosen model, the slope of hemifield and the slope of the interaction between amplitude and hemifield are always significant (except for hemifield and the interaction for 20°, $t < 1.6$). The difference in AIC values is of great interest. On average, the AIC is 314 points lower for the chosen than for the base model, and the difference is in all cases highly significant (all

**Table 2** Comparison of the base models and chosen models from the regression analyses (based on the difference in AIC scores, the rightmost column). The parameters of the chosen model are all highly significant except the slope of hemifield and the interaction of hemifield and amplitude in the 20° amplitude condition. The large AIC difference between base and chosen models is noteworthy (see main text for further detail)

| Amp (°) | Base model | | | | | | Chosen model | | | | | | AIC difference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Intercept | | Slope of Amplitude | | Intercept | | Slope of Amplitude | | Slope of Hemifield[a] | | Slope of Amp × hemif[a] | | |
| | °/s | *t* value | °/s | *t* value | °/s | *t* value | °/s | *t* value | °/s | *t* value | °/s | *t* value | |
| 5 | 203.2 | 12.47 | 17.2 | 21.13 | 187.2 | 11.37 | 19.8 | 12.11 | 47.8 | 3.64 | −7.7 | 3.46 | 218 |
| 8 | 247.1 | 23.29 | 14.2 | 20.29 | 204.2 | 15.67 | 19.1 | 17.37 | 70.0 | 5.25 | −7.4 | 4.91 | 507 |
| 10 | 240.6 | 13.61 | 17.3 | 26.65 | 214.0 | 10.88 | 20.0 | 15.11 | 75.7 | 3.86 | −7.3 | 3.57 | 87 |
| 20 | 292.1 | 17.06 | 11.2 | 18.66 | 302.3 | 13.65 | 10.7 | 11.09 | −40.9 | 1.56 | 2.0 | 1.45 | 130 |

[a] In the regression, the nasal visual hemifield was coded as 0 and the temporal visual hemifield as 1

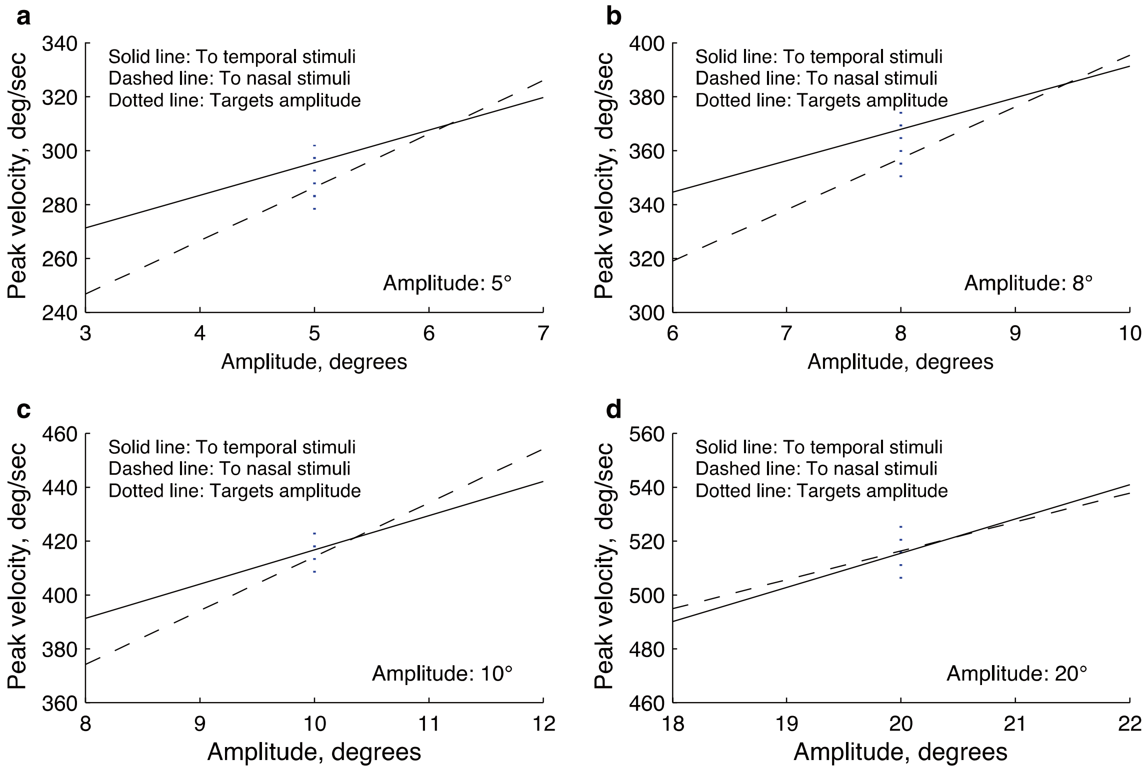

**Fig. 2** The predicted peak velocity and amplitude relationship from the chosen regression models for the different amplitudes. The predicted peak velocities are clearly higher for saccades toward temporal than nasal stimuli in the 5° and 8° amplitude conditions (the *top row*). The difference is smaller in the 10° amplitude condition (*bottom left*) and in the 20° condition (*bottom right*) the difference is almost nil. The slope of saccades toward nasal stimuli is higher than of saccades toward temporal stimuli (except for the 20° condition)

$p$'s < .001). From this, we can conclude that the higher amplitude of saccades toward stimuli in the temporal than the nasal hemifields does not explain the NTA in peak velocity. In other words, when hemifield is added to the regression models, the variation in peak velocity is much better accounted for (and significantly so), demonstrating its' strong effects.

In Fig. 2, [3] we plot the chosen models' predicted relationship[4] between peak velocity and 4 different amplitudes (5°, 8°, 10°, 20°). The figure shows that for all amplitudes except 20° (panel d), the peak velocity of saccades toward temporal stimuli is higher (panels a, b, and c). Because the slopes of the saccades toward nasal stimuli are steeper than of saccades toward temporal stimuli, the figure also suggests that the peak velocity increases faster for saccades toward nasal than temporal stimuli at the lower amplitudes. For the 20° amplitude, there is no difference between the hemifields, but the slope of amplitude is highly significant as expected (*the main sequence*) but neither the slope of hemifield nor the slope of the interaction was significant. Again, Fig. 2 suggests that the difference in peak velocity between saccades toward temporal and nasal stimuli decreases with increased amplitude and, accordingly, the difference in slopes (temporal − nasal) decreases from −7.7 to 2°/s for the amplitudes of 5° and 20°, respectively.

In sum, our results indicate that a model which includes the effect of hemifield fits the data better and predicts peak velocities better than a model without hemifield effects. Furthermore, latency seems not play any role in determining peak velocities. Finally, the results suggest that NTAs in PV become smaller as amplitude increases, since for the 20° amplitude, models with hemifield as an independent variable and the base model were not significantly different (although the difference was numerically in the direction of a similar NTA as for the other amplitudes).

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[3] Caution is needed for predictions of PV values at the outermost points in the graphs since they represent relatively few data points, especially for the higher amplitudes (toward the right of the graphs).

[4] The regression equation for the chosen model is: $y$ = intercept + amplitudeSlope × amplitude + hemifieldSlope × hemifield + interactionSlope × amplitude × hemifield. To take an example a calculation for 5° amplitude and a saccade into the temporal hemifield yields: $187.2 + 19.8 \times 5 + 47.8 \times 1 + (-7.7 \times 5 \times 1) = 295.5°/\text{s}$.

### Saccadic peak velocities during binocular presentation

In an additional experiment run especially for this project, we measured saccadic peak velocities toward the nasal and temporal visual hemifields during binocular presentation to test whether NTAs in peak velocities are idiosyncratic to monocular presentation, or in other words situations where the input is purely nasal or temporal.

#### Method

##### *Participants*

Twenty students (aged 20–53 years, $M = 26.6$ years, SD = 7.4 years; 15 women) from the University of Iceland voluntarily participated and received course credit for participation.

##### *Stimuli and procedure*

We used the same stimuli as in experiment 3 in Jóhannesson et al. (2012), the procedure was similar, and we recorded the movements of the dominant eye and the only difference was that neither of the observer's eyes was blocked. Each observer participated in 2 blocks of 36 trials, 72 in total.

#### Results

Trials with latencies shorter than 80 ms and trials where latency, amplitude, or peak velocity deviated more than 3 SD from their mean were excluded, so 53–72 trials for each observer were analyzed. Figure 3, panel a, shows the results. The average difference between the PV of saccades toward nasal and temporal stimuli is small and so is the difference in amplitude between them. The average peak velocity toward temporal stimuli was 343.6°/s (SD = 67.8°/s), and toward nasal stimuli, it was 334.7°/s (SD = 119.8°/s). The difference 8.9°/s was not significant ($F(1, 19) = 0.79$, $p = .385$). The average landing point deviation from the target's position was 0.46° (SD = 0.9°) for temporal hemifield stimuli, and for nasal hemifield stimuli, the average deviation was 1.1° (SD = 1.1°). Again, the difference, 0.6°, was not significant ($F(1, 19) = 0.79$, $p = .385$). The average latency of saccades toward temporal stimuli was 178 ms (SD = 41.3 ms), and the latency of saccades toward nasal stimuli was 173 ms (SD = 40.7 ms). This 5 ms difference was not significant ($F(1, 19) = 2.69$, $p = .118$).

As in the analyses of the monocular data, we used the *lmer* (Bates 2010) function in R to find the best-fitting model. The intercept of the base model was 206.2 ($t = 11.09$) and the slope of amplitude was 18.1 ($t = 8.53$). The intercept of the chosen model was 232.3 ($t = 10.57$), the slope of amplitude was 14.10 ($t = 5.16$), the slope of hemifield was—44.77 ($t = 2.07$), and the slope of the interaction between amplitude and hemifield was 6.71 ($t = 2.26$). The slope of the interaction is only marginally significant, but all other parameters are significant. In this model, the same pattern holds as in the model for the 20° monocular data; the slope of hemifield is negative and the interaction slope is positive, but the peak velocity is higher for saccades toward the temporal than nasal hemifield. As in the monocular data, the model with amplitude and hemifield as independent variables better predicts peak velocity than a model without hemifield and latency. The AIC for the chosen model was 4 points lower than for the base model, and the difference was significant ($X^2(2) = 7.5$, $p = .023$). The predicted effects of

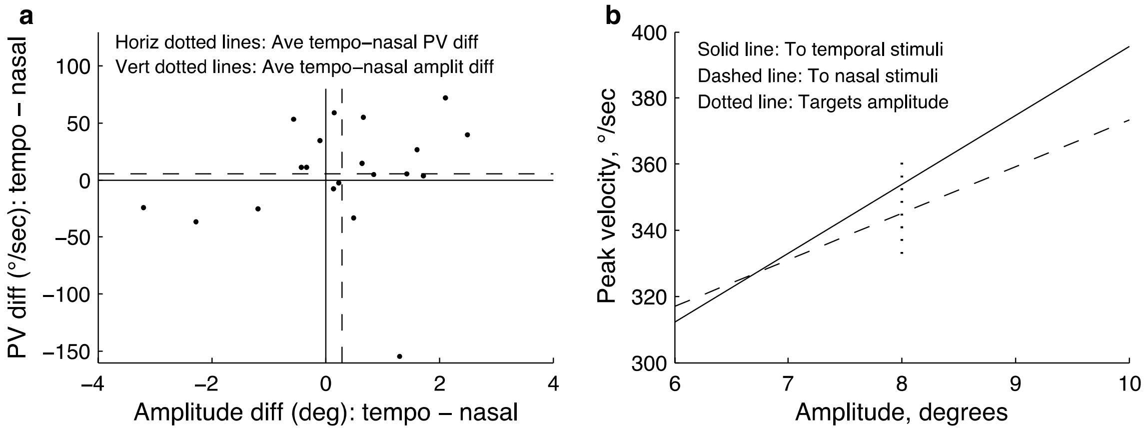

**Fig. 3** The results of the experiment with binocular presentation. In **a,** there are more data points above the line of no difference in peak velocity, but there are equal number of data points to the *left* and *right* of the line of no difference in amplitude. In **b,** at the target's position, the predicted peak velocity of saccades toward stimuli in the temporal hemifield is higher (and the slope also) than of saccades toward stimuli in the nasal hemifield

the chosen model are depicted in Fig. 3, panel b. Note that even if the same analyses as for the monocular data reveal an effect of hemifield, the difference between hemifield PVs is 6.3 % for monocular presentation, while for binocular presentation, it is 2.6 % for the 8° amplitude.

What we can conclude from the foregoing analyses is that the peak velocity NTA is strongly diminished (but not completely absent; see also Vergilino-Perez et al. 2012) during binocular presentation suggesting that naso-temporal differences in anatomy are likely to explain the strong NTA in peak velocity seen during monocular presentation.

## General discussion

The current results provide clear evidence of differences in saccade peak velocity between hemifields under monocular presentation. Importantly, the asymmetries are not accounted for by differences in saccade amplitude between hemifields, although the saccades to nasal hemifield stimuli were, overall, more hypometric than the ones toward temporal hemifield stimuli. The main sequence relation between peak velocity and amplitude (Bahill et al. 1975) does, in other words, not explain the asymmetry.

The results accord well with findings on preferences in saccadic choice tasks (Bompas et al. 2008; Posner and Cohen 1980). When observers are freely allowed to choose targets to saccade to in the temporal or nasal hemifields under monocular presentation, they strongly prefer the temporal target. There are also differences in attentional performance between the hemifields with larger attentional effects for temporal hemifield stimuli. When a target location is cued in the temporal hemifield, the cue-benefit is greater than when cue and target appear in the nasal hemifield. When the cue is presented in one hemifield and the target in the other, the cost of the invalid cue is greater in the temporal, than the nasal hemifield (Rafal et al. 1991). One complication, though, is that one would also expect NTAs for latency, which have proved hard to find consistently (see Bompas et al. 2008; Honda 2002; Jóhannesson et al. 2012; Kristjánsson et al. 2004; Walker et al. 2000).

### Notes on related findings

In our binocular experiment, the amplitude was 8° and the NTA in PV was quite small (8.9°/s), favoring the temporal hemifield, but in the 8° condition under monocular viewing, the difference was much larger (23.1°/s) also favoring the temporal hemifield. This shows that NTAs in PV are much larger for monocular, than binocular, viewing. Vergilino-Perez et al. (2012) reported results broadly consistent with ours. They found that the PVs of 10° saccades into the temporal hemifield with no temporal gap between fixation and target were 358°/s, and for the nasal hemifield, they were 329°/s. In our results, the PVs of 8° saccades into the temporal hemifield were ≈344°/s, and the PVs of 8° saccades into the nasal hemifield were 335°/s. Boghen et al. (1974) concluded that the range of PVs is between ≈190°/s and ≈400°/s for 10° saccades and the above-mentioned PVs lie in between those values. Robinson (1964) found, for monocular viewing, that the velocities of saccades toward temporal stimuli were higher than of saccades into the nasal hemifield and the saccades into the nasal hemifield had on average longer durations than saccades in the opposite direction. Unfortunately, Robinson did not clarify whether peak velocities or mean velocities were measured. Fricker (1971) measured the movement of one eye with the other eye's view blocked finding that 10° saccades into the temporal hemifield had about 50°/s higher PVs than corresponding saccades in the opposite direction and no difference between left and right eye was found. Overall, the results from Robinson (1964) and Fricker (1971) are in good accordance with our results. Boghen et al. (1974) found that monocular saccades to the nasal hemifield (nasal saccades) had higher PVs for amplitudes of 30° than saccades into the temporal hemifield but found no significant difference at other amplitudes (5°, 10° and 20°). Our results are partly consistent with this as the difference between saccades toward temporal and nasal targets seems to decrease with increased amplitude and the difference is smallest at 20°. Their results are, however, somewhat hard to interpret, since their main characteristic was a large interobserver variability. Finally, Furuya et al. (1986) found that a majority (≈60 %) of saccades toward the nasal hemifield had higher PVs than saccades in the opposite direction, which is on the surface inconsistent with our results. Note, however, that each subject only made 16 saccades in total with both eyes which means that there were only 4 saccades of each eye in each direction. In addition, the amplitude of the saccades in Furuyas's et al. experiment was 20°, and for this amplitude, the NTAs in PV in our results were the smallest. Most importantly, Furuya et al. (1986) did not analyze PVs as a function of amplitude, which is crucial according to our analyses.

### Potential neural mechanisms

It is important to note that the fact that the asymmetry is massively reduced during binocular presentation strongly indicates that the velocity difference is accounted for by input NTAs, not movement NTAs. As discussed above, asymmetries exist in both retinotectal and corticotectal pathways (a ratio of about 1.55–1, Williams et al. 1995; see also, Hubel et al. 1975; Itaya and Van Hoesen 1983; Sterling 1973; Tigges and Tigges 1981). In addition, Curcio and Allen (1990) reported that the density of ganglion cells decreases faster in the temporal retina than in the nasal retina.

An obvious question is whether there is any reason to suspect that anatomical NTAs can result in differential peak velocities. This anatomical asymmetry finds its way to neurons likely to have a strong influence on saccade performance, including velocity. It is known that the superficial layers of the superior colliculi (SCs) project to the frontal eye fields (FEF; Johnston and Everling 2011, but according to White and Munoz 2011 this projections might be through the pulvinar and lateral intraparietal cortex), which further project to the saccadic brainstem generator (SBG). The proposed functional projection between SCs and the intermediate layers of superior colliculi (SCi; Doubell et al. 2003) and the projection from FEF could mediate the nasal/temporal asymmetry leading to higher PVs of saccades to temporal stimuli. Brainstem structures below the level of the SC are involved in generating the neural pulse that influences saccade velocity. There is a tight correlation between the discharge rate of saccadic burst cells in the paramedian pontine reticular formation (PPRF; Cullen and Van Horn 2011) and saccade velocity, and premotor neurons responsible for saccade generation primarily encode velocity signals (Leigh and Zee 2006). There is a correlation between the firing rate of burst neurons (BN) of the brainstem saccade generator and saccade velocity. There is also a correlation between saccade duration and the duration of the burst of the BN (Sparks 2002). This could lead to higher PVs of saccades toward temporal, than nasal, stimuli.

One might still ask why anatomical NTAs are not seen consistently for saccadic latency but are seen for PVs. One possible reason may be that the larger projection from nasal than temporal retina may transfer more signals, but the transfer time is the same. Given, that the NTA in signal strength is the same when it reaches the motor neurons, the stronger signals from the nasal retina might lead to faster contraction of the lateral rectus than of the medial rectus produced from the weaker signals from temporal retina, explaining the NTA in PV, but not predicting a concurrent latency NTA.

A protest regarding our proposal might involve that the retinotectal pathway projects to the superficial (visual) layers of the superior colliculus, not the deeper layers that have saccade-related activity. There is, however, evidence for interconnections between SCs and SCi in the cat (Doubell et al. 2003), and it is not fully known where the border between SCs and SCi is located (White and Munoz 2011). Furthermore, the SCs project to the FEF (Johnston and Everling 2011), which further projects to the SCi (White and Munoz 2011). While this account is quite speculative, we argue that it is not farfetched to propose that anatomical NTAs relate to differences in PVs.

## Conclusions

We conclude that the peak velocities of monocular saccades toward the temporal hemifield are higher than toward the nasal hemifield. There was meager evidence of any NTAs in PVs of binocular saccades on the other hand. We propose that signals from the nasal retina are stronger, than from temporal retina—because of NTAs in anatomy—and that stronger signals lead to higher peak velocities.

## References

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Autom Control 19:716–723

Baayen RH, Davidson DJ, Bates DM (2008) Mixed-effects modeling with crossed random effects for subjects and items. J Mem Lang 59:390–412. doi:10.1016/j.jml.2007.12.005

Bahill A, Clark M, Stark L (1975) The main sequence, a tool for studying human eye movements. Math Biosci 24:191–204

Bates D (2010) lme4: mixed-effects modelling with R. http://lme4.r-forge.r-project.org/book/

Becker W (1991) Saccades. In: Carpenter RHS (ed) Vision and visual dysfunction: vol 8, Eye movements. CRC, Boca Raton, pp 95–137

Beydagi H, Yilmaz A, Süer C (1999) The effect of direction on saccadic eye movement parameters. J Basic Clin Physiol Pharmacol 10:73–77

Boghen D, Troost B, Daroff RB et al (1974) Velocity characteristics of normal human saccades. Investig Ophthalmol Vis Sci 13: 619–623

Bompas A, Sterling T, Rafal RD, Sumner P (2008) Naso-temporal asymmetry for signals invisible to the retinotectal pathway. J Neurophysiol 100(1):412–421

Burnham K, Anderson DR (2004) Multimodel inference understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304

Cambridge Research Systems (2006) Video eyetracker toolbox, user manual. Cambridge Research Systems, Rochester

Collewijn H, Erkelens C, Steinman R (1988) Binocular co-ordination of human horizontal saccadic eye movements. J Physiol 404(1):157–182

Cullen KE, Van Horn MR (2011) Brainstem pathways and premotor control. In: Liversedge L, Gilchrist ID, Everling S (eds) Oxford handbook of eye movements. Oxford University Press, Oxford, pp 151–172

Curcio CA, Allen KA (1990) Topography of ganglion cells in human retina. J Comp Neurol 300(1):5–25

Deubel H, Schneider WX (1996) Saccade target selection and object recognition: evidence for a common attentional mechanism. Vis Res 36(12):1827–1837

Dixon P (2008) Models of accuracy in repeated-measures designs. J Mem Lang 59:447–456

Dodds C, Machado L, Rafal R, Ro T (2002) A temporal/nasal asymmetry for blindsight in a localisation task: evidence for extrageniculate mediation. NeuroReport 13(5):655–658

Doubell TP, Skaliora I, Baron J, King AJ (2003) Functional connectivity between the superficial and deeper layers of the superior colliculus: an anatomical substrate for sensorimotor integration. J Neurosci 23(16):6596–6607

Fahle M, Schmid M (1988) Naso-temporal asymmetry of visual perception and of the visual cortex. Vis Res 28(2):293–300

Fricker SJ (1971) Dynamic measurements of horizontal eye motion I. Acceleration and velocity matrices. Invest Ophthalmol Vis Sci 10:724–732

Furuya N, Yabe T, Chiba Y (1986) Predominance of nasal over temporal saccades in fast eye movement. Auris Nasus Larynx (Tokyo) 13:53–62

Greenberg G (1960) Eye-dominance and head-tilt. Am J Psychol 73(1):149–151

Hoffman JE, Subramaniam B (1995) The role of visual attention in saccadic eye movements. Percep Psychophys 57(6):787–795

Honda H (2002) Idiosyncratic left-right asymmetries of saccadic latencies: examination in a gap paradigm. Vis Res 42:1437–1445

Hubel D, LeVay S, Wiesel T (1975) Mode of termination of retinotectal fibers in macaque monkey: an autoradiographic study. Brain Res 96(1):25–40

Itaya SK, Van Hoesen GW (1983) Retinal projections to the inferior and medial pulvinar nuclei in the old-world monkey. Brain Res 269(2):223–230

Jóhannesson ÓI, Ásgeirsson ÁG, Kristjánsson Á (2012) Saccade performance in the nasal and temporal hemifields. Exp Brain Res 219(1):107–120. doi:10.1007/s00221-012-3071-2

Johnston K, Everling S (2011) Frontal cortex and flexible control of saccades. In: Liversedge L, Gilchrist ID, Everling S (eds) Oxford handbook of eye movements. Oxford University Press, Oxford, pp 279–302

Kowler E, Anderson E, Dosher B, Blaser E (1995) The role of attention in the programming of saccades. Vis Res 35(13):1897–1916

Kristjánsson Á (2007) Saccade landing point selection and the competition account of pro- and antisaccade generation: the involvement of visual attention? A review. Scand J Psychol 48:97–113. doi:10.1111/j.1467-9450.2007.00537.x

Kristjánsson Á (2009) Learning in shifts of transient attention improves recognition of parts of ambiguous figure-ground displays. J Vis 9(4):1–11

Kristjánsson Á (2011) The intriguing interactive relationship between visual attention and saccadic eye movements. In: Liversedge L, Gilchrist ID, Everling S (eds) Oxford handbook of eye movements. Oxford University Press, Oxford, pp 455–470

Kristjansson A, Nakayama K (2003) A primitive memory system for the deployment of transient attention. Percep Psychophys 65:711–724

Kristjansson A, Chen Y, Nakayama K (2001) Less attention is more in the preparation of antisaccades, but not prosaccades. Nat Neurosci 4(10):1037–1042

Kristjansson A, Vandenbroucke M, Driver J (2004) When pros become cons for anti-versus prosaccades: factors with opposite or common effects on different saccade types. Exp Brain Res 155(2):231–244

Kustov AA, Robinson DL (1996) Shared neural control of attentional shifts and eye movements. Nature 384:74–77

Leigh R, Zee D (2006) The neurology of eye movements. Oxford University Press, Oxford

Posner MI, Cohen Y (1980) Attention and control of movements. In: Stelmach GE, Region J (eds) Tutorials in motor behavior. North Holland Publishing, Amsterdam, pp 243–258

Rafal R, Calabresi P, Brennan C, Sciolto T (1989) Saccade preparation inhibits reorienting to recently attended locations. J Exp Psychol Hum Percep Perform 15(4):673–685

Rafal RD, Henik A, Smith J (1991) Extrageniculate contributions to reflex visual orienting in normal humans: a temporal hemifield advantage. J Cogn Neurosci 3(4):322–328

Robinson DA (1964) The mechanics of human saccadic eye movement. J Physiol 174:245–264

Rohrschneider K (2004) Determination of the location of the fovea on the fundus. Invest Ophthalmol Vis Sci 45(9):3257–3258. doi:10.1167/iovs.03-1157

Rolfs M, Vitu F (2007) On the limited role of target onset in the gap task: support for the motor-preparation hypothesis. J Vis 7(10):1–20. doi:10.1167/7.10.7

Sparks DL (2002) The brainstem control of saccadic eye movements. Nature Rev Neurosci 3:952–964

Sterling P (1973) Quantitative mapping with the electron microscope: retinal terminals in the superior colliculus. Brain Res 54:347–354

Tigges J, Tigges M (1981) Distribution of retionfugal and corticofugal axon terminals in the superior colliculus of squirrel monkey. Invest Ophthalmol Vis Sci 20:149–158

Tomalski P, Johnson MH, Csibra G (2009) Temporal-nasal asymmetry of rapid orienting to face-like stimuli. NeuroReport 20(15):1309–1312. doi:10.1097/WNR.0b013e32832f0acd

Vergilino-Perez D, Fayel A, Lemoine C et al (2012) Are there any left-right asymmetries in saccade parameters? Examination of latency, gain, and peak velocity. Invest Ophthalmol Vis Sci 53:3340–3348

Walker R, Mannan S, Maurer D et al (2000) The oculomotor distractor effect in normal and hemianopic vision. Pro R Soc London B Biol Sci 267:431–438

White BJ, Munoz DP (2011) The superior colliculus. In: Liversedge L, Gilchrist ID, Everling S (eds) Oxford handbook of eye movements. Oxford University Press, Oxford, pp 195–214

Williams C, Azzopardi P, Cowey A (1995) Nasal and temporal retinal ganglion cells projecting to the midbrain: implications for “blindsight”. Neurosci 65:577–586