Saccade performance
in the nasal and temporal hemifields

Ómar Jóhannesson

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Preface

This MSc thesis (60 ECTS) in psychology was written under the guidance of Dr. Árni Kristjánsson; it was a privilege to have such an excellent mentor. Special thanks to my son, Benedikt, for his assistance in my first steps – and many, many steps there after – in Matlab programming and for the great web based booking system he wrote for me. I want to thank my daughter, Jóhanna, for her great support during my master study. I want also to thank my grandson, Merkúr, my best friends Helena and Börkur, my daughter-in-law, Berglind and all my other friends for filling up some empty spaces in my live. Árni Gunnar Ásgeirsson gets his share of my gratitude for his good introduction to the eye-tracker system. At last I want to thank the examiner, the staff at the Department of Psychology and the many participants for their contributions to this thesis.

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 saccade latency, landing point accuracy and peak velocity 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 and peak velocity. While this lack of asymmetry is surprising in light of previous findings, it may reflect that cortical input to midbrain eye control centers dampens any asymmetry.

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Introduction

When we walk down the street we perceive the buildings as motionless while people and cars move around. Usually we do not think about those facts because this seems normal to us and we know the buildings cannot move. But as we move the image of the environment is constantly shifting on the retina but the visual system somehow manages to keep the environment "in place". The movements of the eyes play an important role in visual function and because of them our gaze can follow a moving car or we can concentrate on an important, stationary part of the environment while we walk. There are seven types of eye movement but those that are of interest here are the saccadic eye movements (saccades), their onset, end point accuracy and peak velocity.

The eye is a sphere and it is located in a socket in the head and the movements of the eye are therefore rotations. Because the eyes' movements are rotations it is both convenient and rational to measure the movement of the eye in degrees (of an arc) or minutes when measuring small rotations. Amplitude refers to the size or the magnitude of the rotation of the eye and is measured in degrees. The center of the eye splits the retina into nasal and temporal parts. It is conventional to talk about the lateral part of the retina (right part of the right eye) as temporal or the temporal hemiretina and the medial part of the retina (left part of the right eye) as nasal or the nasal hemiretina. Accordingly people also talk about the nasal and temporal visual hemifields. The temporal hemifield for the right eye is the area in the visual field, which is to the right of the ventral–dorsal centerline of the eye, and the nasal hemifield for the right eye is the area to left of the ventral–dorsal centerline. A stimulus presented in the temporal hemifield projects to the nasal hemiretina and when a stimulus is presented in the nasal hemifield it projects to the temporal hemiretina.

Visual acuity is by far the highest in the fovea, which is located in the center of the dorsal part of the eye, because there the cone density is highest. Cone density – and visual acuity – declines rather fast with increased eccentricity and the ratio of rods against cones becomes higher. It is therefore important to keep the visual stimulus of interest on the fovea for high precision processing. The fovea is rather small, it's diameter is less than 1 mm (Kandel, Schwartz & Jessel, 2000), and the main purpose of the saccades is to keep – or to bring – the target of interest to the center of the fovea. The time from onset of the target of interest to the initiation of the saccades varies greatly,

both between people and within the same individual. When referring to the time from target onset to initiation of the saccade in the saccadic literature the word latency is usually used but sometimes reaction time (RT) is used instead.

Saccades and smooth pursuit

Saccades are extremely fast movements of the eye within the socket and probably the fastest movements of the body; their peak velocity can reach more than 500°/sec. There is an approximately linear relationship between the amplitude and the peak velocity of the saccade for the first 20° from the center position (Leigh & Zee, 1999). The relationship between the peak velocity and amplitude is well documented and has been termed "the main sequence" (Bahill, Clark & Stark, 1975). There is also a close-to linear relationship between the duration and the amplitude (from 1° to 50°) of the saccade and a typical duration for a saccade of 50° amplitude is about 100 ms. There is, however, some variability in peak velocity and among components that influence the peak velocity are the directions of the saccades, and whether they are made towards a target (prosaccade) or away from a target (antisaccade). Centripetal movements (towards the center position of the eye) tend to have higher peak velocities than centrifugal movements (away from the center position) (Leigh & Zee, 1999) and the abducting eye (moves away from the nose) seem to have higher peak velocities than the adducting eye (moves towards the nose) (Collewijn, Erkelens & Steinman, 1988). When people fixate on a target (e.g. on a computer screen) and a stimulus appears to the right of the fixation point and they saccade to the stimulus they are making a prosaccade. If the stimulus appears 8° to the right of the fixation point then the amplitude of the saccade is 8°. An antisaccade is a saccade in opposite direction to the prosaccade; i.e. in this case the task is to make a saccade to the left of the fixation point and of the same amplitude as the prosaccade or 8° to the left. The latency of antisaccades is usually longer than of prosaccades (but see Kristjánsson, Chen & Nakayama, 2001; Kristjánsson, Vanderbroucke & Driver, 2004; and Liu et al. 2010) and people tend to make more errors on antisaccades than prosaccades but the difference decreases with practice (Leigh & Zee, 1999). The duration of the saccades are too short for visually guided information to influence a planned saccade but if the information reaches the saccadic system before the eye starts to move the saccade can be modified after it's initiation (Leigh & Zee,

1999; Ludwig, Mildinhall & Gilchrist, 2007). It seems therefore, that the saccades are not always completely ballistic.

Another type of eye movement, which also keeps the target at the fovea, is the smooth pursuit movement. Saccades have high velocity and short duration and their role is to move the eye quickly from one position to another to keep the target on the fovea. The role of smooth pursuit is also to keep the target at the fovea but smooth pursuit is a continuous movement that follows the velocity and direction of the moving target. The latency of smooth pursuit is shorter than of saccades and a typical latency is between 100 and 130 ms (but can be as low as 70 ms; Leigh & Zee 1999). In smooth pursuit the eye follows the target almost perfectly up to a velocity of 20°/sec with a ratio of 0.9 to 1.0 between the target's and the eye's velocity (Barnes, 2011). At the initiation of the smooth pursuit the eye tends to overshoot the target's position and velocity but after a very short time the eye follows the target closely, even if the target disappears for a moment. When the target stops, the velocity of the eye declines and the duration of the negative acceleration is rather constant (around 90 ms). The maximum velocity of the smooth pursuit is about 95°/sec and if the eye has to follow a target with higher velocity the eye does it with saccadic movements (Leigh & Zee, 1999). The latency of smooth pursuit is probably too short for visual perception to guide the direction and velocity of the movement at the onset of the smooth pursuit. But the ganglion cells of the retina send information about motion to the nucleus of the optic tract (NOT; and to the lateral geniculate nucleus, LGN) and from there through the pontine nuclei and the inferior olive to the ocular motor neurons (Leigh & Zee, 1999). It is likely that the necessary information for the onset of the smooth pursuit is mediated through this pathway. After the onset of smooth pursuit the movements are visually guided and information from the retina travels from the LGN to the striate cortex, middle temporal visual area (MT), medial superior temporal visual area (MST), and to the frontal and supplementary eye fields (FEF and SEF) which both interact with MT and MST. Signals from FEF, SEF, MT and MST are combined in the pontine nuclei and from there they go to the cerebellar cortex and through few other brain areas to the ocular motor neurons (Leigh & Zee, 1999).

The neurology of saccades

The eye rotates around three axis, two of them are horizontal and one is vertical, the z-axis. The one horizontal axis, the x-axis, is ventral-dorsal and the other one, the y-axis is medial-lateral. The eye is rotated by six muscles in three pairs, one pair for horizontal movements only (the medial rectus and lateral rectus) but the other two pairs work together in a complicated way to control vertical movements and rotation around the x-axis (Kandel et al., 2000). Together those six ocular muscles can induce saccades in any direction and all obey similar principles and therefore we will take a look at the horizontal saccades (around the z-axis). The lateral rectus gets its signals through the abducens nerve (cranial nerve VI) from a nucleus in the brain stem and the medial rectus gets its signals through the oculomotor nerve (cranial nerve III) from the midbrain (Kandel et al., 2000). When making a saccade to a target in the periphery the amplitude of the target seems to be converted to peak velocity and a command – the pulse command – is sent to the lateral rectus, which then pulls on the eye and the result is a positive acceleration until the eye reaches the desired peak velocity. When the lateral rectus stops pulling the eye a negative acceleration begins and the eye comes to a stop – there is, in other words, no active braking of the eye's movement. At this time both the lateral rectus and the medial rectus are commanded, by the step command, to adjust their pulling force to the eye so the eye is kept in the new position (Leigh & Zee, 1999). The pulse and the step commands come from the brainstem where the motor circuits for the saccades are located (Kandel et al., 2000).

The neurons in the motor circuits for the saccades can be divided into two main groups, omnipause neurons (OPNs) and burst neurons (BNs). The BNs can be further divided into three groups, excitatory burst neurons (EBNs), inhibitory burst neurons (IBNs) and long-lead burst neurons (LLBNs). Those four types of neurons all play different roles in the generation of saccades. During fixation the OPNs are active but they are silent during a saccade. The BNs start firing about 12 ms prior to the saccade and are active during saccade, but silent under fixation. When the eyes are to be rotated to the right, the OPNs stop firing and the EBNs (in the paramedian pontine reticular formation, PPRF) send excitatory signals (the pulse) to the lateral rectus of the right eye and the medial rectus of the left eye and the muscles contract and rotate the eyes. At the same time the IBNs (in the rostral medulla) send inhibitory signals to the medial rectus

of the right eye and the lateral rectus of the left eye. It is assumed that the OPNs synchronize the activity of the IBNs and EBNs before the saccade starts and it is important for the velocity of the of the saccade that the lateral and medial rectus of the left and right eyes, respectively, are inhibited before the pulling recti starts to rotate the eyes. LLBNs in the midbrain receive projections from the superior colliculus (SC) and project to OPNs, IBNs and EBNs. The LLBNs start firing about 40 ms before the saccade begins. At the end of the saccade the fixation neurons in the rostral pole of SC start firing at a higher rate than before the saccade (at least higher for the neurons that signal the medial and lateral rectus in previous example) to keep the eyes in the chosen position; this is the *step* part of the saccade (Leigh & Zee 1999).

There is good evidence indicating that the SC plays a large role in the saccadic system. The SC receives direct input from the retina and in SC's dorsal superficial layers is a retinotopic map but more ventral is what Leigh and Zee (1999) call "motormap". The SC also receives direct input from the parietal eyefield (PEF), the frontal eyefield (FEF) and the supplementary eye field (SEF). The FEF and SEF projects to the caudate nucleus which projetcs to substantia nigra pars reticulata (SNr, a part of basal ganglia) which in turn projects to the SC (Leigh and Zee, 1999) and therefore the FEF and SEF seem to have both direct and indirect projections to the SC. The projections from SNr to SC are inhibitory and are believed to play an important role in controlling the saccadic EBNs (White and Munoz, 2011). The superior colliculus projects directly to the motor circuit for the saccades and to the intramedullary lamina of the thalamus. There are connections between the retinotopic map and the motormap in the SC but connections to the motormap from cortical areas (e.g. parietal cortex and the frontal lobes) seem to be more important.

The ventral layers of SC contain buildup neurons, the previously mentioned fixation neurons, and more rostrally are collicular-burst neurons (CBNs). During a saccade there is more activity on the motormap where the target is coded than in other areas on the motormap. This increased activity is also seen in the CBNs and is in good accordance with where the neurons on the motormap are most active. This leads to the conclusion that this is where the amplitude and direction of the saccades is encoded (Leigh & Zee, 1999) and this might be mediated through the SC's projection to LLBNs.

The FEF and SEF are indirectly connected to the saccadic generator through nucleus reticularis tegmenti pontis (NRTP) and the cerebellum but seem also to have weaker but nevertheless direct connections to the generator. It has been shown that saccades can be made without the SC or without the FEF but not without both the SC and FEF. Therefore neither the SC nor the FEF are necessary for the saccades. The FEF seems to be involved in voluntary saccades because neurons in it show activation related to both direction and amplitude of voluntary saccades. The FEF also contains neurons that are active in relation to memory-guided saccades (saccades made to a remembered non-visible position). FEF neurons may participate in selection of the target and in scanning of visual scene and the FEF also contain neurons that encode the target and the saccade to it. The function of the SEF seems to be similar to the function of the FEF but might be more involved with some learned saccadic tasks, such as the antisaccade task and memory guided saccades (Leigh & Zee, 1999).

The superior colliculi appear to play a key role in the generation of reflexive saccades while for voluntary saccades the frontal eyefield plays a vital role. There are, however many other brain areas that contribute to the generation and programming of the saccades.

Naso-temporal asymmetry

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 Schmidt (1988) showed that for the central 10° of the retina Vernier acuity declines rather symmetrically but at higher eccentricities there is a quite pronounced nasal-temporal asymmetry (NTA) in acuity. 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. 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, not in the lateral geniculate nucleus nor 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 in the literature 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. Another intriguing result is that hemianopes could use distractor signals in the blind half of the 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 centers.

In another example, Rafal et al. (1991) measured attentional benefits from valid cues and costs from invalid cues and found that both effects were stronger for cues presented 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 seemingly 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, considering the tight coupling between attentional orienting and saccadic eye movements (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 in the nasal hemiretina (which receives visual input from the temporal hemifield) the well-known relationship between attention and saccades might 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 superior colliculus, 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) found an NTA in prosaccade and antisacade latency such that saccades towards temporal stimuli were faster. Walker et al. (2000) also found evidence of faster saccades towards temporal stimuli but only under attentional load. Another example is that when distractor stimuli are presented simultaneously contralateral to a target stimulus, 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 hemifields 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 if they exist at all. 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 towards and away from the midline as well as sweeping 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, while in experiment 6 we tested high amplitude saccadic eye movements. We report latencies and landing point accuracy of the saccades.

General methods

Six within-subject design experiments were conducted. In experiments 1 and 2 observers tracked a stimulus jumping unpredictably between locations and the saccades were of two different amplitudes (5°) and (10°). In experiment 1 only the movement of the dominant eye 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 landing points (at screen center and 5° towards right or left). The observers never knew which would be the upcoming landing point. This entailed, however, that when observers fixated on the left or right stimulus, they always knew the direction of the upcoming saccade (if not the amplitude) possibly influencing performance. This possibility was eliminated in experiment 2 by adding stimuli to the left and right of the peripheral stimuli from experiment 1 (stimuli 4 and 5 in figure 1A). In experiments 3, 4 and 5 the observers performed 8° saccades unpredictably towards the left or right while in experiment 6 they performed 20° saccades. 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 1750 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 grey background (<1 cd/m^2; RGB = [0 0 0][1]).

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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.
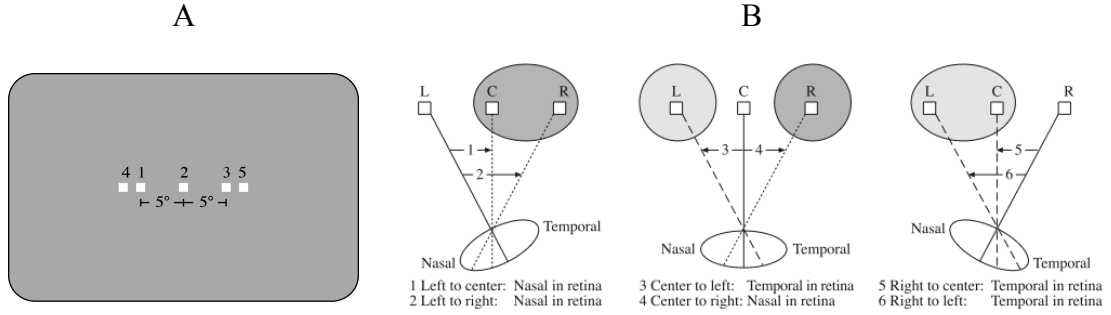
Figure 1. Experimental setup and the different possible movement types tested in experiments 1 and 2. Panel A shows the possible landing points in experiment 1 (positions 1, 2 and 3) and experiment 2 (positions 1 through 5). The stimulus that the observers were instructed to follow appeared randomly in positions 1, 2 or 3 while in experiment 2 the stimulus could appear in positions 4 and 5 as well. Panel 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

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° from Cambridge Research Systems was used. To find the direction of the observer's gaze the eyetrecker 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: 1140 x 900 px) while in experiments 3 to 5 on a 100 Hz 19" Hansol CRT monitor (model: 920D resolution: 800 x 600 px). To maintain the same viewing distance in experiment 6 where large amplitude (20°) eye movements were tested, the stimuli were displayed on a 60 Hz 24" Dell LCD monitor (model: 2407WFP, resolution 1920 x 1200 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[2] extension used to display the stimuli and functions from the eyetracker toolbox[3] 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 when 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). 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).

Statistical analyses

In all experiments mean latency and landing point accuracy for each participant were calculated for each task. Trials with latencies shorter than 80 ms were excluded from all analyses. Latencies or landing point values that deviated more than 3 SD from the mean for each observer were removed before analysis. To compare different task types in each experiment repeated measure ANOVAs and Mauchly's Test of Sphericity were used. When appropriate the degrees of freedom were corrected (Greenhouse-Geisser) and post-hoc comparisons were made with Bonferroni corrected *p*-values. For experiments 2 through 6, the left and right eyes were compared and the dominant and non-dominant eyes to find out if there are 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.

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[2] Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997; Kleiner et al. 2007).
[3] Video Eyetracker Toolbox, version 3.11. Cambridge Research Systems Ltd.

Experiment 1

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 to 1.33 Hz (randomly decided on each trial) between three different locations at left, right or centre (see figure 1A). The fixation point moved between locations. 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 female; 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/m^2; RGB = [255 255 255]) with a smaller dark grey square (<1 cd/m^2; RGB = [0 0 0]) in the middle appeared at the center of the screen. At a random interval varying from 750 ms to 1750 ms (a rate of 0.57 Hz to 1.33 Hz) this stimulus appeared randomly either 5° to the left or the right of centre. On subsequent trials, the stimulus appeared randomly at the central (1/3 of trials), left (1/3 of trials) or right position (1/3 of trials) but never twice in a row in the same position, see figure 1A. This means that there were six possible movement types (see figure 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 to 939 trials were analysed 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 figure 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

towards temporal stimuli (movement type 2) was 156 ms (SD = 8.7 ms), towards 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 (2x2 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.

Landing point accuracy. There were no outliers in the landing point data and 833 to 943 trials were analysed 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 centre were also hypometric, landing left of the central stimulus when saccading from the left and right of it when saccading from the 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 2x2 ANOVA to find out if there was an interaction between the amplitude (short versus long) and hemifield (nasal versus 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 the low-amplitude saccades was 0.95° (SD = 0.51°) and for the 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 in the latency results were that high amplitude sweeping saccades from one visual field to the other across the midline had shorter latencies than low-amplitude saccades and landing point accuracy was better for low- than for high-

amplitude saccades. Experiment 2 is similar in nature to experiment 1, except that there we deal with a possible confound from experiment 1.

Experiment 2

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. Experiment 2 was therefore similar to experiment 1 except that the possible landing positions were 5 rather than 3. We only analyzed the data for the three central positions, while the two most lateral positions were used to eliminate the possibility of directional motor preparation since the upcoming saccade direction was never predictable.

Method

 Participants and procedure. Six volunteers participated (3 female; 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 ($\approx$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 landing points at left and right, methods were identical to those described for experiment 1. On subsequent trials, the stimulus appeared randomly at positions 1 to 5 (1/5 of trials each), but never twice in a row in the same position, see figure 1A.

Results

All trials where stimulus position was either 4 or 5 (38.6% of the data; see figure 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 to 278 trials were analysed 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) and 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 towards temporal stimuli (movement type 2) was 158 ms (SD = 5.2 ms), while towards nasal stimuli (movement type 6) it was 156 ms (SD = 6.1 ms) and no significant difference was found ($F(1, 4) = 5.843$, $p = .073$). In a 2x2 ANOVA comparing low versus high amplitude and hemifield, the main effect of amplitude was significant ($F(1, 4) = 23.511$, $p = .008$) but there was no main effect of hemifield ($F(1, 4) = 1.119$, $p = .350$) and no interaction ($F(1, 4) = 0.007$, $p = .939$). The latency of high-amplitude saccades was 157 ms (SD = 5.4 ms) and for low-amplitude saccades it was 169 ms (SD = 10.2 ms).

Landing point accuracy. There were no outliers in the landing point data and 253 to 286 trials were analysed 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 the temporal stimuli was 0.47° (SD = 0.24°) and for the 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 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 2x2 ANOVA the main effect of amplitude was close to significance ($F(1, 4) = 7.188$, $p = .055$) 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 6 we will search for NTAs in saccade

performance using more traditional saccade tasks, including some attentional manipulations.

Experiment 3

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 to 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 add attentional manipulations.

Method

Participants. Ten volunteers participated (5 female; 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 grey (<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 grey (<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 (at a random timepoint between 750 and 1350 ms) 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 latency analyses (0.7% of the data) and 92 to 102 trials were analysed for each participant dependent on 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. There were no outliers in the landing point data and 92 to 102 trials were analysed for each participant dependent on error rate. Once again, 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 towards an NTA in accuracy as 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[4] 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).
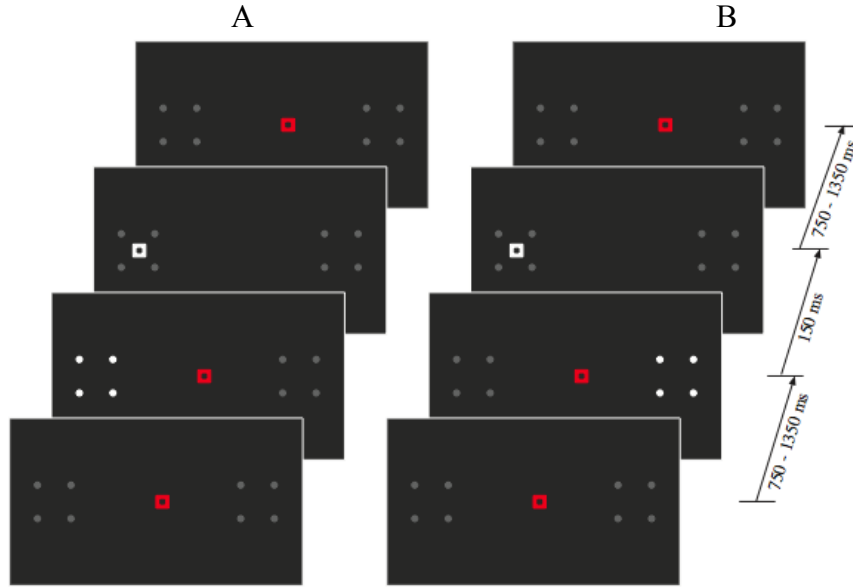
Experiment 4

Method

Participants. 14 volunteers participated (8 female; 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 was excluded because of high error rates (>20%). Of those 9 remaining participants 2 had left eye dominance.

Stimuli. The central fixation and target stimuli were the same as in experiment 3. Four dark-grey dots forming an illusory square (2.8° x 2.8°; 1 cd/m^2; 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 the placeholder on one side briefly brightened up (from 1 cd/m^2 to 39 cd/m^2) (see figure 2).

Procedure. At the beginning of each trial a fixation stimulus was displayed at screen center along with the placeholders (see figure 2). After observers' fixation was confirmed and following a random interval between 750 and 1350 ms, 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.

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[4] 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.

Figure 2. The procedure in experiment 4. Panel A shows the procedure in the valid cue condition while panel B shows the procedure in the invalid cue condition

Results

Trials with latencies shorter than 80 ms (2.4% of the data and all towards 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 towards an invalid cue: 48.5% towards a nasal cue and 38.6% towards 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 which deviated more than 3 SD (0.8%) from the mean were not included in the latency analyses and 258 to 301 trials trials for each observer were analysed depending on their error rate. The average latency for temporal stimuli with a valid cue was 234 ms (SD = 13.4 ms) and for the nasal stimuli with a valid cue it was 232 ms (SD = 15.7 ms). This 2 ms difference was not significant ($F(1, 8) = 0.865$, $p = .380$). For the invalid cue the average latency for temporal stimuli was 229 ms (SD = 25.0 ms) and 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. There were no outliers in the landing point data and 259 to 302 trials for each observer were analysed depending on their error rate. The saccades

were again hypometric on average. In the valid cue condition the saccades towards temporal stimuli deviated from the landing point by 0.43° (SD = 0.81°) and the saccades towards 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 was some evidence that the saccades towards nasal stimuli are more hypometric than to temporal stimuli. When the cue was invalid, the landing points were also hypometric on average. Landing point deviation towards temporal stimuli was 0.58° on average (SD = 0.90°) and towards nasal stimuli it was 0.83° (SD = 0.54°). This NTA (0.25°), was not significant ($F(1, 8) = 0.526$, $p = 0.489$).

Experiment 5

Method

   Participants. The participants were the same 14 volunteers as in experiment 4. Data from five participants (not the same as in experiment 4) was 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 grey (2 cd/m^2; RGB = [60 60 60]) and light grey (3 cd/m^2; 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 figure 3). At the end of each trial a response display was presented in the same position as the discrimination stimuli (see figure 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.
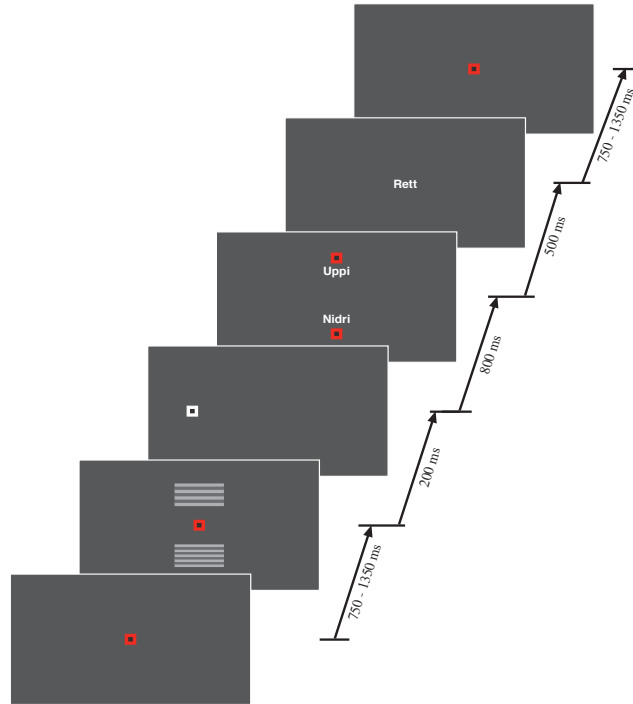
Figure 3. The procedure in experiment 5. The target stimulus was displayed randomly to the left or right of central fixation and the target rectangle with the lower spatial frequency appeared randomly above or below the fixation stimuli while the distractor rectangle (of higher spatial frequency) appeared in the other location.

Procedure. The target rectangle was the one of lower spatial frequency and it appeared at random above or below fixation (and the higher spatial frequency square appeared in the other position). When the saccade target appeared (randomly to the right or left of the fixation stimulus) the discrimination stimuli disappeared followed 800 ms later by the response stimuli. The participants were supposed to shift their gaze towards the appropriate response stimulus (above or below the words) indicating whether the low spatial frequency target was above or below fixation. Eight observers participated in 3 blocks of 50 trials and 1 observer 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 to the discrimination task (5.6% of the data) were not analyzed.

Latency. Trials with latencies larger than 3 SD from the mean were excluded from latency analyses (3.6% of the data) and 192 to 291 trials for each observer were analysed depending on their error rate. 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, $p = .105$).

Landing point accuracy. There were no outliers in the landing point data and 195 to 300 trials for each observer were analysed depending on their error rate. For trials with correct responses on the discrimination task the saccades were hypometric. 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 experiment 3 to 5 reveal little evidence for any NTA in saccade performance, certainly not for latency, while there is some trend for saccades towards nasal stimuli being more hypometric than towards temporal stimuli, in line with the effect seen in experiment 2. The evidence for this potential NTA cannot be considered strong, however.

Experiment 6

Apart from the evidence from experiment 2 (and some tendency in experiments 1, 3, 4 and 5) that saccades into the nasal hemifield are more hypometric than saccades into the temporal hemifield, we have so far found little nasal/temporal asymmetries in saccade performance. Our final test was inspired by reported differences in cone and ganglion density between the two hemifields. As eccentricity from the fovea increases, 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 figure 6A and 6C). 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°) than in previous tests here.

Method

    Participants. Five volunteers participated (4 female, 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 response time shorter than 80 ms (0.3% of the data) and trials with 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 to 513 trials for each observer were analysed dependent on error rate. 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. There were no outliers in the landing point data and 462 to 519 trials for each observer were analysed dependent on error rate. For both nasal and temporal stimuli the saccades were hypometric. The average deviations for nasal and temporal stimuli were identical, 2.74° (SD = 1.74°) for temporal stimuli and 2.74° (SD = 1.10°) for the nasal stimuli.

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

Peak velocity

The peak velocity of the saccades increases as the amplitude of it gets higher. This linear relationship between amplitude and peak velocity (called *the main sequence*) is well known (Bahill et al., 1975; Leigh & Zee, 1999) but as far as we know comparisons of peak velocities between nasal and temporal stimulation have not been made. Here we report our investigation of peak velocity based on the data we collected in the six experiments described above.

Peak velocities in experiment 1. Trials with peak velocities more than 3 SD from the mean were excluded from velocity analyses (32 trials; 0.9% of the data). For low-amplitude saccades the peak velocity towards temporal stimuli was 216.3°/sec (SD = 61.7°/sec) and towards nasal stimuli it was 213.9°/sec (SD = 32.8°/sec). The peak velocity for the high-amplitude saccades towards temporal stimuli was 292.2°/sec (SD = 53.0°/sec) and towards nasal stimuli it was 291.5°/sec (SD = 35.2°/sec). Neither of the above differences were significant (both *F*-values < 0.1) When short versus long and nasal versus temporal saccades were compared (2x2 ANOVA) the main effect of amplitude was significant ($F(1, 5) = 219.460$, $p < .001$) but there was no main effect of hemifield ($F(1, 5) = 0.024$, $p = .884$) nor was there an interaction ($F(1, 5) = 0.031$, $p = .868$). The peak velocity for high-amplitude saccades was 291.86°/sec (SD = 42.88°/sec) and for low-amplitude saccades it was 215.11°/sec (SD = 47.16°/sec). This is of no surprise because higher amplitude of the saccades leads to higher peak velocity of it and is in line with the "main sequence" (Bahill et al., 1975; Leigh & Zee, 1999).

Peak velocities in experiment 2. Trials with peak velocity more than 3 SD from the mean were excluded from velocity analyses (0.1% of the data). For low-amplitude saccades the peak velocity towards temporal stimuli was 215.2°/sec (SD = 47.6°/sec) and towards nasal stimuli it was 195.6°/sec (SD = 45.7°/sec). The difference was 19.6°/sec and significant ($F(1, 4) = 124.760$, p < .001). The peak velocity for the high-amplitude saccades towards temporal stimuli was 306.8°/sec (SD = 42.8°/sec) and towards nasal stimuli it was 284.4°/sec (SD = 47.4°/sec). The difference was 22.4°/sec and significant ($F(1, 4) = 70.742$, $p = .001$. When short, long, nasal and temporal saccades were compared (2x2 ANOVA) the main effect of amplitude and hemifield was significant ($F(1, 4) = 498.770$, $p < .001$; $F(1, 4) = 158.210$, $p < .001$) respectively but there was no interaction ($F(1, 4) = 0.877$, $p = .402$). The peak velocity for high-

amplitude saccades was 295.59°/sec (SD = 44.21°/sec) and for low-amplitude saccades it was 205.41°/sec (SD = 45.19°/sec). The peak velocity for saccades towards temporal stimuli was 260.99°/sec (SD = 64.45°/sec) and for saccades towards nasal stimuli it was 240.00°/sec (SD = 64.15°/sec).

Peak velocity in experiment 3. Trials with peak velocity more than 3 SD from the mean were excluded from velocity analyses (0.8% of the data). The peak velocity for saccades towards temporal hemifield was 357.88°/sec (SD = 62.11°/sec) and for saccades towards nasal hemifield it was 324.67°/sec (SD = 51.19). The difference, 33.21°/sec was significant ($F(1, 9) = 12.932, p = .006$).

Peak velocities in experiment 4. Trials with peak velocity more than 3 SD from the mean were excluded from velocity analyses (0.6% of the data). The peak velocity of saccades towards temporal stimuli in the valid cue condition was 373.48°/sec (SD = 58.21°/sec) and of towards nasal stimuli it was 344.65°/sec (SD = 53.26°/sec (SD = 53.26°/sec). The difference was 28.83°/sec and was close to significant ($F(1, 8) = 4.571$, $p = .065$). For the invalid cue the peak velocities towards nasal and temporal targets were 349.00°/sec (SD = 53.33) and 374.16°/sec (SD = 55.66°/sec), respectively. The difference was 25°/sec and almost significant ($F(1, 8) = 5.120, p = .054$).

Peak velocities in experiment 5. Trials with peak velocities more than 3 SD from the mean were excluded from velocity analyses (0.3% of the data). The peak velocity of saccades in response to temporal stimuli was 351.06°/sec (SD = 42.99°/sec) and for saccades in response to nasal stimuli it was 334.94°/sec (SD = 49.91°/sec) when the answers to the discrimination task were correct. The difference was 16.12°/sec and not significant ($F(1, 8) = 2.044; p = .191$).

Peak velocities in experiment 6. Trials with peak velocities more than 3 SD from the mean were excluded from velocity analyses (1.5% of the data). The peak velocity towards temporal stimuli was 518.01°/sec (SD = 91.14°/sec) and towards nasal stimuli it was 506.65°/sec (SD = 112.1°/sec). The difference was 11.36°/sec and not significant ($F(1, 4) = 0.724, p = .443$).

As expected the peak velocity of saccades with higher amplitude (10°) in experiments 1 and 2 was significantly higher than of saccades with lower amplitude (5°). The peak

velocity of saccades in experiment 6 (20°) was also significantly higher than of saccades in experiment 3 (8°). These results are in good accordance with "the main sequence". What is of more interest is the difference we found between peak velocity of saccades towards nasal and temporal stimuli in experiments 2 and 3 with higher peak velocity of saccades towards temporal stimuli. The same trend was observed in all the other experiments and in experiment 4 this difference was very close to significance whether the cue was valid or invalid.

In the experiments described above, we measured eye movements monocularly but Collewijn et al. (1988) concluded that there is only a minimal difference between the main parameters of the saccades whether the target was viewed mono- or binocularly. According to Collewijn et al. (1988) we might expect to find higher peak velocity when saccading towards stimuli presented in the temporal hemifield (abducting movement) than towards stimuli presented in the nasal hemifield (adducting movement) but in some types of movement the effect of centripetal and centrifugal might influence this assumption. In experiments 1 and 2 the high amplitude saccades included centripetal and centrifugal movements and were either abduction or adduction movements (movement 2 and 6 in figure 1, respectively). The data for low amplitude saccades towards stimuli in the temporal hemifield (movements 1 and 4 in figure 1) and low amplitude saccades towards stimuli in the nasal hemifield (movements 3 and 5 in figure 1) included both centripetal and centrifugal moments. We might therefore expect the effect of centripetal and centrifugal to be minimal. For both low and high amplitude saccades the peak velocity towards stimuli in the temporal hemifield was significantly higher than towards stimuli presented in the nasal hemifield. In experiments 3 through 6 the saccades were centripetally and either abducting (saccades towards stimuli in the temporal hemifield) or adducting (saccades towards stimuli in the nasal hemifield). In experiment 3 the peak velocity was significantly higher towards stimuli in the temporal hemifield than towards stimuli in the nasal hemifield, in experiment 4, both conditions, this difference was close to significant and the trend in peak velocity in experiments 5 and 6 was in the same direction. The results suggest there might be some performance asymmetry in peak velocity of the saccades between nasal and temporal hemifields.

General Discussion

There are enticing reasons to predict differences in saccade characteristics depending on whether the stimuli project to the nasal or temporal hemifield. 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 internally 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), 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 trends in experiments 1, 3, 4 and 5) where landing point accuracy was higher for temporal stimuli (they were less hypometric than saccades towards nasal stimuli). This very modest evidence for any saccadic 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 towards 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 NTA's in attentional function do not result in corresponding saccade latency.

One cue towards why NTAs 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 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 (Seagraves and Goldberg 1987). According to Sommer and Wurtz (2000) the corticotectal 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 $\approx 10\%$ 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 are not as unitary as sometimes thought (see also Schall et al. 2004 and discussion in Kristjánsson 2011).

Conclusions

We conclude that NTAs are generally not seen for saccades except maybe 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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