RESEARCH ARTICLE

Saccade performance in the nasal and temporal hemifields

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Abstract There are numerous asymmetries in anatomy between the nasal and temporal hemiretinae, which have been connected to various asymmetries in behavioral performance. These include asymmetries in Vernier acuity, saccade selection, and attentional function, in addition to some evidence for latency differences for saccadic eye movements. There is also evidence for stronger retinotectal neural projection from the nasal than the temporal hemiretina. There is, accordingly, good reason to predict asymmetries in saccadic performance depending on which hemifield the saccade trigger stimuli are presented in, but the evidence on this is mixed. We tested for asymmetries in both saccade latency and landing point accuracy in a variety of different saccade tasks. We found no evidence for any asymmetries in saccade latency and only modest evidence for asymmetries in landing point accuracy. While this lack of asymmetry is surprising in light of previous findings of attentional asymmetries, it may reflect that cortical input to midbrain eye control centers mitigates any retinal and retinotectal asymmetry.

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Introduction

There are several notable anatomical differences between the nasal and temporal hemiretinae in humans, such as differences in cone and ganglion cell density especially at higher eccentricities (Curcio and Allen 1990). Consistent with this, Fahle and Schmid (1988) showed that for the central 10° of the retina, Vernier acuity declines relatively symmetrically, but at higher eccentricities, there is a quite pronounced nasal-temporal asymmetry (NTA) in acuity, and at 20°, it is around 70 % higher for the temporal hemifield. Neurophysiological work on cats (Hubel et al. 1975; Sterling 1973) old world (Itaya and Van Hoesen 1983) and new world monkeys (Tigges and Tigges 1981) has then revealed asymmetries in projections from the hemiretinae to the superior colliculus (SC). Consistent with this, Sylvester et al. (2007) found that the fMRI response to contrast reversing (8 Hz) checkerboards was stronger for temporal than nasal stimuli, and this NTA in the BOLD signal was only present in the superior colliculus, but not the lateral geniculate nucleus nor the visual cortex. The evidence is, however, mixed with regard to whether these anatomical differences are unique to retinotectal projection (Williams et al. 1995).

Such anatomical asymmetries have been connected with various NTAs in visual performance. Some remarkable findings have surfaced. A hemianopic patient examined by Dodds et al. (2002) showed intact performance for forced-choice localization in the temporal hemianopic visual field, while in the nasal hemianopic visual field, the performance

was at chance, a result most straightforwardly explained by stronger retinotectal projections from the temporal hemifield assuming that the retinotectal projections provide enough information to perform the task. Another intriguing result is that hemianopes could use distractor signals in the blind half of their visual field to inhibit saccades toward targets in their intact visual field, but this was only seen for stimuli projecting to the temporal hemifield (Rafal et al. 1990; but see Walker et al. 2000), again indicating stronger influence from the nasal hemiretina on saccadic control.

In another example, Rafal et al. (1991) measured attentional benefits from valid cues and costs from invalid cues (see e.g., Kristjánsson and Sigurdardottir; Posner and Cohen 1984) and found that both effects were stronger in the temporal than the nasal hemifield. Rafal et al. (1989) also reported such NTAs for the inhibition of return effect. This hemifield asymmetry has then been connected to differences in saccadic latencies (Kristjánsson et al. 2004; Walker et al. 2000), but this has proved controversial (cf. Bompas et al. 2008).

Given the demonstrated difference in retinotectal projection and anatomical differences between the two hemiretinae, there is good reason (see e.g., Honda 2002) to predict that there will be an asymmetry in saccade performance in response to temporal versus nasal stimulation. The difference in the strength of collicular projections from the two hemiretinae might lead to a deficit for stimuli presented in the nasal hemifield (projecting to the temporal hemiretina). This possibility becomes even more likely in light of the findings of Rafal et al. (1989, 1991) for attentional orienting, since attentional orienting and saccadic eye movements appear to be tightly linked (Deubel and Schneider 1996; Hoffman and Subramaniam 1995; Kowler et al. 1995; Kristjánsson et al. 2001; see Kristjánsson 2007 for review). If attentional performance is better for stimuli projecting to the nasal hemiretina (which receives visual input from the temporal hemifield), the well-known relationship between attention and saccades could result in better saccade performance in response to stimuli in the temporal hemifield (see Honda 2002 for similar predictions). There are in other words at least two good reasons to predict NTAs in saccade performance in response to unilateral stimuli. But there are other possibilities. For example, the attentional benefit may not lead to NTAs if it does not translate into a quicker saccade generation signal in the SC, or if the NTA only leads to speeded target selection but not speeded execution. Some authors have indeed not found NTAs for saccade latencies (Bompas et al. 2008; Honda 2002). Another possibility is that cortical input to midbrain saccade control centers may dilute any NTA in saccades.

It has, in other words, been unclear whether NTAs in saccadic performance exist. In a task where prosaccades and antisaccades were interleaved, Kristjánsson et al. (2004; experiment 1) found that saccade latency toward temporal stimuli was generally shorter than toward nasal stimuli. Walker et al. (2000) tested saccade latencies for healthy and hemianopic observers in three conditions, with no distractor, a static distractor or a flickering distractor. For the hemianopic observers, saccade latency toward temporal stimuli was shorter than toward nasal stimuli in all conditions, but for the healthy observers, differences were found in both distractor conditions but none in the no distractor condition. Bompas et al. (2008) did not find any NTA in their single target experiment (experiment 5), consistent with the symmetry of saccadic latency Walker et al. (2000) found for healthy observers without attentional distraction.

Another example is that when distractor stimuli are presented simultaneously contralateral to a saccade target, saccadic latency is increased (the remote distractor effect; Walker et al. 1997) and this distracting effect is stronger when the distractor appears in the temporal than in the nasal hemifield. Saccade amplitude is, however, not affected by a contralateral distractor (Walker et al. 2000). Furthermore, when stimuli are presented simultaneously in the temporal and nasal hemifield, observers show a clear preference for saccading to temporal stimuli (Posner and Cohen 1980; see also Bompas et al. 2008). The temporal visual field may thus have preferential access to saccadic decision systems during free-choice saccade tasks.

No study has, however, specifically been performed to answer this question of whether NTAs arise for saccadic performance, nor have potential hemifield-specific speed-accuracy trade-offs been addressed. Our aim was to fill this void by providing a comprehensive test of whether such NTAs in saccadic performance (latency and accuracy) are seen on a number of different tasks, with and without attentional manipulations. Answers to these questions may shed light upon to what degree anatomical differences correspond to performance differences, at least for saccadic eye movements. To preview the results, our results indicate that any NTAs in saccade performance are small. The only sign of NTAs was some evidence that landing point accuracy was higher for temporal than nasal hemifield stimuli.

Overview of experiments

The aim with experiments 1 and 2 was to ask whether any NTAs would surface in saccade performance in a task where the observers followed the fixation point between 3 (experiment 1) or 5 (experiment 2) different locations on the screen. This allowed us to compare saccades of different amplitudes both toward and away from the midline

as well as large amplitude eye movements from one visual field to the other (crossing the midline). In experiments 3 through 5, a more conventional saccade task was used, with, or without, attentional manipulations. In experiment 6, we tested high-amplitude saccadic eye movements while in experiment 7, we contrasted high-, medium-, and low-amplitude saccades within trial blocks. We report the latencies and landing point accuracy of the saccades.

General methods

Seven within-subject design experiments were conducted. In experiments 1 and 2, observers tracked a stimulus jumping unpredictably between locations and the saccades were of different amplitudes (5° and 10°). In experiment 1 and 7, only the movement of the dominant eye (Greenberg 1960) of each participant was recorded while the other eyes' view was blocked with a medicinal eye patch. In experiments 2 through 6, both eyes of each observer were tested on separate occasions (the other eye always patched). In experiment 1, there were 3 possible target locations (at screen center and 5° toward right or left). The observers never knew which would be the upcoming target location. This entailed, however, that when observers fixated on the left or right stimulus, they always knew the direction (if not the amplitude) of the upcoming saccade. This possibility was reduced in experiment 2 by adding stimuli to the left and right of the peripheral stimuli from experiment 1 (stimuli 4 and 5 in Fig. 1a). In experiments 3, 4, and 5, the observers performed 8° saccades unpredictably toward the left or right while in experiment 6 they performed 20° saccades, and in experiment 7, three saccade amplitudes were tested, 5°, 10°, and 20°. The optic disk is located $15.5° \pm 1.1°$ nasal to the fovea (Rohrschneider 2004), so none of the chosen target locations were in the observers' blind-spot. In experiments 1 and 2, each block began with a central fixation stimulus and observers were simply instructed to follow the fixation dot while it moved at a random interval (from 750 to 1,750 ms) from one of the 3 (experiment 1) or 5 (experiment 2) possible positions to another. In all experiments, the stimuli were displayed on dark-gray background (<1 cd/m^2; RGB = [0 0 0][1]).

In all experiments, a high-speed (250 Hz) monocular eyetracker based on infrared reflection technology with a tracking accuracy from 0.125° to 0.25° with a horizontal range of $\pm40°$ from Cambridge Research Systems (2006) was used. To find the direction of the observer's gaze, the eyetracker used the pupil and dual first Purkinje reflection. This method (more often with single first Purkinje

reflection) has been dominant in eyetracking for about two decades (Holmqvist et al. 2011). The observer's head was stabilized with chin- and headrests. All experiments were run in a sound-proof booth, and the only illumination came from the CRT monitor used to present stimuli and the LCD monitor used by the experimenter. Viewing distance in all experiments was 53 cm. The participants were told they could take breaks between blocks as needed.

In experiments 1 and 2, the stimuli were displayed on an 85 Hz 19″ Dell CRT monitor (model: P992 resolution: 1,140 × 900 px) while in experiments 3–5 on a 100 Hz 19″ Hansol CRT monitor (model: 920D resolution: 800 × 600 px). To maintain the same viewing distance in experiment 6 and 7 where large amplitude (up to 20°) eye movements were tested, the stimuli were displayed on a 60 Hz 24″ Dell LCD monitor (model: 2407WFP, resolution 1,920 × 1,200 px). All the experiments were run on a Dell computer (Intel Core Duo 2.33 GHz, working memory: 1.95 GB, operating system: Microsoft Windows XP 2002). For all experiments, a main script was written in Matlab to control the experimental procedure. The main script utilized functions from the Psychtoolbox (Brainard 1997; Pelli 1997; Kleiner et al. 2007) extension used to display the stimuli and functions from the eyetracker toolbox (Video Eyetracker Toolbox) to record the eye movements.

Eyetracker data analysis

A custom made script was written in Matlab to analyze the eyetracker data. Following target appearance, the velocity of the eye movement and gaze position was checked at each time point in the eye trace. If the velocity exceeded 30°/sec (Leigh and Zee 1999; Walker et al. 1997) at time point N, the saccade was considered to have started at time point $N - 1$ if the angular distance between $N - 1$ and N was at least 1° (Rolfs et al. 2010). The saccade was considered valid if it was made in the right direction and the amplitude exceeded half the distance to the target stimulus (2.5° in experiments 1 and 2; 4° in experiments 3, 4, and 5; 10° in experiment 6; 2.5°, 5°, and 10° in experiment 7). At the first point in time after the velocity dropped below 30°/sec, the saccade was considered to have ended and the corresponding position of gaze was judged to be its' landing point (Leigh and Zee 1999; Walker et al. 1997). The percentage of non-tracking trials (such as from eye blinks or signal loss) and of saccades with amplitudes less than half the distance to the target and of saccades in the wrong direction were calculated for each subject, and if this summed percentage exceeded 20 % (30 % in experiment 7 because of more target locations), the observers data were excluded from further analyses.

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[1] The sensitivity of our photometer was limited, giving the cd/m^2 values as integers, so we report the RGB value as well.
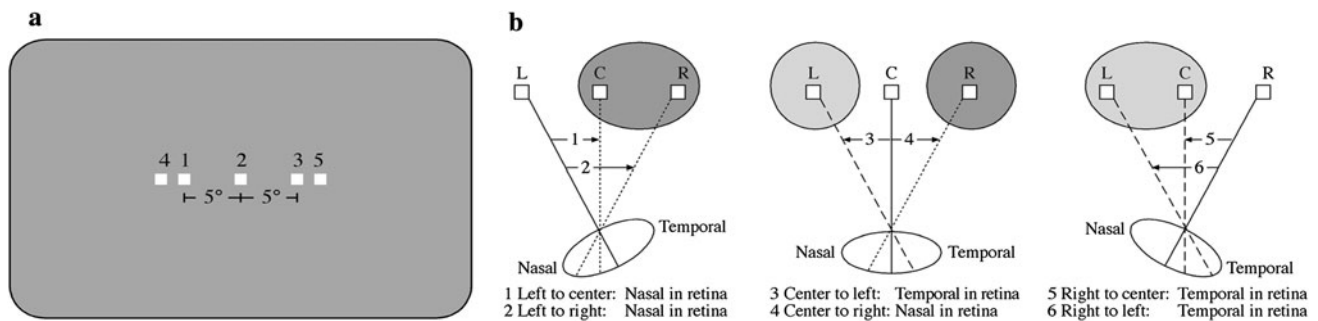
Fig. 1 Experimental setup and the different possible movement types tested in experiments 1 and 2. **a** Shows the possible target locations in experiment 1 (positions 1, 2, and 3) and experiment 2 (positions *1* through *5*). The stimulus that the observers were instructed to follow appeared randomly in positions *1, 2,* or *3* while in experiment 2, the stimulus could appear in positions *4* and *5* as well. **b** Shows the six types of movement (for the right eye) analyzed in experiments 1 and 2. The figure shows the direction and the hemifield that the target projected to for the 6 different movement types

Statistical analyses

In all experiments, mean latency and landing point accuracy for each participant were calculated for each task. Trials with saccadic latencies shorter than 80 ms were excluded from all analyses since these saccades are most likely not target driven but anticipatory (Becker 1991; Rolfs and Vitu 2007). In the statistical analyses, we used one subset for latency and another for landing point accuracy (because of different exclusion criteria). Latencies that deviated more than 3 SD from their mean, and landing point values that deviated more than 3 SD from their mean were removed for each observers' data before analysis. To compare different task types in each experiment, repeated measure ANOVAs and Mauchly's Sphericity tests were used. When appropriate, the degrees of freedom were corrected (Greenhouse–Geisser) and post hoc comparisons were made with Bonferroni corrected *p*-values. Since latency distributions tend to be positively skewed we used the egfit.m (Lacouture and Cousineau 2008) function for Matlab to fit our data to ex-Gaussian distributions (Ratcliff 1993) and estimated the parameters of the ex-Gaussian fit. The ex-Gaussian distribution is a convolution of a Gaussian and an exponential distribution with a longer right than left tail and usually fits latency and response time data well. To describe the ex-Gaussian distribution, the parameters, μ and σ, are used for the mean and standard deviation of the Gaussian and τ denotes the mean of the exponential part (Ratcliff 1993; Matzke and Wagenmakers 2009). We compared different tasks in each experiment with ANOVAs for μ and Wilcoxon signed-rank tests for τ and for the combined mean ($\mu + \tau$) of the ex-Gaussian distribution. The results of these tests are reported when their results differ from the tests based on the normal distribution.

For experiments 2 through 6, the left and right eyes were compared and the dominant and non-dominant eyes to

check for any performance differences. No differences were found, however, so the data for the two eyes were combined. When calculating landing point accuracy, the absolute value of the landing point was subtracted from the position of the center of the target stimulus. Details for each experiment will be described below, in specific sections for each respective one.

Experiment 1: Three target locations with saccadic amplitudes of 5° and 10°

In the first experiment, we tested eye movement performance during which observers followed a small square as it moved at a rate of 0.57–1.33 Hz (randomly decided on each trial) between three different locations at left, right, or center (see Fig. 1a). This allowed us to contrast lateral versus medial saccades, as well as saccades of different amplitudes (5° or 10°).

Method

Participants

Seven volunteers participated (5 women; aged from 19 to 30 years; M = 23.0 years, SD = 3.6 years) all with a dominant right eye, but 1 was excluded because of high error rates (>20 %). All were students at the University of Iceland and received course credit for participating.

Procedure

On the first trial of each block, a small white square (0.5°; 39 cd/m²; RGB = [255 255 255]) with a smaller dark-gray square (<1 cd/m²; RGB = [0 0 0]) in the middle appeared at the center of the screen. At a random interval varying from 750–1,750 ms (a rate of 0.57–1.33 Hz), this stimulus

appeared randomly either 5° to the left or the right of center. On subsequent trials, the stimulus appeared randomly at the central (1/3 of trials), left (1/3 of trials), or right positions (1/3 of trials) but never twice in a row in the same position, see Fig. 1a. This means that there were six possible movement types (see Fig. 1b). Each observer participated in 20 blocks of 50 trials.

Results

Trials with latencies shorter than 80 ms (2.7 % of the data) and trials with recording errors (such as signal loss, 7.0 % of the data) were excluded from all statistical analyses. There were no differences for medial versus lateral saccades.

Latency

Trials with latencies longer than 3 SD from the mean (3.3 % of the data) were excluded, and 816–939 trials were analyzed for each participant depending on their error rate. For the low-amplitude saccades, the average latency for temporal stimuli (movement types 1 and 4 in Fig. 1b) was 175 ms (SD = 14.6 ms), and for nasal stimuli (movement types 3 and 5), it was 166 ms (SD = 11.9 ms). This 9 ms difference was not significant [$F_{(1, 5)} = 2.696, p = .162$]. The average latency for high-amplitude saccades toward temporal stimuli (movement type 2) was 156 ms (SD = 8.7 ms), and toward nasal stimuli, the average latency was 149 ms (SD = 8.3 ms). This 7 ms difference was not significant [$F_{(1, 5)} = 5.132, p = .073$]. When low- and high-amplitude saccades and nasal versus temporal saccades were compared (2 × 2 ANOVA), the main effect of amplitude was significant [$F_{(1, 5)} = 21.212, p = .006$] but neither the main effect [$F_{(1, 5)} = 3.925, p = .104$] of hemifield nor the interaction [$F_{(1, 5)} = 0.355, p = .577$] reached significance. The average latency of low- and high-amplitude saccades was 170 ms (SD = 13.8 ms) and 152 ms (SD = 8.9 ms), respectively. The mean of the exponential part (τ) of the ex-Gaussian distribution for high-amplitude saccades toward temporal stimuli was 16 ms, and toward nasal stimuli, it was 13 ms. This 3 ms difference was significant ($V = 21$; $p = .031$). This suggests that there are more extreme values in the latencies for temporal than nasal stimulation for the high-amplitude saccades. The mean of the ex-Gaussian distribution ($\mu + \tau$) for high-amplitude saccades toward temporal stimuli was 156 ms, and toward nasal stimuli, it was 149 ms and this difference, 7 ms, was significant ($V = 21$; $p = .031$).

Landing point accuracy

All deviations were within 3 SD's from the mean, so no trials were excluded and 833–943 trials were analyzed for

each participant depending on their error rate. On average the saccades were hypometric for both nasal and temporal stimuli (consistent with Collewijn et al. 1988). When saccading to the periphery, the landing points were medial to the target stimuli on average. The saccades to the center were also hypometric, landing left of the central stimulus when saccading from left and right of it when saccading from right. For the low-amplitude saccades, the average deviation for temporal and nasal stimuli was 0.69° (SD = 0.27°) and 1.21° (SD = 0.58°), respectively. The difference (0.52°) was not significant [$F_{(1, 5)} = 3.267, p = .131$]. The average deviation for temporal stimuli for the high-amplitude saccades was 1.19° (SD = 0.33°), while for nasal stimuli, it was 1.78° (SD = 1.08°) and the difference, 0.59°, was not significant [$F_{(1, 5)} = 3.037, p = .142$]. We used a 2 × 2 ANOVA to find out if there was an interaction between the amplitude (short vs. long) and hemifield (nasal vs. temporal). The main effect of amplitude was significant [$F_{(1, 5)} = 6.893; p = .047$] but the main effect of hemifield was not [$F_{(1, 5)} = 3.265, p = .131$], and there was no interaction [$F_{(1, 5)} = 0.277, p = .621$]. The average deviation for low-amplitude saccades was 0.95° (SD = 0.51°), and for high-amplitude saccades, it was 1.49° (SD = 0.82°).

The main result with regard to our experimental question of possible NTAs in saccade performance is that no such asymmetries were observed in latency nor accuracy. The only significant effects were between low- and high-amplitude saccades. In the latency results, high-amplitude saccades from one visual field to the other across the midline had shorter latencies than low-amplitude saccades. And the landing point accuracy was better for low- than for high-amplitude saccades. This absence of any NTA is shown to occur both for centrifugal saccades (away from the eyes central position) and centripetal saccades (to the central position). Experiment 2 was similar in nature to experiment 1, except that there we deal with a possible confound from experiment 1.

Experiment 2: Testing the role of motor preparation

A potential problem with the design of experiment 1 was that when observers' gaze was fixed at the leftmost or rightmost point, they always knew in which direction they were supposed to move their eyes next, allowing directional motor preparation, which may have affected the results. Consistent with this, the latencies for the high-amplitude saccades, whose direction was always predictable, were indeed shorter. Knowledge of the amplitude and the direction of the upcoming saccade can result in motor preparation, leading to shorter latencies (Paré and Munoz 1996) due to greater activity of buildup neurons in the SC

(Dorris and Munoz 1998). And if the retinotectal projections are asymmetric, this pattern might even be stronger for stimuli appearing in the temporal than in the nasal hemifield. But as the number of possible amplitudes and target locations increases, motor preparation effects tend to be smaller because of increased uncertainty (Paré and Munoz 1996). Experiment 2 was, therefore, similar to experiment 1 except that the possible target locations were 5 rather than 3. We only analyzed the data for the three central positions, while the two most lateral positions were used to reduce the possibility of motor preparation since the upcoming saccade direction was never predictable.

Method

Participants and procedure

Six volunteers participated (3 women; aged from 19 to 33 years; M = 24.4 years, SD = 5.2 years) all with a dominant right eye. One was excluded because of high error rates (≈ 40 % of the net data). All were students at the University of Iceland and received course credit for participating. Apart from the addition of the two possible target locations at left and right (at 6° away from central fixation), methods were identical to those described for experiment 1. On subsequent trials, the stimulus appeared randomly at positions 1–5 (1/5 of trials each), but never twice in a row in the same position, see Fig. 1a.

Results

All trials where stimulus position was either 4 or 5 (38.6 % of the data; see Fig. 1a, for the positions) and all trials where the stimulus on the preceding trials was in positions 4 or 5 (29.8 % of the total data) were not analyzed. Trials with recording errors (5.8 % of the remaining data) and trials with latencies shorter than 80 ms (3.1 % of the remaining data) were excluded from the statistical analyses.

Latency

Trials with latencies larger than 3 SD from the mean (1.0 % of the data) were excluded, and 251–278 trials were analyzed for each participant depending on their error rate. For the low-amplitude saccades, the average latency for temporal stimuli (movement types 1 and 4) was 169 ms (SD = 8.4 ms); for nasal stimuli (movement types 3 and 5), it was 168 ms (SD = 12.8 ms); and unsurprisingly, this 1 ms difference was not significant [$F(1, 4) = 0.224$, $p = .661$]. The average latency for high-amplitude saccades toward temporal stimuli (movement type 2) was 158 ms (SD = 5.2 ms), while toward nasal stimuli

(movement type 6), it was 156 ms (SD = 6.1 ms) n.s. [$F(1, 4) = 5.843$, $p = .073$]. In a 2×2 ANOVA comparing low versus high-amplitude hemifield, the main effect of amplitude was significant [$F(1, 4) = 23.511$, $p = .008$], but there was no main effect of hemifield [$F(1, 4) = 1.119$, $p = .350$] nor any interaction [$F(1, 4) = 0.007$, $p = .939$]. The latency of the high-amplitude saccades was 157 ms (SD = 5.4 ms), and for the low-amplitude saccades, it was 169 ms (SD = 10.2 ms).

Landing point accuracy

All deviations from the mean were within 3 SD's from it, and 253–286 trials were analyzed for each participant depending on their error rate. As in experiment 1, the saccades were on average hypometric. For the low-amplitude saccades, the average deviation for temporal stimuli was 0.47° (SD = 0.24°), and for nasal stimuli, it was 1.34° (SD = 0.34°). The difference was 0.87° and quite significant [$F(1, 4) = 21.505$, $p = .010$]. For the high-amplitude saccades, the average deviation for temporal stimuli was 0.61° (SD = 0.56°) while for nasal stimuli, it was 1.96° (SD = 0.51°). The difference was 1.35° and again highly significant [$F(1, 4) = 59.922$, $p = .002$]. In a 2×2 ANOVA, the main effect of amplitude was close to significant [$F(1, 4) = 7.188$, $p = .055$] and the main effect of hemifield was significant [$F(1, 4) = 38.997$, $p = .003$]. The interaction between amplitude and hemifield was significant [$F(1, 4) = 43.911$, $p = .003$]. The average deviation for high-amplitude saccades was 1.28° (SD = 0.87°), and for low-amplitude saccades, it was 0.90° (SD = 0.54°). The average deviation (pooled over amplitude) from temporal landing points was 0.54° (SD = 0.41°), and from nasal landing points, it was 1.65° (SD = 0.52).

In experiment 2, there was a significant NTA in that the landing point accuracy for temporal stimuli was higher than for nasal stimuli. Whether this is a general pattern for nasal versus temporal saccades is not clear, however, since it did not appear in experiment 1. In experiments 3 through 7, we will search for NTAs in saccade performance using more traditional saccade tasks, including some attentional manipulations and within-experiment amplitude variation.

Experiment 3: Testing NTAs with a standard saccade task

In experiments 1 and 2, saccades of different amplitude (5° and 10°) were interleaved so the movements were from the center to periphery and vice versa, in addition to high-amplitude saccades across the midline. We found no NTAs in terms of latency, nor accuracy in experiment 1 while in

experiment 2, landing point accuracy was higher for temporal stimuli.

In previous experiments where saccadic NTAs have been reported, attentional manipulations have been used (e.g., Kristjánsson et al. 2004; Walker et al. 2000). In experiments 3–5, we contrast different attentional loads for a "standard" saccade task where the observers simply fixate on a central stimulus and then saccade to it when it moves to the left or to the right. In experiment 3, there was no secondary attentional load to test for any "baseline" NTAs, while in experiments 4 and 5, we added attentional manipulations.

Method

Participants

Ten volunteers participated (5 women; aged from 19 to 42 years; M = 29.7 years, SD = 7.0 years). All were students at the University of Iceland, and 2 had a left dominant eye.

Stimuli

The central fixation stimulus was a small red square (0.7°, 8 cd/m^2; RGB = [202 2 2]) with a smaller dark-gray (<1 cd/m^2; RGB = [0 0 0]) square in the middle. The target stimulus was a small white square (0.7°; 39 cd/m^2; RGB = [255 255 255]) with a smaller dark-gray (<1 cd/m^2; RGB = [0 0 0]) square in the middle.

Procedure

At trial start, the fixation point was displayed at screen center. When central fixation had been confirmed by the eye tracker, the fixation point disappeared (following an interval between 750 and 1,350 ms, determined randomly) and simultaneously the target stimulus appeared either 8° to the left or right (determined randomly). The observers participated in 1 block of 52 trials for each eye.

Results

Trials with latencies shorter than 80 ms (1.1 % of the data) and trials with recording errors (5.8 % of the data) were excluded from all statistical analyses.

Latency

Trials with latencies larger than 3 SD from the mean were excluded from the latency analyses (0.7 % of the data), and 92–102 trials were analyzed for each participant dependent on their error rate. The average latency for temporal stimuli was 186 ms (SD = 13.3 ms), and for nasal stimuli, it was 184 ms (SD = 18.3 ms). This 2 ms difference was not significant [$F(1, 9) = 0.522, p = .488$].

Landing point accuracy

All deviations from the mean were within 3 SD's from it, so 92–102 trials were analyzed for each participant dependent on their error rate. As before, the saccades were hypometric on average. The average deviation for temporal stimuli was 0.36° (SD = 0.65°), and for nasal stimuli, it was 1.13° (SD = 1.10°), the difference (0.77°) was, however, not quite significant [$F(1,9) = 3.318, p = .102$], presumably because the difference in variance with regard to the conditions is very large compared to the difference in means.

In sum, experiment 3 revealed no NTAs for saccade latency nor landing point accuracy although there was a notable trend toward a similar NTA in accuracy as was found to be significant in experiment 2.

A note on Experiments 4 and 5

In previous studies where conflicting findings regarding potential nasal/temporal differences have been reported, various types of task have been tested. Kristjánsson et al. (2004) found such an NTA in latency in a task where prosaccades and antisaccades (see e.g., Munoz and Everling 2004; Kristjánsson 2007 for review) were interleaved within blocks. In Walker et al. (2000), there was evidence of NTAs when distractors were presented along with the saccade target. This opens up the possibility that NTAs may surface under attentional load but might at the same time be less likely to occur in a more simple and straightforward saccade task. In experiments 4 and 5, we therefore added two types of attentional manipulation to the simple saccade task tested in experiment 3. In experiment 4, we used a "pre-cue"-design[2] (Posner and Cohen 1984; see also Kristjánsson and Sigurðardóttir 2008) where a non-predictive stimulus "cued" one side or the other before saccade execution, and in experiment 5, a secondary discrimination task was presented along with the saccade target (as in experiment 1 in Kristjánsson et al. 2001).

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[2] Note that even though we follow the convention of referring to a stimulus of this sort as a pre-cue, it did not really "cue" the target position, as such, since it was non-predictive of the upcoming saccade target location.

Experiment 4: Measuring NTAs in a pre-cue design

Method

Participants

Fourteen volunteers participated (8 women; aged from 19 to 55 years; M = 32.1 years, SD = 9.3 years). All were students at the University of Iceland. Data from 5 participants were excluded because of high error rates (>20 %). Of the 9 remaining participants, 2 had left eye dominance.

Stimuli

The central fixation and target stimuli were the same as in experiment 3. Four dark-gray dots forming an illusory square (2.8° × 2.8°; 1 cd/m²; RGB = [40 40 40]) with their center ±8° from screen center (in both hemifields) acted as placeholders for the pre-cue and were always visible. These placeholders also served as a cue when those on one side briefly brightened (from 1 cd/m² to 39 cd/m²; see Fig. 2).

Procedure

At the beginning of each trial, a fixation stimulus was displayed at screen center along with the placeholders (see Fig. 2). After observers' fixation was confirmed and following an interval between 750 and 1,350 ms (randomly determined), the left or right side placeholder brightened for 150 ms, serving as a pre-cue. When the cue disappeared

(by returning to the "baseline" illumination of the placeholders), the fixation stimulus disappeared and the target stimulus appeared randomly either to the left or to the right. The cue was thus non-predictive of the target location (valid on 50 % of the trials). The observers participated in 3 blocks of 52 trials for each eye.

Results

Trials with latencies shorter than 80 ms (2.4 % of the data and all toward a valid cue) and with recording errors (3.7 % of the data) were excluded from all statistical analyses. Furthermore, 6.0 % of the trials were excluded because the saccade was made in the wrong direction and of those 87.0 % were toward an invalid cue: 48.5 % toward a nasal cue and 38.6 % toward a temporal cue (the difference between these proportions was not quite significant; $z = 1.867$; $p = .062$). Only 13.0 % of the direction errors occurred when the cue was valid, and the difference between nasal (6.5 %) and temporal (5.9 %) movements was small and not significant ($z = 0.225$, $p = .818$).

Latency

Latencies that deviated more than 3 SD (0.8 %) from the mean were not included in the latency analyses, and 258–301 trials for each observer were analyzed depending on their error rate. For the valid cue, the average latency for temporal stimuli was 234 ms (SD = 13.4 ms), and for the nasal stimuli, it was 232 ms (SD = 15.7 ms). This 2 ms difference was not significant [$F(1, 8) = 0.865$, $p = .380$].

Fig. 2 The procedure in experiment 4. **a** The procedure in the valid cue condition while **b** shows the procedure in the invalid cue condition
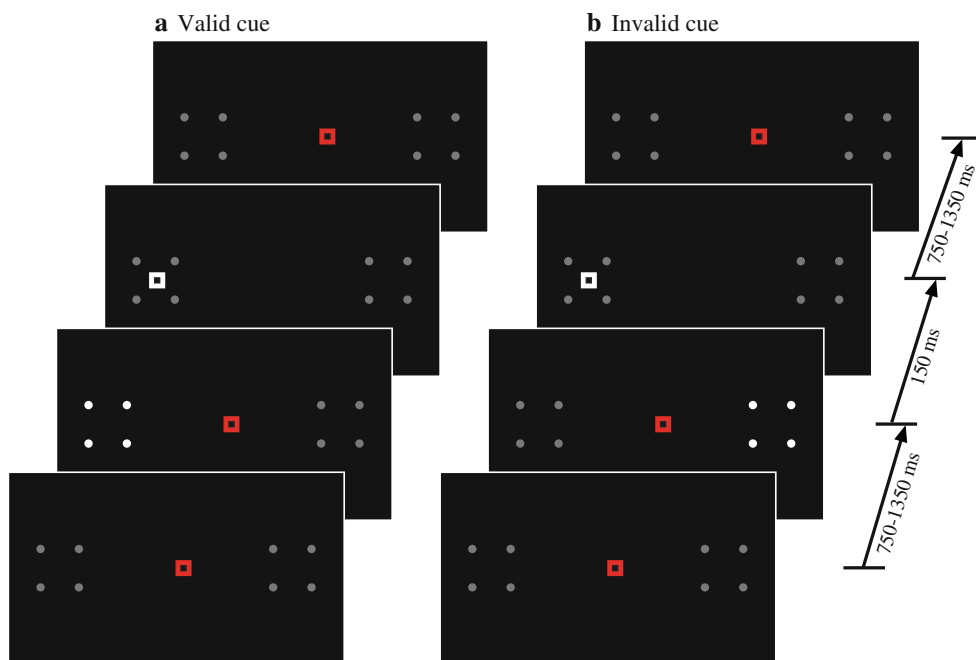
For the invalid cue, the average latency for temporal stimuli was 229 ms (SD = 25.0 ms); for nasal stimuli, it was 224 ms (SD = 21.9 ms); and again this 5 ms difference was not significant [$F(1, 8) = 4.035$, $p = .079$].

Landing point accuracy

All deviations from the mean were within 3 SD's from it, and 259–302 trials for each observer were analyzed depending on their error rate. The saccades were again hypometric on average. In the valid cue condition, the saccades toward temporal stimuli deviated from the target position by 0.43° (SD = 0.81°) and the saccades toward the nasal stimuli deviated by 0.99° (SD = 0.63°). This difference, 0.56°, was not significant [$F(1, 8) = 2.143$, $p = .181$], although once again there were some indications that the saccades toward nasal stimuli are more hypometric than to temporal stimuli. When the cue was invalid, the saccades were also hypometric on average. Landing point deviation toward temporal stimuli was 0.58° on average (SD = 0.90°), and toward nasal stimuli, it was 0.83° (SD = 0.54°). This trend toward an NTA (0.25°) was not significant [$F(1, 8) = 0.526$, $p = 0.489$].

Experiment 5: Measuring saccadic NTAs with a secondary discrimination task

Method

Participants

The participants were the same 14 volunteers as in experiment 4. Data from five participants (not the same as in experiment 4) were excluded because of high error rates (>20 %). Of those 9 remaining participants, 2 had a left dominating eye.

Stimuli

The fixation and target stimuli were the same as in experiment 4. The discrimination stimuli were two rectangles with a horizontal square wave pattern (dark gray (2 cd/m²; RGB = [60 60 60]) and light gray (3 cd/m²; RGB = [80 80 80]); $w = 3.78°$; $h = 1.65°$) of different spatial frequency (4.24 cycles/degree and 5.45 cycles/degree), which were displayed 2.74° (center/center) above and below the center of the fixation stimulus (see Fig. 3). At the end of each trial, a response display was presented in the same position as the discrimination stimuli (see Fig. 3). Above the center of the screen, the word "Uppi" ("above" in Icelandic) was displayed, and below the center, the word "Niðri" ("below" in Icelandic) was displayed.

Procedure

At the beginning of each trial when observers' central fixation had been confirmed by the program, the two rectangles for the discrimination task appeared (800–1,800 ms following confirmation, determined randomly), one above the fixation stimulus and the other below it. The rectangle with lower spatial frequency appeared randomly above or below the fixation stimulus (and the other rectangle in the opposite position). During this part of the trial, the observers' task was to judge—without shifting gaze—whether the rectangle with the lower spatial frequency appeared above or below fixation. When the saccade target appeared 200 ms following the discrimination stimuli, the rectangles disappeared and the participant's task was to saccade to the suddenly appearing stimulus. The saccade target was visible for 800 ms, and as soon as it disappeared, the response stimuli appeared above and below the center of the screen (see Fig. 3, fourth frame from bottom). The participants were supposed to shift their gaze toward the appropriate response stimulus (above or below the words) indicating whether the low spatial frequency target had appeared above or below the fixation stimulus. Eight observers participated in 3 blocks of 50 trials and 1 observer
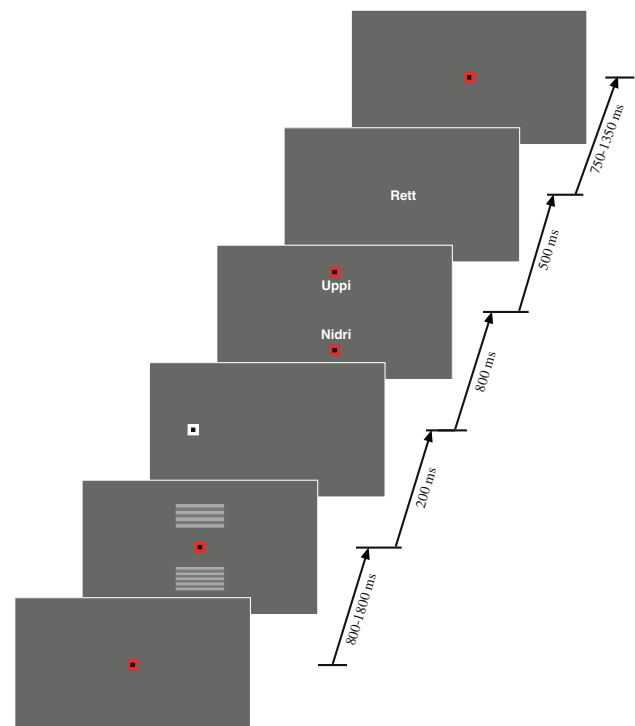
Fig. 3 The procedure in experiment 5. The first frame denotes the time when central fixation had been confirmed. The target stimulus was displayed randomly to the *left* or *right* of central fixation and the target *rectangle* with the lower spatial frequency appeared randomly above or below the fixation stimuli while the distractor *rectangle* (of higher spatial frequency) appeared in the other location

in 2 blocks of 50 trials for each eye in the experiment. In other respects, the methods were similar to experiment 4.

Results

Saccades with latencies shorter than 80 ms (0.07 % of the data) with recording errors (2.3 % of the data) or direction errors (4.4 % of the data) were excluded from all statistical analyses. Trials with incorrect responses on the discrimination task (5.6 % of the data) were not analyzed.

Latency

Trials with latencies larger than 3 SD from the mean were excluded (3.6 % of the data), and 192–291 trials for each observer were analyzed depending on error rates. For trials with correct responses on the discrimination task, the average latency for temporal stimuli was 244 ms (SD = 41.6 ms), and for the nasal stimuli, it was 237 ms (SD = 36.0 ms). This 7 ms difference was not significant [$F(1, 8) = 3.336$, $p = .105$]. The mean of the exponential part (the τ-parameter) of the ex-Gaussian distribution for saccades toward temporal stimuli was 67 ms, and toward nasal stimuli, it was 53 ms. This 14 ms difference was significant ($V = 43$; $p = .012$). This suggests that long latencies are more frequent and variability in latency higher for temporal than nasal stimuli.

Landing point accuracy

All deviations from the mean were within 3 standard deviations from it, and 195 to 300 trials for each observer were analyzed depending on error rates. For trials with correct responses on the discrimination task, the saccades were hypometric on average. Landing point error for temporal stimuli was 0.60° on average (SD = 0.78°), and for nasal stimuli, it was 0.99° on average (SD = 0.82°). The difference, 0.39°, was not significant [$F(1, 8) = 1.748$, $p = 0.223$].

Overall, the results from experiments 3–5 reveal little evidence for any NTA in saccade performance, certainly not for latency, while there is some trend for saccades toward nasal stimuli being more hypometric than toward temporal stimuli, in line with the effect seen in experiment 2. The evidence for this potential NTA cannot be considered very strong, however.

Experiment 6: Two target locations with large amplitude saccades (20°)

Apart from the evidence from experiment 2 (and some tendency in experiments 1, 3, 4, and 5) for more hypometric saccades into the nasal than temporal hemifield, we have so

far found little nasal/temporal asymmetries in saccade performance. Our test in experiment 6 was inspired by reported differences in cone and ganglion density between the two hemifields. With increased eccentricity from the fovea, density drops more quickly in the temporal than nasal hemiretina (Curcio and Allen 1990) and at 20° in the periphery, this asymmetry becomes quite pronounced (Curcio and Allen 1990, figures 6A and 6C). At the nasal edge of the optic disk, the ganglion cell density is 1.4 times that in the temporal retina and this ratio increases to 4.2 at the retinal edges. Our question was whether these density differences at eccentric locations in the retina might result in different saccade characteristics for stimuli presented peripherally to each respective hemiretina, in this case more peripherally (20° from central fixation) than in previous tests.

Method

Participants

Five volunteers participated (4 women, aged from 23 to 39 years; M = 27.0 years, SD = 6.7 years). All were students at the University of Iceland and all but 1 had a right dominating eye.

Stimuli, experimental design, and procedure

The target stimulus appeared randomly 20° to the right or left of center, the viewing distance was 53 cm, and there were 5 blocks of 52 trials for each eye in the experiment. Otherwise the stimuli, experimental design, and procedure were similar to experiment 3.

Results

Trials with latencies shorter than 80 ms (0.3 % of the data) and recording errors (5.6 % of the data) were excluded from all statistical analyses.

Latency

Trials with latencies larger than 3 SD from the mean were excluded from the analyses (1.1 % of the data), and 452–513 trials for each observer were analyzed dependent on error rates. The average latency for temporal stimuli was 213 ms (SD = 33.2 ms), and for nasal stimuli, it was 208 ms (SD = 28.1 ms). This 5 ms difference was not significant [$F(1, 4) = 0.732$, $p = .441$].

Landing point accuracy

All deviations were within 3 SD's from the mean, and 462–519 trials for each observer were analyzed dependent

on error rates. For both nasal and temporal stimuli, the saccades were hypometric on average. The average deviations for nasal and temporal stimuli were identical, 2.74° (temporal SD = 1.74°; nasal SD = 1.10°).

Experiment 6 did not reveal any evidence of NTAs in saccade performance, generally consistent with what we have seen in the 5 preceding experiments.

Experiment 7: Contrasting different saccade amplitudes within blocks

In experiment 2—where the influence of motor preparation might have been modest because of the number of target locations—we found some evidence for NTA in landing point accuracy for both of the tested amplitudes (5° and 10°). To investigate this further, we conducted the 7th experiment in which there were three amplitudes (5°, 10°, and 20°), and therefore, the target stimulus could appear in any of 6 positions on the screen and the fixation point at the center of the screen was the 7th position. The number of target locations might minimize the effect of motor preparation and their distribution might clarify any influence of anatomical NTAs (Curcio and Allen 1990).

Method

Participants

Twelve volunteers participated (7 women; aged from 21 to 48 years; M = 31.6 years, SD = 8.0 years) seven with a dominant right eye but 3 were excluded because of high error rates (>30 %). All were students at the University of Iceland and received course credit for participating.

Stimuli, experimental design, and procedure

The target stimulus appeared randomly 5°, 10°, or 20° to the right or left of center, the viewing distance was 53 cm, and there were 18 blocks of 60 trials for the dominant eye in the experiment. In the previous experiments, no differences were found between left and right eyes nor between the dominant and non-dominant eyes so we measured the dominant eye only. Otherwise the stimuli, experimental design, and procedure were similar to experiment 3.

Results

Trials with response times shorter than 80 ms (0.3 % of the data), trials with recording errors (3.3 % of the data), and trials where the amplitude of the saccade was smaller than half the distance to the target stimulus (10.7 %) were excluded from all statistical analyses.

Latency

Trials with latencies larger than 3 SD from the mean were excluded from the analyses (0.05 % of the data), and 95–177 trials for each observer were analyzed depending on error rates. The effect of amplitude was significant [$F_{(2, 16)} = 5.17$, $p = .019$] but not of hemifield [$F_{(1, 8)} = 0.71$, $p = .425$] while the interaction between amplitude and hemifield was significant [$F_{(2, 16)} = 4.15$, $p = .035$]. The average latency in the 20° condition for temporal stimuli was 203 ms (SD = 13.6 ms), and for nasal stimuli, it was 196 ms (SD = 13.4 ms). In the 10° condition, the latency was 192 ms (SD = 17.1 ms) and 192 ms (SD = 11.8 ms) for temporal and nasal stimuli, respectively. The average latency in the 5° condition for temporal stimuli was 196 ms (SD = 17.3 ms), and for nasal stimuli, it was 195 ms (SD = 11.0 ms). The differences were all small and none of them significant (all p's > .5). The significant interaction reflects the small difference between nasal and temporal hemifields for the largest amplitude.

Landing point accuracy

Trials with deviations larger than 3 SD from the mean were excluded from the analyses (0.04 % of the data), and 95–177 trials for each observer were analyzed depending on error rates. The effects of amplitude [$F_{(2, 16)} = 46.38$, $p < .001$] and hemifield [$F_{(1, 8)} = 6.25$, $p = .037$] were significant as well as the interaction between the two [$F_{(2, 16)} = 4.24$, $p = .033$]. On average, the saccades toward temporal stimuli at 5° were hypermetric, but in all other cases, the saccades were hypometric. In the 20° condition, the average deviation for temporal stimuli was 1.61° (SD = 0.72°) and for nasal stimuli, it was 3.25° (SD = 1.70°). In the 10° condition, the deviations was 0.34° (SD = 0.74°) and 1.67° (SD = 1.20°) for temporal and nasal stimuli, respectively. The average deviation in the 5° condition for temporal stimuli was 0.26° (SD = 0.80°), and for nasal stimuli, it was 0.90° (SD = 11.0°). The differences in accuracy between temporal and nasal stimuli were all small and none of them significant (all p's > .3).

The results from experiment 7 are in good accordance with results from experiments 1 through 6 in revealing no significant NTA in latency while landing point accuracy is lower for the nasal stimuli at the highest eccentricity. The interactions between hemifield and eccentricity were significant for both latency and landing point accuracy. This could argue for a slight difference in speed/accuracy trade-offs for the two hemifields (see the "General discussion"), especially at the higher eccentricities. Another possibility is that significant NTAs in latency might surface at even larger eccentricities than 20° because the between-

hemifield ganglion and cone density asymmetries increase with eccentricity. Both of these questions need to be addressed in future experiments.

General discussion

There are enticing reasons to predict differences in saccade characteristics depending on whether the stimuli project to the nasal or temporal visual hemifields. Structural differences in the retinae and in projections to saccade control centers in the midbrain are one reason, and the other is evidence for asymmetries in attentional function between the hemifields. But the experimental findings with regard to saccade NTAs have not proved consistent.

Our study is the first to address this question explicitly with a variety of different tasks (in other studies this has at best been a secondary aim; e.g., Bompas et al. 2008; Kristjánsson et al. 2004; Rafal et al. 1991; Walker et al. 2000), with measures both of latency and accuracy. Our conclusion is that any NTAs in saccadic performance are small. The only evidence for such NTAs comes from experiment 2 and 7 (and trends in experiments 1, 3, 4, and 5) where landing point accuracy was higher for temporal stimuli (they were less hypometric than saccades toward nasal stimuli). This rather modest evidence for any NTA is surprising in light of previous results. One obvious question is why reported differences for attentional function do not translate into differences in saccade performance. Temporal signals have a larger effect upon attention (Rafal et al. 1989; 1991) and are more effective in automatically triggering saccadic eye movements toward them (Posner and Cohen 1980) consistent with what is known about retinotectal neural projections. Honda (2002) observed little evidence for NTAs in saccade latencies and shares our surprise at the fact that NTAs in attentional function do not result in corresponding saccade latency.

One subtle pattern that does pop-up more than once in our results is lower accuracy for saccades toward nasal stimuli (that project to the temporal hemiretina). At the same time, the latencies were often slightly lower (by a few milliseconds) for the nasal hemifield stimuli even though this was never significant. This raises the possibility that speed-accuracy tradeoffs are more likely or larger for the nasal hemifield, while the current paradigms are not sensitive enough to pick up this subtle pattern consistently. Experiments are under way in our laboratory to address this more thoroughly.

One cue toward why NTAs in attention are not found for saccades may come from the studies of Bompas et al. (2008) who found that observers are more likely to choose to saccade to temporal stimuli as Posner and Cohen (1980) had observed previously. Importantly, Bompas et al. also found

such saccade-choice NTAs for s-cone stimuli, which are not visible to non-color-opponent retinotectal neurons. The saccade-choice NTA was therefore not unique to retinotectal projection. Also, in a recent unpublished study, Bompas and Sumner (2011) argue that saccade choice and latency can be dissociated which could mean that attention (choice) need not necessarily lead to saccade latency benefits.

The response properties of the SC are modulated by input from brain areas receiving direct retinogeniculate input (Wilson and Toyne 1970; Fries 1984). This may dilute any manifest asymmetry. This is not unlikely since preparatory set-related activity in SC neurons during saccades is mediated, at least in part, by direct descending projections from the FEF to the SC (Segraves and Goldberg 1987). According to Sommer and Wurtz (2000), the cortico-tectal projections from FEF strongly influence the SC throughout the saccade generation process. This raises the possibility that the saccade NTAs observed by Kristjánsson et al. (2004) and Walker et al. (2000) are mediated via different processes than the extrageniculate pathway between the retina and the colliculus.

We should keep in mind that probably no more than ≈ 10 % of retinal ganglion cells have primary projections to the SC (e.g., Perry and Cowey 1984), so their influence may be small on saccadic performance, and any asymmetries subtle. Finally, it is worthwhile to note that the "tight coupling" between attention and saccades may not be as tight as sometimes thought. Sato and Schall (2003) found that one-third of FEF neurons exhibited response patterns where saccade target selection and attentional selection were not correlated (see also Schall et al. 2004 and discussion in Kristjánsson 2011).

An unexplored question, however, is whether nasal/temporal asymmetries might be stronger for *express* saccades (Edelman et al. 2007; Fischer and Boch 1983; Ross and Ross 1980; Saslow 1967), typically seen in a 'gap' paradigm where the fixation point in a standard saccade task disappears 100–200 ms before the saccade is to be executed. Express saccades have sometimes been thought to correspond to the visuomotor grasp reflex, the tendency to shift gaze to a sudden stimulus, which might be more strongly influenced by retinotectal projections than "regular" saccades. Future experiments may uncover whether this is the indeed the case.

Conclusions

We conclude that NTAs are generally not seen for saccades except perhaps with attentional manipulations. Why the well-known attentional benefit for temporal stimuli does not translate into a saccade latency advantage is, to our minds, still unclear. This may reflect that the control of

simple saccades to luminance based stimuli is not at all a purely retinotectal process but is strongly modulated by other pathways such as from frontal lobe control structures.

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