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The influence of spatial frequency and contrast on saccade latencies

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Abstract

We characterised the impact of spatial frequency and contrast on saccade latencies to single Gabor patches. Saccade latencies decreased as a function of contrast, and increased with spatial frequency. The observed latency variations are qualitatively similar to those observed for manual reaction times. For single target detection, our findings highlight the similarity in the visual processes that support both saccadic and manual responses.

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1. Introduction

A number of studies have investigated the visual properties that determine saccade latency to single targets. For example, Doma and Hallett (1988) studied the relationship between contrast and latency, and a number of groups have investigated the effect of eccentricity on saccade latency (Hodgson, 2002; Kalesnykas & Hallett, 1994). Following on from this work, in this article we describe the relationship between saccade latency and spatial frequency across a range of contrasts, at two peripheral eccentricities.

The current study also complements the extensive literature on the relationship between manual reaction time (MRT) and spatial frequency. The basic observation is that MRTs to sinusoidal gratings increase with spatial frequency (Breitmeyer, 1975; Felipe, Buades, & Artigas, 1993; Gish, Shulman, Sheehy, & Leibowitz, 1986; Lupp, Hauske, & Wolf, 1976; Mihaylova, Stomonyakov, & Vassilev, 1999). Vassilev, Mihaylova, and Bonnet (2002) showed that MRTs to sinusoidal gratings presented in foveal vision, decreased as a power function of the product of contrast and grating period. This finding suggests that the MRT variation is largely due to local intensity factors (i.e. the contrast integrated over one grating period). Alternatively, the MRT differences might be largely due to underlying differences in contrast sensitivity. Various methods have been used to attempt to equate the visibility of gratings with different spatial frequencies: matching apparent contrast (Breitmeyer, 1975), matching detection performance (Gish et al., 1986), and presenting the grating at some fixed multiple of the contrast threshold (Lupp et al., 1976). Under these conditions, MRTs still increase with spatial frequency.

In the current study we have measured saccade latency to Gabor patches of a range of spatial frequencies and contrasts, and we have measured the contrast sensitivity function for each observer. These data allow us to characterise the relationship between saccade latency, spatial frequency and contrast. In addition, we assess to what extent the latency variations can be accounted for in terms of (a) contrast, (b) local intensity factors and (c) differences in contrast sensitivity.

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2. Methods

2.1. Participants

Three men, aged between 22 and 32, acted as observers. All three had extensive experience with psychophysical eye tracking experiments. CL and IDG are authors; HP was naïve to the purpose of the study. All three observers had normal or corrected-to-normal vision.

2.2. Equipment and stimuli

The displays were generated using custom written software for a VSG 2/3 graphics card (Cambridge Research Systems Ltd.). Stimuli were presented on a 21'' gamma corrected monitor (Eizo FlexScan T965) running at 80 Hz with a 1024×770 pixel resolution. The monitor was viewed from a distance of 57 cm with the head stabilised by a chinrest.

The stimuli were horizontal Gabor patches in sine phase presented at 4° (near) and 8° (far) left or right of the central fixation point on the horizontal meridian. The fixation point was a $0.3^{\circ} \times 0.3^{\circ}$ black cross. The spatial frequencies of the patches were 1, 2, 4, 8, and 16 c/deg. The standard deviation of the spatial envelope was 0.5° . Contrast is defined as the Michelson contrast $[(L_{max}-L_{min})/(L_{max}+L_{min})]$ of the underlying sinusoid—that is, the nominal contrast (Peli, 1997). The contrast was varied around a grey background with a mean luminance of 51.4 cd/m².

Each spatial frequency was tested at five contrast levels, spaced 0.25 log units apart. On the basis of pilot data, we set a different starting contrast level for each spatial frequency: the lowest contrast increased with 0.1 log units for each octave increase in spatial frequency. As such, contrast ranged from 0.03 to 0.64 across all spatial frequencies. This sampling scheme ensured that almost all of the targets were detectable, yet still within a range of suprathreshold contrast in which latency strongly varied with contrast.

Eye movements were monitored with the EyeLinkII (SR Research Ltd., Mississauga, Ontario, Canada). This infrared tracking system uses the centre of the pupil and the corneal reflection (if available) to sample eye position at 250 Hz. Tracker noise is reduced by a heuristic filter (Stampe, 1993) to a level of below 0.01° (fixation stability of an artificial pupil; measurements by SR Research). The filter replaces noise pulses by the average of the preceding and subsequent sample values. The average spatial error was 0.3° for all three observers. Saccades were detected using velocity and acceleration criteria of 30 deg/s and 8000 deg/s², respectively. The eye movement data were analysed off-line.

2.3. Experimental procedure

A single Gabor could appear at the two eccentricities in the left or right visual field. Besides position, the independent variables were spatial frequency and contrast. Combining the four positions with the five frequencies and contrast levels, resulted in 100 different displays. These displays were randomly intermixed within a block. Each observer performed 10 sessions spread over various days with each session containing five blocks of 100 trials.

A trial started with the presentation of the central fixation point. The target appeared after a random fore period of 200–1000 ms. The central fixation point disappeared simultaneously with the target onset. The stimulus remained visible for 1000 ms after which the trial ended.

We measured the contrast sensitivity of our observers under similar conditions. The onset of the Gabor was accompanied by a tone. The observer then had to indicate the location of the patch by pressing the corresponding key (1-4, going from left to right) on a standard keyboard. The contrast of the Gabor was adjusted according to a three-down, one-up rule, targeting a performance level of 79% correct (Leek, 2001). The contrast step size was 0.002. There was one staircase for each combination of position and spatial frequency. Thus, in total 20 staircases were randomly interleaved to yield a contrast sensitivity function for each of the four positions. Threshold was defined as the mean of the final six reversal points. In order to achieve the minimum six reversals, around 1500 trials were run in a single session lasting approximately 1.5 h. Observers were allowed a break after each block of 25 trials. Eye movements were not monitored during these measurements. Observers had to maintain central fixation throughout a block. Previous experiments with the same observers indicated they had no difficulty complying with these instructions.

3. Results

Only the first saccade after display onset was analysed. Trials were excluded when (i) gaze deviated more than 1° from the display centre at the time of target presentation, (ii) the eye movement was anticipatory (latency < 80 ms; Wenban-Smith & Findlay, 1991), and (iii) the saccade was inaccurate (landing outside a 2° region from the centre of the target). For each combination of position, spatial frequency, and contrast, the mean latency of the first saccade was computed (the observed patterns were similar for the median latencies). Each mean for each observer in the current experiment was based on 29–50 trials. Only those conditions in which the saccade accuracy was greater than 62.5%

correct (representing a sensitivity threshold of d' = 1.2 in 4AFC) were included in this analysis.

For each of the four positions, there were five latency vs contrast functions (one for every frequency). Fig. 1 plots the five functions at each spatial position for the three observers. Error bars have been omitted for the sake of clarity. Pooled over target location, the standard error ranged from 2 to 12 ms for IDG; 1-16 ms for CL, and 2-19 ms for HP. Variability covaried with mean latency in that it was largest at the lowest contrast levels where the latencies were longest, and target uncertainty greatest (Luce, 1986). The variation of latency with contrast is well described by a power function, or Piéron function, of the form SRT(c) = $\beta c^{-\alpha} + t_0$; where c is the contrast, and β , α , and t_0 are constants (Pins & Bonnet, 1996). This function was fit to the data using the Levenberg-Marquardt algorithm with each mean latency weighted by the reciprocal of its variance. The best-fitting power functions are shown as the solid lines.

Even though there are clear differences in the saccade latencies across observers, the impact of contrast on latency, and the rank ordering of the functions was very similar for all three observers. Like MRTs, saccade latency increased with spatial frequency. The increase was particularly pronounced for the higher frequencies (8 and 16 c/deg). The latencies of saccades to 1–4 c/ deg Gabor patches overlapped considerably. IDG showed a strong lateral bias [ANOVA with side and eccentricity as factors: F(1, 4432), p < 0.01]: the latency of his rightward saccades was on average 35 ms shorter than that of leftward movements. HP showed a small, 6 ms, bias in the opposite direction [F(1, 4699), p < 0.05]. The ANOVAs revealed no consistent eccentricity effects across the three observers.

Fig. 2 illustrates the proportion of saccades that landed outside the 2° target region. Note that the vast majority of the data points lie well above the 62.5% correct criterion (i.e. below the dashed horizontal line), and most were close to 100% correct. Errors were most frequent when the spatial frequency was 1 or 16 c/deg, at the two lowest contrast levels. The clustering of errors at the low end of the contrast scale suggests that the observed variation in mean latency with contrast cannot be attributed to a speed-accuracy trade-off. Instead, it seems likely that the long latencies of saccades to low contrast Gabors reflect the longer integration time of weak target signals. Finally, note that eccentricity affected the detectability of the patterns at the low contrasts as would be expected on the basis of the reduced contrast sensitivity in the periphery (Pointer & Hess, 1989). The effect is particularly pronounced for the 16 c/deg stimulus.

We examined to what extent the four data sets for each observer (each set containing 22-25 mean

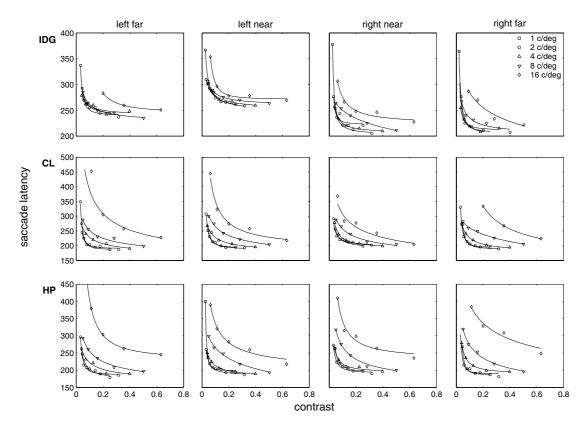


Fig. 1. Saccade latency as a function of contrast for each target frequency, position, and observer. The solid lines are the best-fitting Piéron functions (see text).

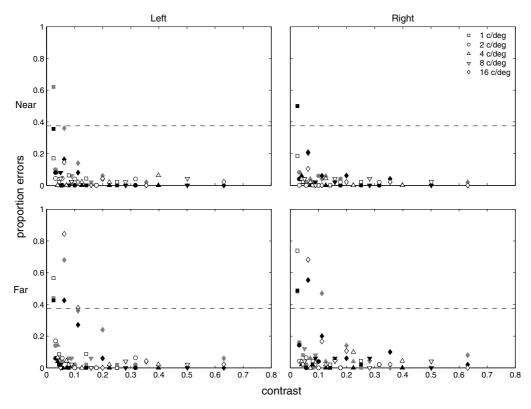


Fig. 2. Proportion of saccades that landed outside a 2° region centred on the target. Observer IDG: open symbols, CL: grey filled symbols, HP: black filled symbols. The dashed horizontal line represents the accuracy criterion (see text for details).

latencies), could be approximated by a single threeparameter function of the same form as described above. We were interested to what extent saccade latency simply covaried with luminance contrast, disregarding spatial frequency. The parameter estimates and adjusted goodness-of-fit r^2 values are reported in Table 1. For observer IDG a substantial part of the variance in the latencies of his leftward saccades was accounted for purely in terms of contrast variations. As for his rightward saccade latencies, and for observers

Table 1 Parameter estimates for the examined models and adjusted r^2 values for each observer

	Parameter	Contrast			Contrast×period			Contrast/contrast threshold		
		IDG	CL	HP	IDG	CL	HP	IDG	CL	HP
Left far	α	1.52	2.03	2.05	0.47	0.53	0.6	1.18	1.59	1.09
	β	0.35	0.12	0.08	5.25	9.58	6.39	118	198	119
	t_0	245	202	199	231	163	167	238	194	190
	r^2	0.67	0.25	0.21	0.45	0.80	0.75	0.86	0.58	0.25
Left near	α	0.90	1.39	1.16	0.24	0.72	0.91	0.85	1.33	1.17
	β	2.74	0.82	1.50	23.6	3.84	1.21	79.1	147	121
		258	204	191	227	178	185	258	199	191
	r^2	0.73	0.25	0.37	0.39	0.90	0.77	0.81	0.50	0.49
Right near	α	0.71	0.53	1.08	0.66	0.79	0.93	0.57	0.80	1.37
	β	6.13	17.2	2.14	2.53	1.90	1.27	84.4	130	134
	t_0	208	179	197	206	195	189	199	191	198
	r^2	0.33	0.39	0.18	0.71	0.86	0.85	0.79	0.66	0.47
Right far	α	1.13	1.98	1.82	0.64	0.42	0.77	1.03	1.27	1.47
	β	1.41	0.14	0.21	3.15	17.4	3.57	131	151	164
		215	206	199	199	153	172	204	194	193
	r^2	0.34	0.34	0.12	0.64	0.76	0.80	0.83	0.60	0.30

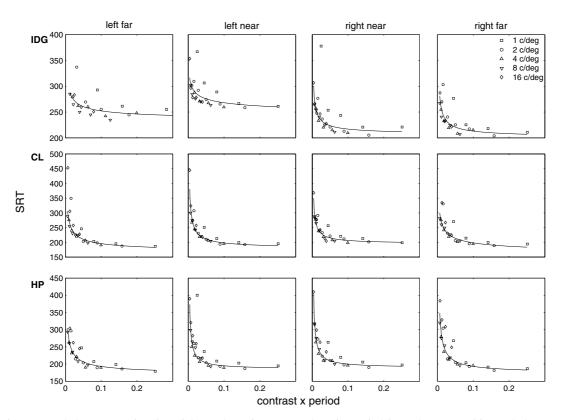


Fig. 3. Saccade latency as a function of the product of contrast and grating period for each target position and observer.

CL and HP, the fits of the contrast-dependent model were much less satisfactory.

We then explored to what extent the fits could be improved by incorporating a spatial frequency modulation. One candidate modulation is to multiply contrast with the grating period (Vassilev et al., 2002). Fig. 3 illustrates the saccade latencies plotted in this way, with the solid line as the best-fitting Piéron function (again using weighted least-squares). This particular modulation resulted in much better fits for observers CL and HP (see Table 1). The model accounted for a large part of the variance in IDG's rightward saccade latencies, which were not well accounted for by the contrast model.

A critical issue in the literature on the relation between MRT and spatial frequency, is to what extent the latency variations are due to underlying differences in contrast sensitivity to patches of different spatial frequencies. The second modulation we examined was to plot saccade latency as a function of multiples of the contrast threshold (cf. Lupp et al., 1976). The resulting plots are shown in Fig. 4, again with the solid line as the best-fitting Piéron function. Certainly for IDG's data this model provided the best fits of all (see Table 1). The fits for CL and particularly HP were worse than those of the contrast×period model.

4. Discussion

We measured saccade latencies to eccentric Gabor patches of different contrasts and in a spatial frequency range of 1–16 c/deg. The latencies follow a similar pattern as that observed for MRTs to sinusoidal gratings presented either centrally or in the parafovea (e.g. Thomas, Fagerholm, & Bonnet, 1999). Like MRTs, saccade latencies decrease with higher contrasts, but increase with spatial frequency. As such, our results highlight the similarity in the visual processes underlying both manual and saccadic responses, at least in the context of single target detection.

4.1. Descriptive models of RT variations

We explored to what extent the saccade latency variations with contrast and spatial frequency could be accounted for by models that have been developed in the MRT literature. We analysed saccade latency as a power function of contrast (pooled over spatial frequency), contrast multiplied by grating period, and multiples of the contrast threshold. In comparison with the contrast based model, some modulation by spatial frequency resulted in superior fits for all observers. For IDG's data we obtained the best fits by expressing contrast in terms of multiples of threshold (adjusted r^2 range 0.79–0.86).

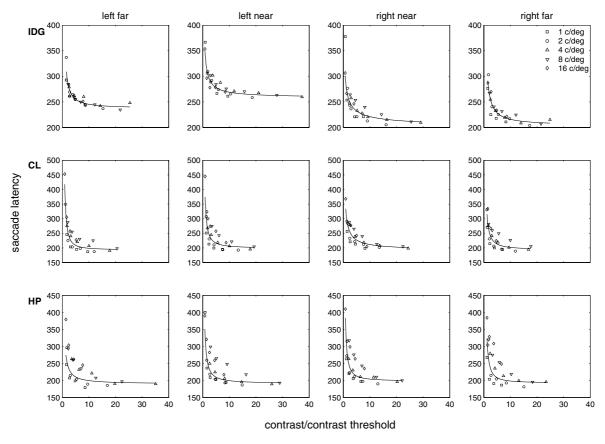


Fig. 4. Saccade latency as a function of multiples of threshold contrast for each target position and observer.

The contrast x period model provided the best fits for observers CL and HP (adjusted r^2 range 0.75–0.90).

The good fits of the model based on the product of contrast and period, suggests that the latency variations of CL and HP can be largely explained by assuming that these observers integrate contrast over an area that is the width of one bar in the Gabor patch (Donner & Fagerholm, 2003; Vassilev et al., 2002). However, as pointed out by Vassilev (2003), it is almost certainly too simplistic to claim that MRT is entirely determined by the luminance contrast of one bar in the grating only, particularly when the spatial frequency is high. Vassilev et al. (2002) reported that the MRTs to 12 c/deg gratings were systematically longer than predicted by contrast×period. Moreover, when fitting the data for each spatial frequency separately, t_0 increased with spatial frequency. Thus, it appears that additional and slower mechanisms are involved in detecting the high spatial frequency patterns.

We did not find a consistent underestimation of the latencies to the high spatial frequency patterns (see Fig. 3). Unfortunately, our estimates of t_0 when fitting the data for each spatial frequency separately, were not sufficiently stable to draw any conclusions about how this parameter varies with spatial frequency. Thus, whether saccades to high spatial frequency patterns are

also dependent on the operation of a slower channel, is still an open question (see below).

We did find that the model systematically underestimated the latency of saccades to the 1 c/deg Gabors, particularly at low contrasts. These deviations were especially pronounced in IDG's data. One possible explanation lies in the small size of the Gaussian window through which the stimulus was viewed, and therefore the small number of visible cycles for the 1 c/deg Gabor. As a general rule, contrast sensitivity improves with increasing the number of cycles up to a critical point (e.g. Hoekstra, Van der Groot, Van den Brink, & Bilsen, 1974). Less is known about how RT depends on the number of cycles. Vassilev et al. (2002) reported evidence that suggested that MRT is independent of the number cycles beyond a minimum of three cycles. On the basis of these considerations, it is possible that the small aperture particularly affected the latency of saccades to the low contrast 1 c/deg targets.

The convergence of the data onto a single function of contrast/contrast threshold for IDG and to a lesser extent CL, evokes interesting questions concerning the relation between perceptual and/or saccade latency on the one hand and suprathreshold contrast perception, or visibility, on the other. The visual system's response to suprathreshold contrast does not depend on spatial frequency in the same way as its response to low contrast levels (Georgeson & Sullivan, 1975). At threshold, the contrast response varies with spatial frequency in a bandpass fashion, but at high suprathreshold contrasts the bandpass function has flattened (an effect termed contrast constancy). Thus, if one multiplies the contrast threshold by some fixed factor (i.e. a parallel shift of the bandpass contrast threshold function along the log contrast ordinate), the perceived contrast of different spatial frequencies should not be the same. The fits in Fig. 4 suggests that such a shift *will* approximately equalise the latency of saccades to Gabors with different frequencies (at least for some observers). However, note that for CL and HP the residual variation in saccade latency did vary systematically with spatial frequency. It can be seen in Fig. 4 that at any one multiple of contrast threshold (or window of close values) low to medium spatial frequency Gabors (1-2 c/deg) triggered saccades with shorter latencies than high spatial frequency Gabors (8–16 c/deg). This pattern matches the results of Lupp et al. (1976) who still found an increase in MRT with spatial frequency when gratings were presented at various multiples of contrast threshold.

Grating period varies with spatial frequency as a linear function with a negative slope on double log coordinates, and the contrast threshold varies with spatial frequency in a bandpass fashion. The effect of both modulations is to attenuate the effective contrast at the high spatial frequency end. Thus, our results suggest that a variety of spatial frequency modulations that share this characteristic can in principle account for RT variations with contrast and spatial frequency. As such, it appears that a good fit of any of these descriptive models does not necessarily point to the mechanisms that underlie the observed latency variations.

4.2. Single vs multiple channel models

The MRT variations with contrast and spatial frequency have been linked to the operation of multiple, parallel channels in the human visual system: a fast, transient channel that is particularly sensitive to low spatial frequency information, and a slower, sustained channel that primarily responds to high spatial frequencies (Legge, 1978; Tolhurst, 1975). An alternative explanation is that target detection is subserved by a single channel with high spatial frequency attenuation (Parker & Salzen, 1977; Thomas et al., 1999).

Murray and Plainis (2003) used the slope of the function relating MRT and reciprocal contrast to characterise the contrast gain of the underlying mechanisms that mediate the response to the target. The contrast gain derived in this way diminished with increasing spatial frequency and at high contrast levels (>0.1). This finding parallels the contrast gain characteristics of the Magnocellular (M) and Parvocellular (P) pathways: the contrast gain of the M channel is high but saturates at low contrast levels, whereas the P channel is much less sensitive but responds over a larger range of contrasts (Kaplan, Lee, & Shapley, 1990). On the basis of their analysis, Murray and Plainis (2003) argued that the M channel is responsible for target detection in typical RT tasks, with the P system contributing only at high spatial frequencies (>7 c/deg) and/or contrasts (>0.1). This hypothesis builds upon the idea that the M channel underlies the largest part of the contrast sensitivity function (Kaplan et al., 1990).

With regard to saccadic eye movements, one can think of an oculomotor centre in which target-related activity gradually builds up to a particular response threshold (Carpenter, 1981). This centre may receive information from a variety of channels, and it integrates the information as it becomes available over time regardless of the source of the information. Thus, the rise to threshold may be jointly determined by M and P signals, with the influence of the P channel becoming manifest only if its signals arrive before the threshold has been crossed on the basis of the M contribution alone. The frontal eye fields (FEF) appear to be a good candidate for this centre: the FEF are extensively connected with virtually all (extra)striate areas of the visual brain (Schall & Thompson, 1999), and its visuomotor activity can be described by a gradual rise to a fixed threshold that is strongly related to saccade latency (Hanes & Schall, 1996).

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