

The spatio-temporal tuning of the mechanisms in the control of saccadic eye movements

Brian J. White^{a,*}, Dirk Kerzel^b, Karl R. Gegenfurtner^a

^a *Justus-Liebig-Universität Giessen, Allgemeine Psychologie, Otto-Behaghel-Str. 10F, D-35394 Giessen, Germany*

^b *Université de Genève, Uni Mail, FaPSE 40 bd du Pont d'Arve, CH-1205 Genève, Switzerland*

Received 2 March 2006; received in revised form 16 June 2006

Abstract

We compared the spatio-temporal tuning of perception to the mechanisms that drive saccadic eye movements. Detection thresholds were measured for Gabor-targets presented left or right of fixation (4 or 8 deg eccentricity), at one of four spatial frequencies (1, 2, 4 or 8 cpd) oscillating at one of three temporal frequencies (1, 8 or 16 Hz). We then measured saccade latency to each target presented at various multiples of detection threshold. Consistent with previous research, latency decreased as a function of contrast. However, at equal detection performance, we found no systematic difference in saccadic latency and no difference in average oculometric performance (% correct saccade direction) across the different target spatio-temporal frequencies. Furthermore, position error remained fairly constant across all conditions. The results are consistent with the idea that the spatio-temporal signals used for perception are the same as those used by the mechanisms driving saccadic eye movements.

© 2006 Elsevier Ltd. All rights reserved.

Keywords: Saccade latency; Spatio-temporal tuning; Temporal frequency; Spatial frequency; Contrast sensitivity

1. Introduction

The patterns of light that enter our eyes during everyday vision are filled with spatio-temporal variation. Because of factors related to both the optics of the eye (Williams, Brainard, McMahon, & Navarro, 1994) and the brain, contrast sensitivity varies as a function of spatio-temporal frequency (e.g., Kelly, 1979) and retinal eccentricity (e.g., Rovamo, Virsu, & Nasanen, 1978; Wright & Johnston, 1983). The spatio-temporal tuning of neurons at different levels of visual processing is well established (e.g., De Valois, Albrecht, & Thorell, 1982; Derrington & Lennie, 1984; Merigan & Maunsell, 1993). However, much less is known about the nature of the visual signals driving the motor system. In terms of saccades, the superior colliculus (SC) and frontal eye fields (FEF) depend on inputs from visual areas that

convey selectivity for features like orientation and color, since visually responsive neurons in the SC and FEF are not believed to be selective for visual features (Bruce & Goldberg, 1985; Robinson & McClurkin, 1989). The question this paper addresses is to what degree do the visuomotor and perceptual systems use the same spatio-temporal signals.

The delay between the appearance of a peripheral target and the onset of a saccade (saccade latency) represents the sum of the visuomotor processes underlying the movement (Findlay & Gilchrist, 2003). Along these lines, saccade latency has been modeled as a decision signal that rises to some response threshold (LATER Model, Carpenter, 1988), at a rate that is influenced by both goal-driven (prior expectations) and stimulus-driven (accumulation of sensory information) factors, the latter of which is the focus here.

Saccade latency has been of considerable interest for several reasons: It can reflect underlying neuronal latencies, and can be indicative of different mechanisms driving the

* Corresponding author. Fax: +49 641 9926119.

E-mail address: brian.j.white@psychol.uni-giessen.de (B.J. White).

movements (e.g., “express saccades” as revealed by a bimodal latency distribution, see Fischer & Ramsperger, 1984). Latencies have also been used to examine the influence of distractors (Trappenberg, Dorris, Munoz, & Klein, 2001; Walker, Deubel, Schneider, & Findlay, 1997; Weber & Fischer, 1994; White, Gegenfurtner, & Kerzel, 2005), and the competition between stimulus-driven (“bottom-up”) and goal-driven (“top-down”) control (Ludwig & Gilchrist, 2002). Furthermore, latencies can be used to investigate the sensitivity of the oculomotor system to various target properties such as contrast (Doma & Hallett, 1988), retinal eccentricity (Kalesnykas & Hallett, 1994), and spatial frequency (SF) (Ludwig, Gilchrist, & McSorley, 2004). For example, Ludwig et al. (2004) reported that, at any given multiple of contrast threshold, targets of low spatial frequency (1–2 cpd) triggered saccades with somewhat shorter latencies than targets of high spatial frequency (8–16 cpd). Earlier studies also reported longer manual reaction times to foveally presented gratings of higher relative to lower spatial frequency (Breitmeyer, 1975; Lupp, Hauske, & Wolf, 1976).

One difficulty in interpreting latency differences between stimuli of different spatial frequency is that contrast sensitivity is not constant across spatial frequency and eccentricity (Rovamo et al., 1978; Wright & Johnston, 1983), and that saccadic latency is highly sensitive to differences in contrast (Doma & Hallett, 1988). If stimuli are not carefully controlled in terms of detection performance, it is difficult to rule out the contribution of contrast. Furthermore, at threshold, saccade latencies are unavoidably noisy, so it is essential to perform a detailed analysis around detection threshold.

Only one study (Ludwig et al., 2004) examined the influence of spatial frequency on saccadic latency. In this study the authors did not present targets specifically at threshold, but fit a Piéron function (Pins & Bonnet, 1996) to each observer’s raw latency data plotted as a function of contrast/contrast threshold (i.e., multiples of threshold). While the higher SF targets showed some deviation (elevation) from the function for two observers, Ludwig and colleagues noted that the data for the third observer in fact converged quite well into a single function ($r^2 = 0.79$ to 0.86 for individual target locations). Furthermore, it is quite remarkable that little difference was seen for spatial frequencies below 8 cpd for either observer. This suggests that, to a large degree, the spatio-temporal tuning for perception is the same for the mechanisms driving saccadic eye movements.

The aim of the current study was to test whether the mechanisms driving saccades do rely on the same spatio-temporal signals as perception, by (1) performing a more detailed examination around detection threshold, (2) by using a greater number of observers than in the Ludwig et al. (2004) study, and (3) by examining targets along the temporal frequency (TF) domain as well, since both spatial and temporal frequency selectivity are important attributes of primate and human visual systems (De Valois et al., 1982; Derrington & Lennie, 1984; Foster, Gaska, Nagler, &

Pollen, 1985). Furthermore, the transient versus sustained nature of the magno- versus parvo-cellular pathways has been a common explanation for differences in response latency (Breitmeyer, 1975; Legge, 1978; Murray & Plainis, 2003; Schwartz, 1992). Neurons in the magno-cellular layers of the LGN respond better to rapidly flickering low spatial frequency targets, whereas neurons in parvo-cellular layers can respond better to low temporal frequencies, and can resolve much higher spatial frequencies (Derrington & Lennie, 1984; Merigan & Maunsell, 1993). It was therefore in our interest to investigate both spatial and temporal target properties.

Thus, our predictions are as follows: If the mechanisms driving saccades do rely on the same spatio-temporal signals as perception, the pattern of saccadic latencies should reflect perceptual sensitivity. That is, at equal detection performance, latencies should be the same regardless of spatio-temporal frequency. Alternatively, if the systems rely on the output of different visual mechanisms, we should observe some systematic variation in latency as a function of spatio-temporal frequency. In addition, we measured saccadic position error. While position error is believed to be independent of latency (Becker & Jurgens, 1979; Findlay & Walker, 1999), a tradeoff may occur when targets are more difficult to detect (Coeffe & O’Regan, 1987), making it pertinent to the current study. We primarily wanted to ensure that accuracy was held constant when making a comparison between latencies. Finally, we also computed oculometric- and psychometric-performance (proportion correct saccade direction versus psychophysical detection) at threshold as a means of comparing the degree to which the systems use the same visual spatio-temporal signals for decision processes. A similar method has been used to compare saccadic- and perceptual-performance during visual search (Beutter, Eckstein, & Stone, 2003), the results of which support the idea that both systems use similar visual processing mechanisms for detection. If saccadic and perceptual decisions rely on the same spatio-temporal signals, oculometric and psychometric performance at threshold should not differ.

2. Methods

2.1. Observers

One of the authors plus five additional naïve observers took part in Experiment 1, and three additional observers took part in Experiment 2. All observers had normal or corrected to normal visual acuity. Observers ranged in age from 20 to 36 years of age. All observers received informed consent before participating, and all experiments followed the ethical guidelines of the Declaration of Helsinki.

2.2. Equipment

Stimuli were displayed on a 21 in. CRT monitor (ELO Touchsystems) driven by an ASUS V8170 GeForce 4 MX440 graphics board at a non-interlaced refresh rate of 100 Hz. The resolution of the monitor was set at 1280×1024 pixels, which corresponded to physical dimensions of 37 cm wide by 29.6 cm high. At a viewing distance of 47 cm, the display occupied

a retinal area of 45 deg horizontally and 36 deg vertically. Eye-movements were measured using EyeLink II (video-based tracker from SR Research Ltd., Mississauga, Ontario) at a sample rate of 250 Hz.

2.3. Stimuli

The target was a vertically oriented Gabor patch ($SD = 0.7$ deg), presented at one of four spatial frequencies (1, 2, 4 or 8 cpd), and oscillating at one of three temporal frequencies (1, 8 or 16 Hz). Targets appeared left or right of center at an eccentricity of 4 deg in Experiment 1, and 4 or 8 deg in Experiment 2. The central fixation stimulus was a black spot approximately 0.2 deg in diameter. Targets were presented on a neutral gray background with a luminance of 32 cd/m².

Because temporal frequency involves the modulation of contrast over time, targets of different temporal frequencies may become visible at different times (e.g., a 16 Hz target will reach peak contrast sooner than a 1 Hz target). This is an obvious difficulty when trying to compare latencies between targets of different temporal frequency. We dealt with this in two ways: for the primary experiment (Experiment 1), targets were onset at their maximum point of modulation for a given contrast, and the temporal oscillation continued from there for 500 ms. This produced an abrupt onset for all targets, which could drive transient mechanisms (Legge, 1978; Murray & Plainis, 2003), and possibly overshadow subtle differences from the target's actual temporal characteristics. A Fourier analysis revealed that only the 1 Hz target showed a significant amount of residual energy, but it was spread out over a large range of frequencies, with most of the energy around 1–2 Hz. A second experiment (Experiment 2) was run where we ramped the onset of the 8 and 16 Hz targets with the sinusoidal temporal contrast function of the 1 Hz target. Here, target duration was 1000 ms to deal with the fact that targets would become visible at a later time. At a monitor refresh of 100 Hz, the 1 Hz target lasted the duration of one complete cycle, and reached maximum contrast after 25 frames (250 ms), or one quarter of the entire cycle. The first quarter of the 8 and 16 Hz targets was multiplied with the first quarter of the 1 Hz sinusoid. So in essence, the 8 and 16 Hz targets retained their primary flicker frequency throughout the entire period. The only difference was their onset was essentially windowed by the 1 Hz contrast modulation. In this way, the time to reach maximum contrast was the same for all targets, 250 ms after initial onset. Analysis of the Fourier energy along the temporal domain showed negligible 1 Hz residual energy for the 8 and 16 Hz targets.

Typically saccade targets are presented with an abrupt onset. Given that response latencies have been attributed to the transient vs sustained nature of the magno- versus parvo-cellular pathways (Breitmeyer, 1975; Legge, 1978; Murray & Plainis, 2003; Schwartz, 1992), it was in our interest to perform tests using both abrupt and slower onset targets.

2.4. Procedure

2.4.1. Thresholds

We used a staircase procedure to determine contrast threshold for each of the 12 targets (4 SFs \times 3 TFs) in a 2-alternative forced choice (2AFC) procedure for Experiment 1 (left versus right), and a 4AFC in Experiment 2 (left-near, left-far, right-near, and right-far). Two staircases per stimulus were initiated, one at a log unit below the starting value, and one at a log unit above. Starting values were set relatively low such that stimuli were just visible. The staircase followed a 3-up 1-down rule yielding the 79% detection threshold (see Macmillan & Creelman, 1991): three correct responses in a row resulted in a contrast decrease of 1 log unit, and one incorrect response resulted in a contrast increase of 1 log unit. The threshold of each stimulus was the mean of eight reversal points (four for each staircase).

Note that eye movements were controlled using the EyeLink II tracker, and the head was stabilized by a chin rest. Calibrations were made before each block of trials (approximately every 50–100 trials), and consisted of fixating 9 consecutive bull's-eye stimuli at various locations on the screen. Average spatial accuracy for each calibration was maintained at 0.35 deg or better.

The fixation stimulus was present before the trial was initiated. Observers had to fixate this stimulus, and then initiate the trial when they were ready by pressing a key on a game-pad. This allowed for a drift correction procedure at the start of each trial. In the event that observers were not fixating accurately (within 1 deg), an error-tone was presented, and the trial had to be reinitiated. If a saccade of greater than 1 degree was made during a trial, a visual and auditory warning was presented, and the trial was aborted with no change in the status of the staircase. This ensured that the resulting thresholds were not confounded by periodically fixating the target. This was aided by the presence of the fixation stimulus throughout the duration of a trial. The target was onset randomly between 800 and 1200 ms after a trial was initiated, and appeared left or right of fixation at an eccentricity of 4 deg in Experiment 1, and 4 or 8 deg in Experiment 2. The target remained present for 500 ms in Experiment 1, and 1000 ms in Experiment 2. All trials were randomly interleaved. Observers simply made a 2AFC (Experiment 1, left, right) or a 4AFC (Experiment 2, left-near, left-far, right-near, and right-far) as to the location of the target.

2.4.2. Eye movements

Once we determined thresholds, each stimulus was presented at various multiples of this during a separate session (0.8, 1, 2, 3, 4 or 10 \times threshold and 100% contrast in Experiment 1, and 1, 1.1, 2, 4 \times threshold and 100% in Experiment 2). Note that due to the inherent noise at threshold, observations from the two lowest contrasts (0.8 and 1 \times threshold for Experiment 1, and 1 and 1.1 \times thresh. for Experiment 2) were later pooled to increase the reliability of the mean at this level of visibility.

Observers were simply requested to make an eye movement to the center of the target when it appeared, and that both speed and accuracy are equally important. The stimulus presentation was identical to the threshold procedure above except that the fixation stimulus was removed at the same time the target was onset. As with the threshold procedure, after each trial, observers made a psychometric decision as to the location of the target by pressing the appropriate key. Eye position and event data were recorded, and all analyses were done offline.

2.5. Analysis

Saccadic latency was used as the primary indicator of the sensitivity of the saccadic system to different spatio-temporal frequencies. Latency was the time (in ms) between target onset and the onset of the first saccade. Saccades were detected by the EyeLink-II system at a velocity threshold of 30 deg/s or an acceleration threshold of 8000 deg/s². We also computed position error which was the Euclidean distance (unsigned) between the end point of the first saccade and the target center in degrees. We primarily wanted to ensure that position error was held constant when making a comparison between latencies. Furthermore, at low contrasts, if position error is large, it suggests that the saccade may not have been driven by the target (but might instead be a voluntary guess). We tried to rule out the contribution of such trials by computing latencies only for trials where position error was less than 2 deg. The same criterion was used by Ludwig and colleagues (2004). Finally, we also measured the proportion of correct saccade directions (oculometric performance) at psychophysical detection threshold to determine the degree to which saccadic and perceptual decisions rely on the same visual signals (i.e., with regard to spatial and temporal frequency). As mentioned earlier, Beutter and colleagues (2003) used a similar method to compare saccadic- and perceptual performance during visual search, and argued that both systems use similar mechanisms for visual detection. For our purposes, this method simply provided an additional dimension for comparing both systems.

Observers completed approximately 1500 trials each in Experiment 1, and 1000 trials each in Experiment 2, with the exception of observers LP and NB in Experiment 1, and observer SO in Experiment 2 who completed just over 500 trials each. No outlier procedure was used, but we considered saccades with latencies less than 80 ms as anticipatory responses (see Wenban-Smith & Findlay, 1991). Trials with saccadic direction errors were also removed from the accuracy and latency analyses. With errors removed, the mean of each target condition consisted of 10–30 observations per observer (with the exception of observers LP, NB and SO who had somewhat fewer on some target conditions).

3. Experiment 1

3.1. Results and discussion

3.1.1. Proportion of errors

Table 1 shows the proportion of saccades and error trials at detection threshold. For brevity, the table shows threshold trials only since this is where most errors occurred. At detection threshold, the proportion of trials in which observers did not make a saccade was less than 25%, with the exception of observers MS and NB. This does not necessarily mean that detection performance was worse for these observers, but that their criterion for making a saccadic response may have been rather high. Note that the proportion of saccade direction errors (saccades in opposite direction to target) was computed from only those trials in which a saccade occurred because the number of direction errors out of the total trials would overestimate performance for those who made less saccades (especially observers MS and NB). To make detection performance comparable to this, it was also computed from saccade trials only. As such, direction and detection performance were quite similar (as seen in Table 1), and close to the predicted threshold performance based on the staircase rule (79%, see Section 2). Furthermore, a correlation between saccade direction errors and detection errors over trials was highly significant for each observer, $\Phi = 0.45$ to 0.77 , $p < .001$ in all cases. Note that except for observers NB and SW, the

proportion of inaccurate trials was low. Most removed trials were due to direction or detection errors at threshold. The last column represents the total proportion of saccade trials used at threshold (errors and inaccurate trials removed).

Fig. 1 shows the mean proportion of saccadic direction versus detection errors at threshold, as a function of target temporal frequency (left plot), and spatial frequency (right plot). The mean was around 25–30% (i.e., 70–75% correct) across all temporal and spatial frequencies, with only slightly higher direction versus detection errors overall, which may be due to the fact that saccades necessarily involve a speeded response, possibly making them more prone to direction errors. A 2×3 (error-type \times temporal frequency) and 2×4 (error-type \times spatial frequency) repeated measures ANOVA did reveal a small effect of error-type only ($F(1,5) = 9.8$, $p < .05$, and $F(1,5) = 9.7$, $p < .05$, respectively). However, F was less than 1 for all remaining effects, which means that oculometric- and psychometric-performance did not differ across spatial or temporal frequency. This supports the idea that saccadic and perceptual decisions rely on the same visual spatio-temporal signals.

3.1.2. Accuracy

As mentioned earlier, an accuracy-latency tradeoff may occur when targets are difficult to detect (Coffe & O'Regan, 1987). This analysis was performed to ensure there was no such tradeoff. A $2 \times 3 \times 4$ (2 contrasts \times 3

Table 1
Proportion of saccades, errors and used trials at detection threshold (Experiment 1)

Observer	Proportion saccades	Direction errors	Detection errors	Proportion correct	Inaccurate/anticipatory	Proportion used (<i>N</i>)
BW	0.89	0.34	0.24	0.64	0.04	0.61 (322)
LP	0.77	0.30	0.28	0.69	0.13	0.60 (87)
MS	0.57	0.29	0.23	0.67	0.06	0.63 (188)
NB	0.39	0.23	0.22	0.76	0.29	0.54 (54)
NZ	0.85	0.26	0.22	0.74	0.16	0.62 (188)
SW	0.76	0.12	0.09	0.88	0.24	0.67 (167)

The proportion of direction and detection errors was computed from trials with saccades only (first column). The proportion correct represents the saccade trials with no direction or detection errors, and the proportion used represents the correct trials (fourth column) that satisfied the inaccuracy/anticipatory criterion (see Section 2).

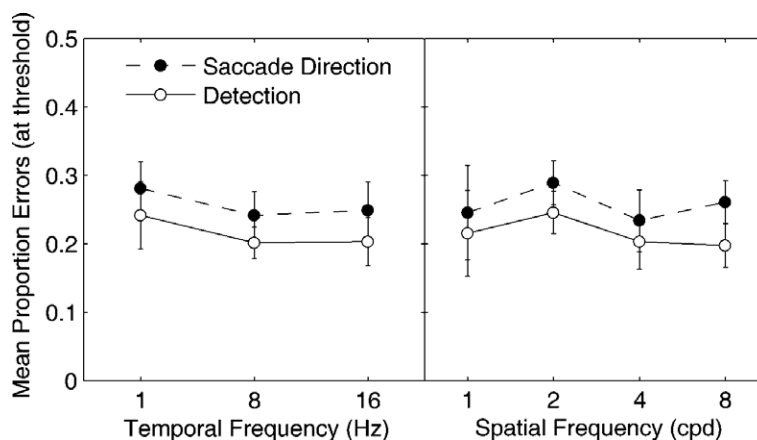


Fig. 1. Mean proportion of saccade direction errors and detection errors at threshold as a function of temporal frequency (left) and spatial frequency (right) (Experiment 1).

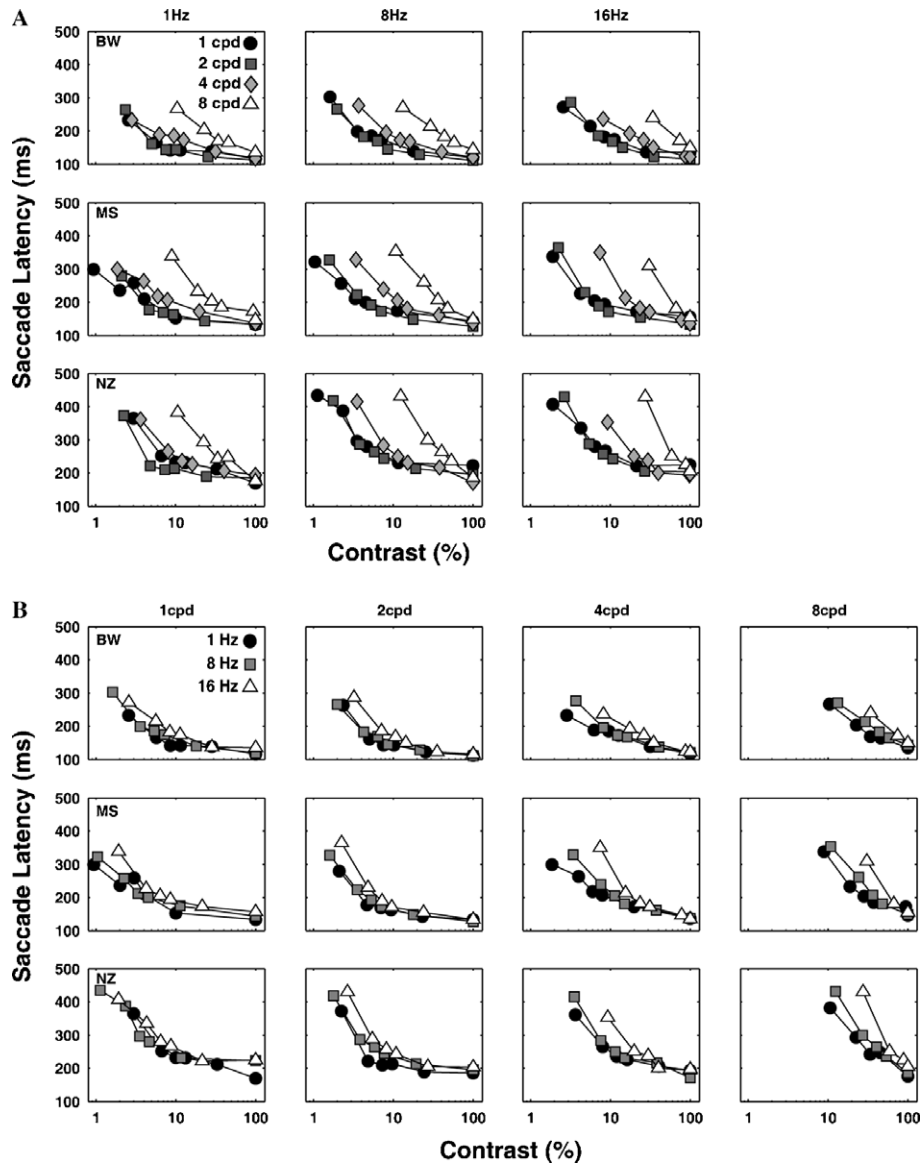


Fig. 2. Saccadic latency as a function contrast (log) for three representative observers (Experiment 1), plotted for comparison between spatial frequencies within a given temporal frequency (A), and between temporal frequencies within a given spatial frequency (B). Errorbars omitted for clarity.

TFs \times 4 SFs) repeated measures ANOVA was run on the data to test whether any differences exist between spatial or temporal frequency. We chose only the two lowest contrasts (threshold and twice threshold) because multiples of threshold greater than this were not possible for all observers on all targets, especially in terms of the high spatial frequencies.¹ If differences do exist, they should be more easily detected near threshold. The ANOVA revealed a small effect of SF ($F(3, 15) = 4.6, p = .017$) and a SF \times contrast interaction ($F(3, 15) = 4.4, p = .021$). No other effects were significant ($p > 0.3$ for all remaining tests). The effect of SF was due to slightly higher error for

1 cpd targets (0.51 deg) relative to 2 cpd targets (0.44 deg), $p < .05$, but no other differences were significant with a Bonferroni correction. In short, there was little difference in saccadic error across targets of different spatio-temporal frequency.

3.1.3. Latency

Fig. 2 shows saccadic latency as a function of contrast for three representative observers. Fig. 2A is plotted for comparison between spatial frequencies within a given temporal frequency, and Fig. 2B is for comparison between temporal frequencies within a given spatial frequency. The first thing to note is the predicted steady decrease in latency as a function of contrast. Second, consistent with the Ludwig et al. (2004) study, at a given contrast, latencies were longer at consecutively higher spatial frequencies (Fig. 2A). This was similar for the highest temporal frequency

¹ Because of limitations in the maximum contrast possible on CRT monitors, contrasts of more than $2 \times$ threshold were not always possible for all observers on all targets, especially in terms of the high spatial frequencies.

(Fig. 2B), but overall there was considerably more overlap between temporal frequencies. The results were similar for the other observers.

Fig. 3 shows the mean saccade latency of the six observers, plotted for comparison between spatial frequencies (top), and between temporal frequencies (bottom). As can be seen, latencies showed a steady decrease as a function of multiples of contrast threshold, but differences between spatial and temporal frequencies were much less evident here.

We ran a $2 \times 3 \times 4$ (2 contrasts \times 3 TFs \times 4 SFs) repeated measures ANOVA on the latency data. As with saccadic error, we chose only the two lowest contrasts (threshold and twice threshold) for the ANOVA because multiples of threshold greater than this were not possible for all observers on all targets. Furthermore, if any differences exist, they should be most detectable near threshold. The ANOVA revealed a strong effect of contrast ($F(1,5) = 54, p = .001$), and a TF \times SF interaction ($F(6,30) = 3.1, p = .017$). No other effects were statistically significant. The effect of contrast was reasonably clear from the plots, but the interaction was difficult to interpret. Table 2 shows the mean latencies (plus SEs) across SF for each TF. We ran a repeated measures ANOVA across SF for each TF, and across TF for each SF while correcting for multiple comparisons. The only significant difference found was across TF for the 2cpd targets ($p = .021$ with Bonferroni correction), with slightly longer latencies at higher TFs (283, 315, and 347ms, for the 1, 8, and 16 Hz targets, respectively). No other significant differences were found ($p > .25$ for all remaining tests).

Thus, at equal detection performance, the results showed little systematic difference in saccade latency as a function of spatial or temporal frequency. While the main effect of temporal frequency was consistent in one direction (longer laten-

Table 2

Mean saccade latency and standard error (in parentheses) for the TF \times SF interaction (Experiment 1)

TF	SF			
	1 cpd	2 cpd	4 cpd	8 cpd
1 Hz	315 ms (30)	283 ms (23)	322 ms (29)	313 ms (21)
8 Hz	343 ms (28)	315 ms (27)	326 ms (22)	332 ms (20)
16 Hz	334 ms (23)	347 ms (28)	323 ms (29)	313 ms (29)

cies at successively higher TFs), it was true only for the 2cpd targets, and no other such consistencies were observed. The lack of an effect of SF here disagrees with the results of the Ludwig et al. (2004) study. In fact, for our latency data, F was less than 1 for both the main effect of SF and the SF \times contrast interaction. It is possible that differences exist at SFs greater than 8cpd, but the effect appeared about the same for 8 or 16cpd targets in the Ludwig et al. study. More importantly, our data showed no indication of a systematic ordering of latencies from low to high spatial frequency as was reported in the Ludwig et al. (2004) study. This would be important for the idea that latency increases as a function of spatial frequency. This was not the case here. In short, the results of Experiment 1 suggest that, to a large degree, the mechanisms controlling saccadic eye movements have access to the same spatio-temporal signals used for perception. It is possible however that the lack of a consistent effect of TF was due to the transient target onset across all conditions. Experiment 2 was designed to test this possibility.

4. Experiment 2

The abrupt onset of the target in Experiment 1 did produce residual high temporal frequency energy, especially in terms of the 1 Hz targets. This may have masked

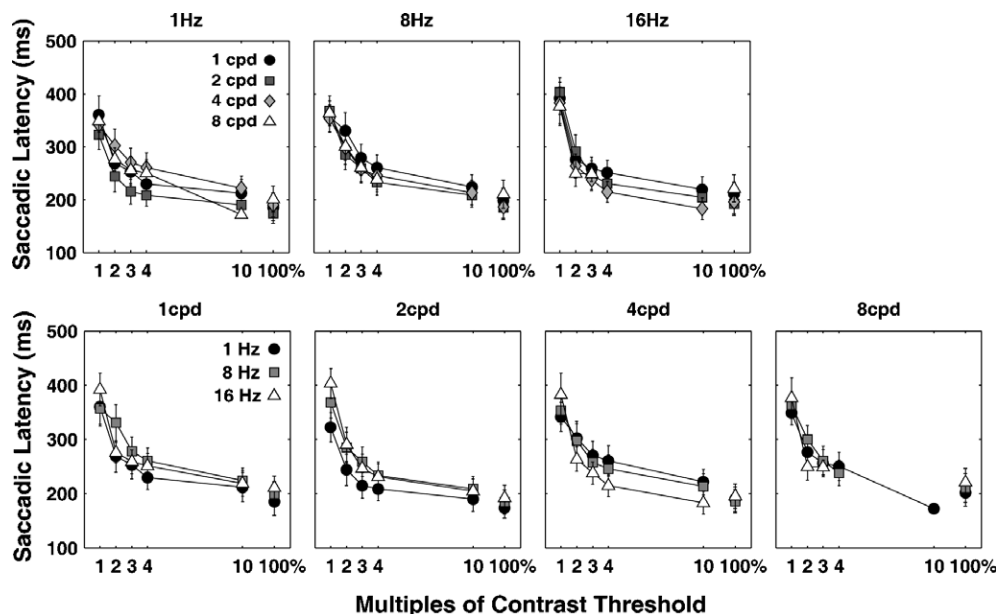


Fig. 3. Mean saccadic latency (6 observers) as a function of multiples of contrast threshold (Experiment 1), plotted for comparison between spatial frequencies within a given temporal frequency (top), and between temporal frequencies within a given spatial frequency (bottom). Errorbars represent ± 1 standard error.

any differences due to the target's actual temporal frequency characteristics. Using an abrupt onset was the simplest way of dealing with the fact that targets of different temporal frequencies reach peak contrast at different times, making latency comparisons difficult. Here, we ramped the onset of the 8 and 16 Hz targets with the sinusoidal contrast function of the 1 Hz target (see Section 2). In addition, we used two target eccentricities (4 or 8 deg) to reduce the predictability of the target's position.

4.1. Results and discussion

4.1.1. Proportion of errors

Table 3 shows the proportion of saccades and error trials at detection threshold for Experiment 2. For brevity, the table shows threshold trials only since this is where most errors occurred. At detection threshold, the proportion of no-saccade trials was less than 10%. As with Experiment 1, direction and detection performance were similar, but slightly higher than the predicted threshold performance based on the staircase rule (79%, see Section 2). This may be due to the extended target duration, or the fact that we pooled data from threshold and $1.1\times$ threshold in this case. The proportion of inaccurate trials was on average slightly higher here ($M=0.18$) than in Experiment 1 ($M=0.15$).

Fig. 4 shows the mean proportion of saccadic direction versus detection errors at threshold, as a function of target temporal frequency (left plot), and spatial frequency (right plot). The mean was around 10–15% (i.e., 85–90% correct)

across temporal and spatial frequencies. A 2×3 (error-type \times temporal frequency) and 2×4 (error-type \times spatial frequency) repeated measures ANOVA revealed no significant differences ($p>.25$ for all effects). The lack of an effect of error-type may be due to the fact that saccadic performance was necessarily computed as a binary response (left versus right), whereas psychophysical performance was a 4AFC procedure (left-near, left-far, right-near, and right-far). Nonetheless, most importantly there was no indication of a difference across spatial or temporal frequency within either response-type. In other words, there was no bias towards a particular spatial or temporal frequency. This again supports our claim that the saccadic and perceptual systems rely on the same spatio-temporal signals.

4.1.2. Accuracy

As with Experiment 1, this analysis was performed to ensure there was no accuracy-latency tradeoff. We ran tests separately for each target eccentricity to include as many threshold multiples as possible. A $2\times 3\times 4$ (2 contrasts \times 3 TFs \times 4 SFs) repeated measures ANOVA was run on the targets at 4 deg eccentricity. The ANOVA revealed an effect of contrast only ($F(1,3)=26.1$, $p=.015$), with slightly higher saccadic error at threshold (0.7 deg) than at the higher contrast (0.59 deg). No other effects at this eccentricity were significant ($p>.15$ for all remaining tests). For the outermost targets, it was only possible to test all SFs and TFs at detection threshold (see Footnote 1). However, none of the effects were significant ($F<1$ for the main effect of

Table 3
Proportion of saccades, errors and used trials at detection threshold (Experiment 2)

Observer	Proportion saccades	Direction errors	Detection errors	Proportion correct	Inaccurate/anticipatory	Proportion used (<i>N</i>)
BW	0.97	0.17	0.15	0.79	0.16	0.66 (247)
DW	0.93	0.06	0.04	0.92	0.14	0.79 (284)
PS	0.91	0.08	0.08	0.89	0.19	0.72 (255)
SO	0.98	0.08	0.18	0.81	0.24	0.62 (117)

The proportion of direction and detection errors was computed from trials with saccades only (first column). The proportion correct represents the saccade trials with no direction or detection errors, and the proportion used represents the correct trials (fourth column) that satisfied the accuracy/anticipatory criterion (see Section 2).

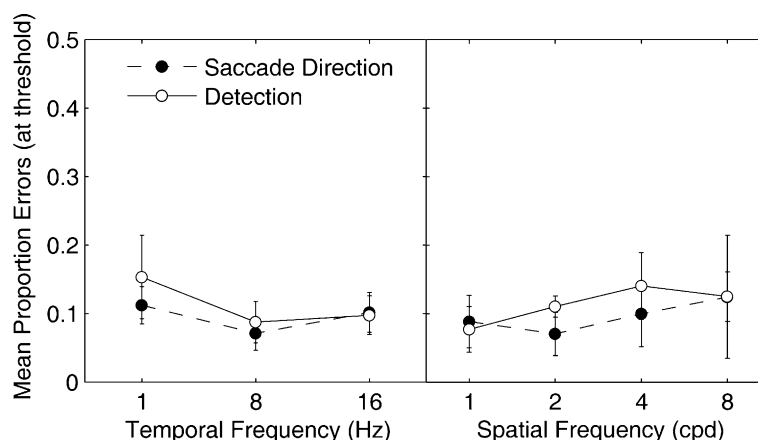


Fig. 4. Mean proportion of saccade direction errors and detection errors at threshold as a function of temporal frequency (left) and spatial frequency (right) (Experiment 2).

TF; $F(3,9)=1.2$, $p=.34$ for the main effect of SF; $F(6,18)=1.1$, $p=.38$ for the TF \times SF interaction). We were able to run another test including two threshold multiples, but only with 2 TFs and 4 SFs ($2 \times 2 \times 4$). Again, only the effect of contrast was significant ($F(1,3)=13.5$, $p=.035$), showing slightly higher saccadic error at threshold (0.89 deg) than at the higher contrast (0.78 deg). In most cases, F was less than 1 (e.g., for the main effect of TF, SF,

TF \times SF, TF \times contrast, and TF \times SF \times contrast). Thus, as with Experiment 1, position error remained fairly constant across target spatio-temporal frequency.

4.1.3. Latency

Fig. 5 shows saccadic latency as a function of contrast for two representative observers. Fig. 5A is plotted for comparison between SFs within a given TF, and Fig. 5B for

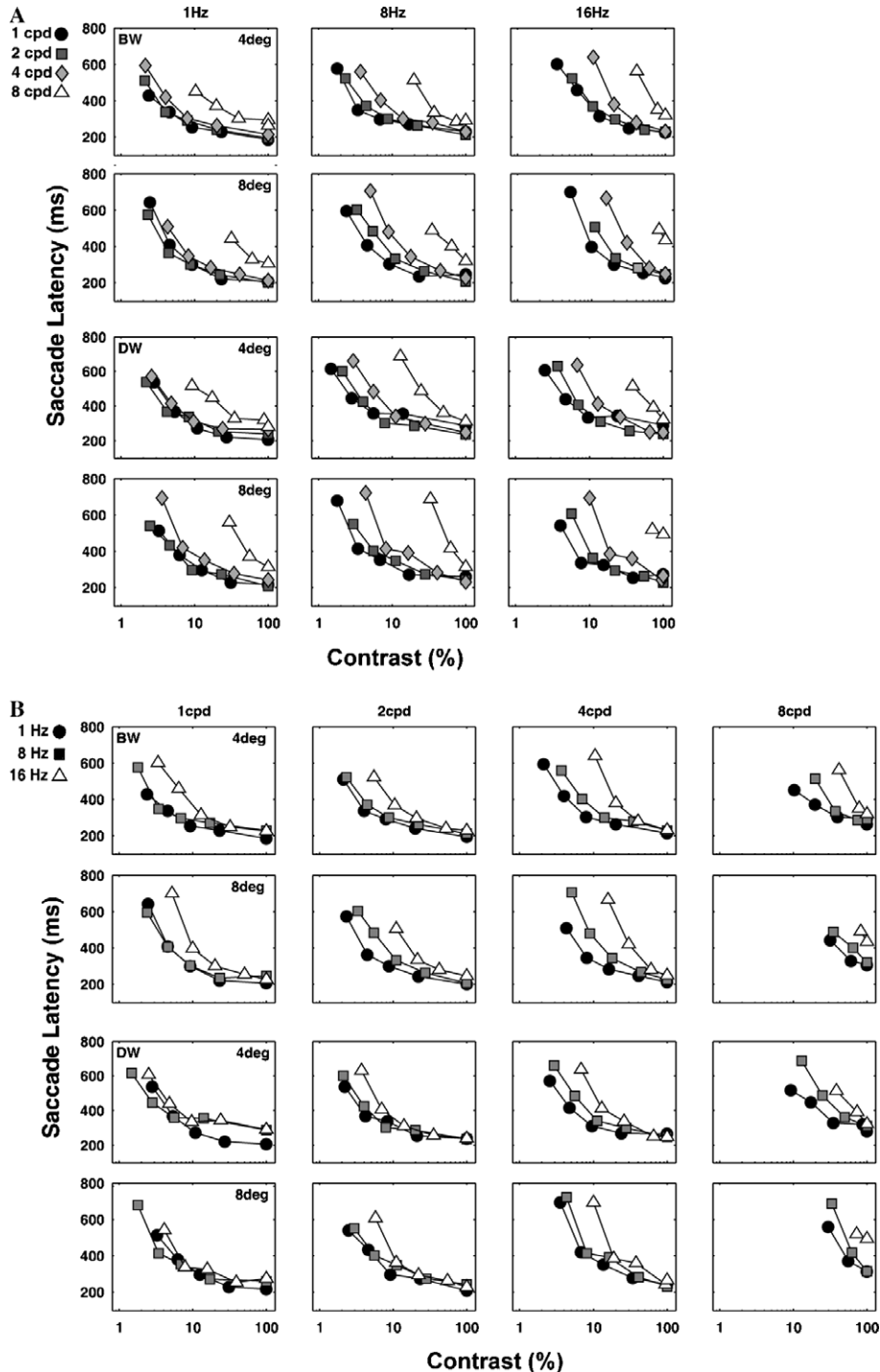


Fig. 5. Saccadic latency as a function contrast (log) for two representative observers (Experiment 2), at two target eccentricities (4 or 8 deg), plotted for comparison between spatial frequencies within a given temporal frequency (A), and between temporal frequencies within a given spatial frequency (B). Errorbars omitted for clarity.

comparison between TFs within a given SF. Latencies were overall much longer here due to the ramped target onset (see Section 2), but the pattern was similar to Experiment 1 in that we see a steady decrease in latency as a function of contrast. The pattern in terms of TF (Fig. 5B) was somewhat different from before: Fig. 5B shows considerable overlap between 1 and 8 Hz targets at lower SFs (which is similar to the pattern in Experiment 1; see Fig. 2B), but there is an increasing separation between the TFs at increasing SFs in Experiment 2 (Fig. 5B) that is not so obvious in Experiment 1 (Fig. 2B). If we consider a fixed contrast at low TF (Fig. 5A), latencies are somewhat longer for higher SF targets, but this difference appears to increase at higher TFs, and with greater target eccentricity (the lines separate more than in Fig. 2A, Experiment 1). This is in fact what we would expect based on the spatio-temporal contrast sensitivity function (Kelly, 1984): spatial contrast sen-

sitivity tends to be band-pass at low TFs and low-pass at high TFs. This means that we are better able to resolve fast flickering low SF patterns than slow flickering high SF patterns, and this difference should be more pronounced further in the periphery due its greater sensitivity to flicker (Baker & Braddick, 1985), and poorer sensitivity to high SF. The data in Experiment 2 are consistent with this.

However, the question is to what extent this difference holds at points of equal detection performance. Fig. 6 shows the mean saccadic latency across threshold multiples for the four observers, plotted for comparison between SFs (top two), and between TFs (bottom two), at each target eccentricity. As with accuracy, latencies were noisier at higher threshold multiples, especially for the higher SFs (4 and 8 cpd) at the outermost eccentricity, because some of these points represent data from as few as one observer

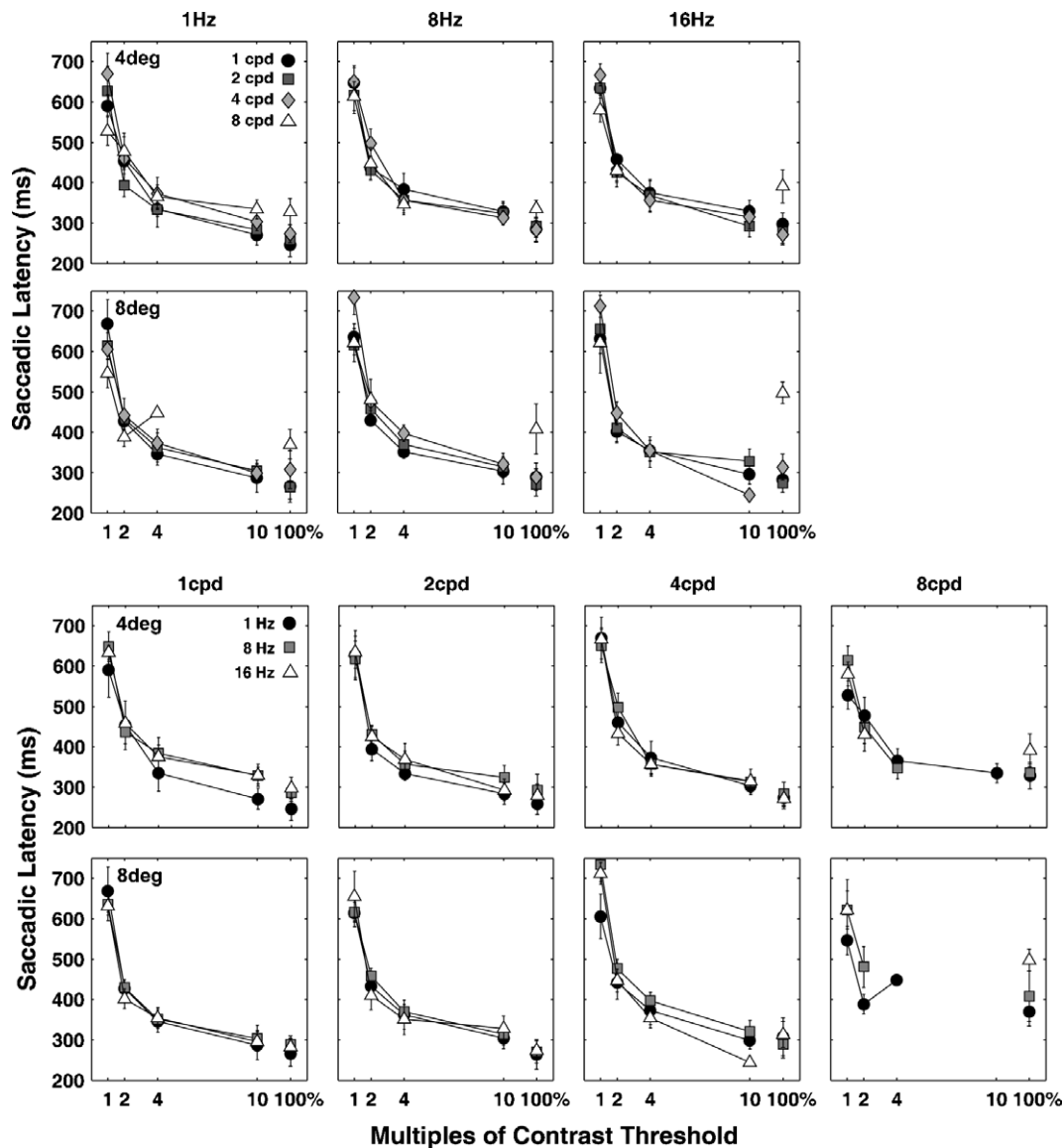


Fig. 6. Mean saccade latency (4 observers) as a function of multiples of contrast threshold (Experiment 2), plotted for comparison between spatial frequencies within a given temporal frequency for each target eccentricity (top two sets of panels), and between temporal frequencies within a given spatial frequency (bottom two sets of panels). Errorbars represent ± 1 standard error.

(Footnote 1). However, at equal detection performance (i.e., near threshold), there appears to be little if any difference.

We ran tests separately for each target eccentricity in order to include as many threshold multiples as possible while ensuring that each condition contained data from all four observers (since most missing cases were for targets at the outermost eccentricity at the highest SF; Footnote 1). We were able to run a $2 \times 3 \times 4$ (2 contrasts \times 3 TFs \times 4 SFs) repeated measures ANOVA on the targets at 4 deg eccentricity. The ANOVA revealed a main effect of SF ($F(3,9)=6.9, p=.01$), and contrast ($F(1,3)=397, p<.001$), plus a TF \times contrast interaction ($F(2,6)=5.4, p=.04$), and a SF \times contrast interaction ($F(3,9)=5.4, p=.02$). No other effects were significant.

The main effect of contrast showed an expected longer latency at threshold (622 ms) than twice threshold (445 ms). However, for the SF main effect, Bonferroni adjusted comparisons between the specific SFs (537, 521, 562, and 513 ms for the 1, 2, 4, and 8 cpd targets respectively) did not reach statistical significance ($p > .09$ for all comparisons). In addition, the interactions showed no obvious systematic differences. Table 4 shows the mean saccade latency (and SEs) for both interactions that reached statistical significance. We ran a repeated measures ANOVA at both contrasts (1 and $2 \times$ thresh) across TF (Table 4A), and then across SF (Table 4B), while correcting for multiple comparisons. Only the effect of SF at threshold was significant ($F(3,9)=9.1, p<.05$), and was

due to slightly longer latency for 4 cpd targets (662 ms) relative to 8 cpd targets (574 ms). Note that this is in fact in the opposite direction to the effect reported by Ludwig and colleagues (2004). In their study, latencies were in fact elevated for SFs ≥ 8 cpd.

For targets at 8 deg eccentricity, it was only possible to test all SFs and TFs at detection threshold (multiples greater than this were not possible for all targets; see Footnote 1). However, none of the effects were significant ($p > .15$ for all effects). We were able to run another test including two threshold multiples, but with only 2 TFs and 4 SFs ($2 \times 2 \times 4$). Again, there was an expected effect of contrast ($F(1,3)=231, p<.001$). The only other effect to reach statistical significance was TF ($F(1,3)=12.7, p=.04$), and was due to slightly longer latencies for 8 Hz (557 ms) than 1 Hz (516 ms) targets.

To reinforce these results, a more stringent test was run at threshold with a single observer using only two SFs (1 and 8 cpd), two TFs (1 and 16 Hz), and one target eccentricity (8 deg). For the staircase, threshold was taken as the mean of 8 reversals (versus 4 previously). We obtained 100 trials per stimulus condition at only one contrast, detection threshold. If saccadic latency is in fact longer for high SFs (Ludwig et al., 2004), it should be detectable here. Fig. 7 shows the results. On the left is saccade latency, and on the right is saccade error, with the percentage of correct saccade directions next to each mean value. Again, there was no indication of longer latencies for high SF targets here.

Table 4
Mean saccade latency and standard error (in parentheses) for the TF \times contrast interaction (A) and the SF \times contrast interaction (B) for Experiment 2

(A)	TF			
	1 Hz	8 Hz	16 Hz	
Threshold	604 ms (50)	632 ms (32)	629 ms (25)	
$2 \times$ Threshold	446 ms (37)	452 ms (30)	437 ms (21)	
(B)	SF			
	1 cpd	2 cpd	4 cpd	8 cpd
Threshold	624 ms (38)	626 ms (44)	662 ms (33)	574 ms (25)
$2 \times$ Threshold	449 ms (30)	417 ms (23)	464 ms (28)	452 ms (37)

5. General discussion

We can conclude from these experiments that perceptual and saccadic performance was remarkably similar: once targets were presented at near equal detection performance, we found little *systematic* difference in saccade latency and no difference in average oculometric performance (% correct saccade direction) across a range of spatial and temporal frequencies. Furthermore, saccadic position error remained fairly constant across all conditions. The only reliable effect was due to contrast. The pattern of latencies as a function of contrast (see Figs. 2 and 5) was what we would expect based on the spatio-temporal contrast sensi-

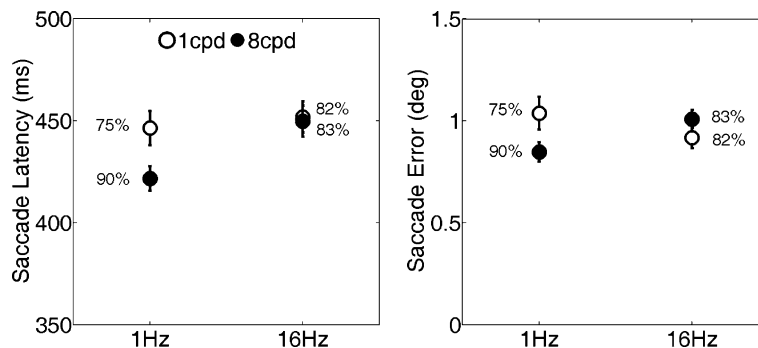


Fig. 7. Saccade latency (left) and saccade error (right) as a function of target spatio-temporal frequency (targets at detection threshold). Errorbars represent ± 1 standard error. Percent correct saccade direction plotted to the side.

tivity function (Kelly, 1984). In short, sensitivity falls at higher SFs, which is reflected in the pattern of latencies as a function of contrast (Figs. 2 and 5) but this difference begins to disappear when we control for contrast sensitivity by performing tests at multiples of threshold (Figs. 3 and 6). Taken together, the results support the idea that the mechanisms driving saccades rely on the same visual spatio-temporal signals as perception.

It is possible that latency differences exist at spatial frequencies higher than was used in the current study (8 cpd). The Ludwig et al. (2004) study used spatial frequencies up to 16 cpd, and they reported a systematic ordering of latencies from medium to high spatial frequencies. However, our setup did not permit an adequate sampling of 16 cpd targets. By our accounts, this was also a problem in the Ludwig et al. study (approximately 2 pixels per cycle at 16 cpd, which is fairly close to a square-wave pattern). Furthermore, we did not find any indication of a systematic ordering of latencies for spatial frequencies up to 8 cpd, so it seems doubtful that we would have found a difference at 16 cpd. However, further tests using a more detailed sampling resolution for spatial frequencies beyond 8 cpd might be useful.

The use of temporal frequency was also an important aspect of this study, and arguably it has been understudied in terms of saccades. It has been suggested that differences in response latencies due to stimuli with different spatio-temporal properties can be attributed to the transient versus sustained nature of the magno- versus parvo-cellular pathways, respectively (Breitmeyer, 1975; Legge, 1978; Murray & Plainis, 2003; Schwartz, 1992). Neurons in the magno-cellular layers of the LGN respond better to rapidly flickering low spatial frequency targets, whereas neurons in parvo-cellular layers can respond better to low temporal frequencies, and can resolve much higher spatial frequencies (Derrington & Lennie, 1984; Merigan & Maunsell, 1993). However, the conduction time from the optic chiasm to the LGN is only about 3–4 ms slower for the P-layers relative to the M-layers (Schiller & Malpeli, 1978), and the difference is only slightly larger in terms of visual response latency, with reports from 7–10 ms (Maunsell et al., 1999; Maunsell & Gibson, 1992). For behavioral differences to match this would require that visual stimuli uniquely isolate each pathway. It seems unlikely then that stimuli believed to isolate these channels would produce a behaviorally significant difference. We used both abrupt-onset targets (Experiment 1) and slow-onset targets (Experiment 2) of different temporal frequencies, but the results showed no clear consistent effect to support this idea. In fact, at equal detection performance, there was no difference across temporal frequency for every spatial frequency except 2 cpd, where the effect was actually opposite to the prediction based on the fast M-path versus the slower P-path (i.e., latencies were slightly longer for successively higher TFs).

One might argue that the few differences we did find (or arguably the lack of any differences) were due to less than perfect thresholds. The staircase method is a quick means of obtaining the threshold for many stimuli simultaneously,

but plotting a psychometric function may be a more accurate approach. Unfortunately, it was not possible to adequately fit a psychometric function to our data (which is often the case for data obtained from a staircase). The alternative is to use a constant stimuli procedure, but the tradeoff is time due to the greater amount of data required to fit a reasonable function. This might be worth exploring with fewer target spatio-temporal frequencies.

In contrast to our results, there has been considerable support for the idea that the visual signals driving perception are distinct from the visual signals used to guide actions (e.g., Goodale & Milner, 1992; Goodale & Westwood, 2004). Part of the support comes from patients with lesions in areas believed to be primarily responsible for motor behavior (so-called “dorsal” areas) versus visual perception (so-called “ventral” areas). For example, patients with lesions in dorsal areas have shown deficits in reaching and grasping certain objects, while their perception of such objects is presumably unaffected (Perenin & Vighetto, 1988). Conversely, patients with ventral lesions have shown perceptual deficits while motor behavior is presumably spared (so-called visual form agnosia; Milner et al., 1991). Since this initial hypothesis however, there has been growing evidence suggesting a high degree of interaction between dorsal and ventral areas, and a much higher level visual representation in the dorsal stream. For example, several studies have reported effects of visual illusions on reaching and grasping behavior (e.g., de Grave, Brenner, & Smeets, 2004; Franz, Gegenfurtner, Bulthoff, & Fahle, 2000; Glover & Dixon, 2001, 2002). In addition, studies are beginning to suggest that the motor system can use pure chromatic signals to guide rapid pointing behavior (Brenner & Smeets, 2004; Schmidt, 2002). Furthermore, there is some evidence for color selectivity in dorsal area LIP (lateral intraparietal area) when color is relevant for the task, in this case a saccade task (Toth & Assad, 2002). Along these lines, the results of the current study support the idea that dorsal areas in the control of saccadic eye movements have access to the same spatio-temporal signals as perception.

Acknowledgments

This research was funded by the Bundesministerium für Bildung und Forschung (“Modkog” 62000177), and the DFG Forschergruppe 560 (“Perception and Action”).

References

- Baker, C. L., Jr., & Braddick, O. J. (1985). Eccentricity-dependent scaling of the limits for short-range apparent motion perception. *Vision Research*, 25(6), 803–812.
- Becker, W., & Jurgens, R. (1979). An analysis of the saccadic system by means of double step stimuli. *Vision Research*, 19(9), 967–983.
- Butter, B. R., Eckstein, M. P., & Stone, L. S. (2003). Saccadic and perceptual performance in visual search tasks. I. Contrast detection and discrimination. *Journal of the Optical Society of America A Optics, Image Science, and Vision*, 20(7), 1341–1355.
- Breitmeyer, B. G. (1975). Simple reaction time as a measure of the temporal response properties of transient and sustained channels. *Vision Research*, 15(12), 1411–1412.

- Brenner, E., & Smeets, J. B. (2004). Colour vision can contribute to fast corrections of arm movements. *Experimental Brain Research*, 158(3), 302–307.
- Bruce, C. J., & Goldberg, M. E. (1985). Primate frontal eye fields I: single neurons discharging before saccades. *Journal of Neurophysiology*, 53, 603–635.
- Carpenter, R. H. S. (1988). *Movements of the eyes*. London: Pion.
- Coeffe, C., & O'Regan, J. K. (1987). Reducing the influence of non-target stimuli on saccade accuracy: predictability and latency effects. *Vision Research*, 27(2), 227–240.
- de Grave, D. D., Brenner, E., & Smeets, J. B. (2004). Illusions as a tool to study the coding of pointing movements. *Experimental Brain Research*, 155(1), 56–62.
- De Valois, R. L., Albrecht, D. G., & Thorell, L. G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. *Vision Research*, 22(5), 545–559.
- Derrington, A. M., & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *Journal of Physiology*, 357, 219–240.
- Doma, H., & Hallett, P. E. (1988). Rod-cone dependence of saccadic eye-movement latency in a foveating task. *Vision Research*, 28(8), 899–913.
- Findlay, J. M., & Gilchrist, I. D. (2003). *Active vision: The psychology of looking and seeing*. Oxford University Press.
- Findlay, J. M., & Walker, R. (1999). A model of saccade generation based on parallel processing and competitive inhibition. *Behavioural and Brain Sciences*, 22(4), 661–674 discussion 674–721.
- Fischer, B., & Ramsperger, E. (1984). Human express saccades: extremely short reaction times of goal directed eye movements. *Experimental Brain Research*, 57(1), 191–195.
- Foster, K. H., Gaska, J. P., Nagler, M., & Pollen, D. A. (1985). Spatial and temporal frequency selectivity of neurones in visual cortical areas V1 and V2 of the macaque monkey. *Journal of Physiology*, 365, 331–363.
- Franz, V. H., Gegenfurtner, K. R., Bulthoff, H. H., & Fahle, M. (2000). Grasping visual illusions: no evidence for a dissociation between perception and action. *Psychological Science*, 11(1), 20–25.
- Glover, S., & Dixon, P. (2001). The role of vision in the on-line correction of illusion effects on action. *Canadian Journal of Experimental Psychology*, 55(2), 96–103.
- Glover, S., & Dixon, P. (2002). Dynamic effects of the Ebbinghaus illusion in grasping: support for a planning/control model of action. *Perception & Psychophysics*, 64(2), 266–278.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25.
- Goodale, M. A., & Westwood, D. A. (2004). An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. *Current Opinion in Neurobiology*, 14(2), 203–211.
- Kalesnykas, R. P., & Hallett, P. E. (1994). Retinal eccentricity and the latency of eye saccades. *Vision Research*, 34(4), 517–531.
- Kelly, D. H. (1979). Motion and vision. II. Stabilized spatio-temporal threshold surface. *Journal of the Optical Society of America*, 69(10), 1340–1349.
- Kelly, D. H. (1984). Retinal inhomogeneity. I. Spatiotemporal contrast sensitivity. *Journal of the Optical Society of America A*, 1(1), 107–113.
- Legge, G. E. (1978). Sustained and transient mechanisms in human vision: temporal and spatial properties. *Vision Res.*, 18(1), 69–81.
- Ludwig, C. J., & Gilchrist, I. D. (2002). Stimulus-driven and goal-driven control over visual selection. *Journal of Experimental Psychology: Human Perception and Performance*, 28(4), 902–912.
- Ludwig, C. J., Gilchrist, I. D., & McSorley, E. (2004). The influence of spatial frequency and contrast on saccade latencies. *Vision Research*, 44(22), 2597–2604.
- Lupp, U., Hauske, G., & Wolf, W. (1976). Perceptual latencies to sinusoidal gratings. *Vision Research*, 16(9), 969–972.
- Macmillan, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. New York: Cambridge University Press.
- Maunsell, J. H., Ghose, G. M., Assad, J. A., McAdams, C. J., Boudreau, C. E., & Noerager, B. D. (1999). Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Visual Neuroscience*, 16(1), 1–14.
- Maunsell, J. H., & Gibson, J. R. (1992). Visual response latencies in striate cortex of the macaque monkey. *Journal of Neurophysiology*, 68(4), 1332–1344.
- Merigan, W. H., & Maunsell, J. H. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, 16, 369–402.
- Milner, A. D., Perrett, D. I., Johnston, R. S., Benson, P. J., Jordan, T. R., Heeley, D. W., et al. (1991). Perception and action in 'visual form agnosia'. *Brain*, 114(Pt 1B), 405–428.
- Murray, I. J., & Plainis, S. (2003). Contrast coding and magno/parvo segregation revealed in reaction time studies. *Vision Research*, 43(25), 2707–2719.
- Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: a specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain*, 111(Pt. 3), 643–674.
- Pins, D., & Bonnet, C. (1996). On the relation between stimulus intensity and processing time: Pieron's law and choice reaction time. *Perceptions & Psychophysics*, 58(3), 390–400.
- Robinson, D. L., & McClurkin, J. W. (1989). The visual superior colliculus and pulvinar. *Review of Oculomotor Research*, 3, 337–360.
- Rovamo, J., Virsu, V., & Nasanen, R. (1978). Cortical magnification factor predicts the photopic contrast sensitivity of peripheral vision. *Nature*, 271(5640), 54–56.
- Schiller, P. H., & Malpeli, J. G. (1978). Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey. *Journal of Neurophysiology*, 41(3), 788–797.
- Schmidt, T. (2002). The finger in flight: real-time motor control by visually masked color stimuli. *Psychological Sciences*, 13(2), 112–118.
- Schwartz, S. H. (1992). Reaction time distributions and their relationship to the transient/sustained nature of the neural discharge. *Vision Research*, 32(11), 2087–2092.
- Toth, L. J., & Assad, J. A. (2002). Dynamic coding of behaviourally relevant stimuli in parietal cortex. *Nature*, 415(6868), 165–168.
- Trappenberg, T. P., Dorris, M. C., Munoz, D. P., & Klein, R. M. (2001). A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience*, 13(2), 256–271.
- Walker, R., Deubel, H., Schneider, W. X., & Findlay, J. M. (1997). Effect of remote distractors on saccade programming: evidence for an extended fixation zone. *Journal of Neurophysiology*, 78(2), 1108–1119.
- Weber, H., & Fischer, B. (1994). Differential effects of non-target stimuli on the occurrence of express saccades in man. *Vision Research*, 34(14), 1883–1891.
- Wenban-Smith, M. G., & Findlay, J. M. (1991). Express saccades: is there a separate population in humans? *Experimental Brain Research*, 87(1), 218–222.
- White, B. J., Gegenfurtner, K. R., & Kerzel, D. (2005). Effects of structured nontarget stimuli on saccadic latency. *Journal of Neurophysiology*, 93(6), 3214–3223.
- Williams, D. R., Brainard, D. H., McMahon, M. J., & Navarro, R. (1994). Double-pass and interferometric measures of the optical quality of the eye. *Journal of the Optical Society of America A Optics, Image Science, and Vision*, 11(12), 3123–3135.
- Wright, M. J., & Johnston, A. (1983). Spatiotemporal contrast sensitivity and visual field locus. *Vision Research*, 23(10), 983–989.