Report

Saccadic Facilitation in Natural Backgrounds

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Summary

In visual systems with a fovea, only a small portion of the visual field can be analyzed with high accuracy. Saccadic eye movements shift that center of gaze around several times a second. Saccades have been characterized in great detail and depend critically on a number of visual properties of the stimuli [1–5]. However, typical experiments have used bright spots on dark backgrounds, while our natural environment has a highly characteristic rich spatial structure [6, 7]. Here we show that the saccadic system, unlike the perceptual system, is able to compensate for the masking caused by structured backgrounds. Consequently, saccadic latencies in the context of natural backgrounds are much faster than unstructured backgrounds at equal levels of visibility. The results suggest that whenever a structured background acts to mask the visibility of the saccade target, it simultaneously preactivates saccadic circuitry and thus ensures a fast reaction to potentially critical stimuli that are difficult to detect in our environment.

Results and Discussion

Our understanding of the mechanisms of vision, and saccadic eye movements in particular, is based primarily on the use of simple stimuli (Figure 1A). However, visual systems are highly adapted to the visual properties conveyed by natural scenes [6, 7] (Figure 1B), and the brain's response to such complex stimuli cannot be completely understood from the use of simpler stimuli [8, 9]. Here we asked how structured backgrounds with similar statistical properties as natural images influence the saccadic response (Figure 1C).

The time required for a saccadic response should depend on the salience of an object relative to its surround (i.e., the signal-to-noise ratio [SNR]). Since saccadic latency is highly dependent upon stimulus contrast [1–5], we asked whether it can be accounted for purely in terms of target visibility irrespective of the background in which it appears. If the saccadic response is entirely determined by the SNR, we would predict the same response latency at equal points of visibility.

A stationary, vertically oriented Gabor target with a carrier spatial frequency of 1 cycle per degree (cpd) was presented on a uniform or structured (stationary) background 8° left or right of center. Observers performed two separate tasks: a detection task that consisted of a two-alternative forced choice (2AFC) as to the direction of the target (left versus right), and a saccade task in which observers launched an eye movement to the target's location. Target contrast was varied in both cases. We measured detection performance and the latency of the first saccade, both as a function of contrast, for targets in each background condition. We then made comparisons between the background conditions at points of equal psychophysical detection performance.

Figure 2 shows the results of a representative observer using the low spatial frequency Gabor target (1 cpd) on a uniform gray (gray lines and symbols) or 1/f background (red lines and symbols). As can be seen, the psychometric function (Figure 2A) for the target in the structured background (red) was shifted significantly to the right, indicating strong visual masking from the dominant low spatial frequency energy of the noise [10–12]. However, saccade latency (correct saccades only) was relatively unaffected by the masking (Figure 2C). Consequently, at equal detection performance (75% correct detection represented by the vertical dotted lines), latencies were in fact substantially shorter for targets in the structured background. This can be clearly seen when plotted as a function of multiples of threshold (Figure 2D). Note that the proportion of correctly directed saccades was significantly above chance along the region represented by the shaded area in Figure 2D, which was the range used to compute a measure of effect size (see Experimental Procedures). In addition, psychometric thresholds ($M_{uniform}$ = 1.7, $M_{structured}$ = 4.8% contrast) were on average only slightly lower than "oculometric thresholds" ($M_{uniform}$ = 2.4, $M_{structured}$ = 6.3% contrast) based on saccade direction performance. More importantly, both psycho- and oculometric measures showed the same relative threshold elevation ($threshold_{structured}$/$threshold_{uniform}$) for the structured background condition (2.8 for psychometric performance versus 2.6 for oculometric performance). As a result, latencies were also shorter for the structured background condition at points of equal *oculometric* performance (i.e., where the proportion of correctly directed saccades was the same for both conditions). The results are therefore not explicable in terms of a speed-accuracy tradeoff (see also Supplemental Data).

The size of the effect in Figure 2D was determined for four additional observers and revealed substantial effect sizes from 50 to 114 ms. This is considerably large as compared to other facilitatory oculomotor effects such as the "gap effect" [13, 14], which can produce very short latency "express saccades" [15, 16] that approach the limits of the shortest neural pathway driving saccades. If we consider the entire latency period for targets on the uniform background at threshold (Figure 2D), facilitation from the structured background accounted for as much as a third of the entire latency period.

The same degree of saccadic facilitation was found when we embedded the low spatial frequency target in backgrounds of actual natural scenes (Figure 3). Here, targets were presented
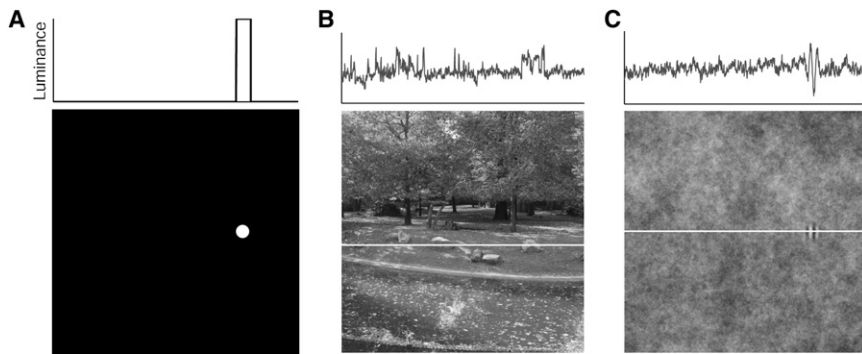
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Figure 1. Visual Signals in Natural Contexts

(A) Saccadic eye movements have been typically characterized using simple stimuli (e.g., bright spots on dark uniform backgrounds).

(B) This is dramatically different from natural scenes, where targets are often subtle signals in noisy backgrounds. Natural visual environments also have a characteristic spatial structure; the amplitude spectrum falls as a function of 1/spatial frequency [6, 7].

(C) A vertically oriented Gabor target embedded in a random noise texture with this naturalistic 1/f property.

at equal psychophysical detection performance for each respective condition (numbers below the bars represent the average oculometric performance, i.e., percent correct saccade directions). The data in Figure 3B represent the mean of five observers.

These results can be interpreted in two ways. First, if the speed of the saccadic decision process depends entirely on the SNR [1–5], then natural backgrounds must increase processing speed. This could happen if the background simply preactivated the neural circuitry underlying the decisions. If this were the case, we would expect any background structure to produce similar results. In fact, one might predict an even earlier response in a case where the background does not mask the target. To test this, we ran a series of control experiments using the same low spatial frequency target (1 cpd) on backgrounds with different visual properties intended to minimize target masking (Figure 4). The first was a form of band-

pass noise (Figure 4A), with a center spatial frequency of 126 cycles per image or 3.5 cpd, which was sufficiently distinct from the target spatial frequency. The second background type was 1/f noise modulated along the red-green (RG) isoluminant axis in color space [17, 18] (Figure 4B). In this case, we expected a reduction in masking because detection of the target should involve primarily luminance-sensitive mechanisms, whereas any effect of the background should involve primarily color-sensitive mechanisms [19]. A third background type consisted of horizontally oriented 1/f noise with orientations greater than ±5° about the horizon removed (Figure 4C). Since cortical areas underlying the control of saccades, such as lateral intraparietal region (LIP) or the frontal eye fields (FEF), are generally not believed to be selective for visual features such as color or orientation [20–23] (see however [24, 25]), any effect of these visual properties on saccade latency should be the result of processes occurring upstream.
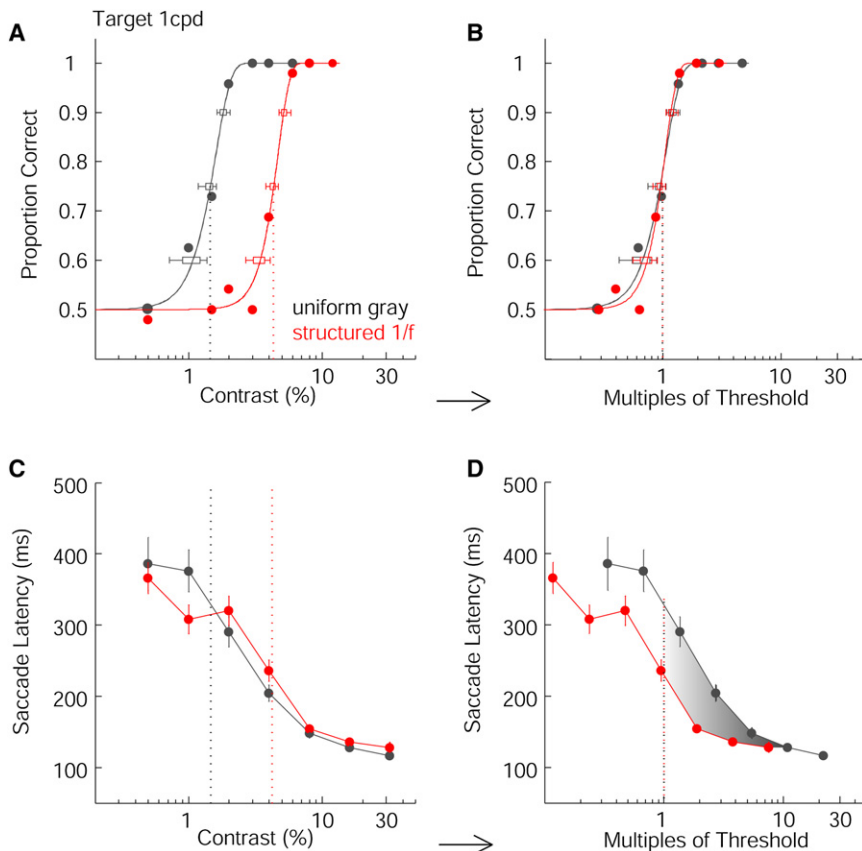

Figure 2. Saccade Latency at Equal Visibility

Results of the detection task (A and B) and the saccade task (C and D) as a function of contrast and multiples of contrast threshold for Gabor targets (1 cpd) embedded in a uniform gray background (gray lines and symbols) versus structured (1/f) backgrounds (red lines and symbols). The vertical dotted lines represent contrast at the 75% correct detection point, and the error bars for the detection task represent the 95% (box) and 99% (whiskers) confidence interval for the threshold estimates. Error bars for the saccade task represent ±1 standard error of the mean. Latencies represent correctly directed saccades only. The shaded area in (D) illustrates the degree of facilitation from the structured background and was restricted to points along the curves where the proportion of correctly directed saccades was significantly above chance.
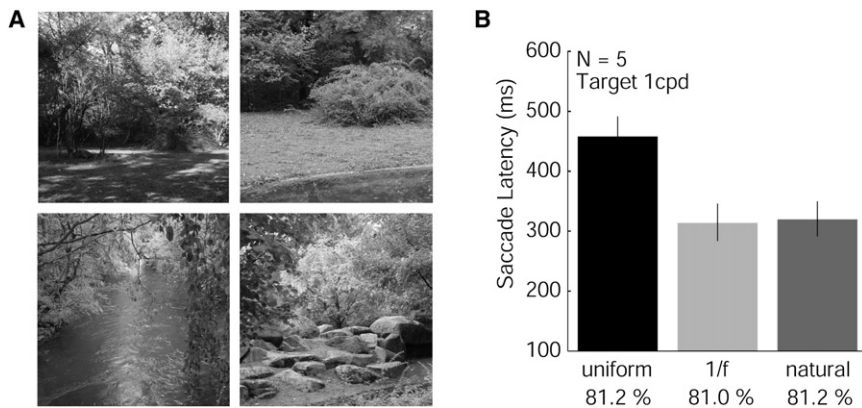
Figure 3. Comparison with Backgrounds of Natural Scenes

(A) Sample of the natural backgrounds used (from a total of 100 randomly selected images). Images consisted of natural scenes containing trees, rocks, and water, with no animate or man-made objects.

(B) Mean saccade latency (five observers) for Gabor targets (1 cpd) on each of the three background types (latencies represent correctly directed saccades only). Targets appeared right or left of center (8°) at contrast threshold for each respective condition. Error bars represent ± 1 standard error of the mean. Numbers below the bars represent the average oculometric performance (percent correct saccade directions).

Figure 4D shows saccadic facilitation (latency$_{structured}$ − latency$_{uniform}$) for four observers using the original 1/f background (black bars), as well as two observers for each subsequent control experiment. While the effect was still present using the band-pass and RG-isoluminant noise, any potential reduction in masking clearly did not enhance the facilitation. For the oriented noise, the effect was virtually absent. However, when we plotted facilitation as a function of masking (Figure 4E), we see a strong linear relationship, $R^2 = 0.86$, $p < 0.0001$; i.e., the facilitation was almost entirely accounted for by the degree of masking. The effect is present only if the target shares properties with its background. In fact, if we instead change the target's properties to minimize masking (e.g., by using a higher spatial frequency target (8 cpd) in the original 1/f noise), we also find little masking and, consequently, little if any facilitation.

These findings make it unlikely that differences in sensory processing speed are responsible for the shortened saccadic latencies in natural scenes. It is possible that neurons in primary visual cortex would produce shorter latencies to signal changes when they are already active (e.g., from the structured background). However, when comparing onset and offset latencies, for example, such differences were observed to be

on the order of 5–20 ms [26]. This could not account for the massive 50–100 ms latency differences we observed.

The alternative interpretation is that saccadic response latency depends on target contrast, and not the SNR. In this case, the saccadic system would respond whenever the activity of visual cortex reaches a fixed contrast at a specific location. *At a fixed contrast*, we would therefore expect a greater proportion of saccade direction errors for targets in the structured background, which is reflected by the corresponding elevation in oculometric thresholds described earlier. In addition, perceptual detection performance and saccadic direction performance were approximately equal. This implies that all relevant stimulus analyses can be done in a relatively short time, and the result of this analysis is used for both saccadic and perceptual decisions [27, 28]. *At equal visibility*, the proportion of direction errors was the same for either background condition, which means that psychophysical target detection processes must have also been about equal at the moment of saccade initiation. This implies that the shorter latencies for the structured background condition must have instead resulted from processes directly related to saccade preparation/initiation [29]. Given the strong dependence on target-background similarity (Figure 4E), the structured background
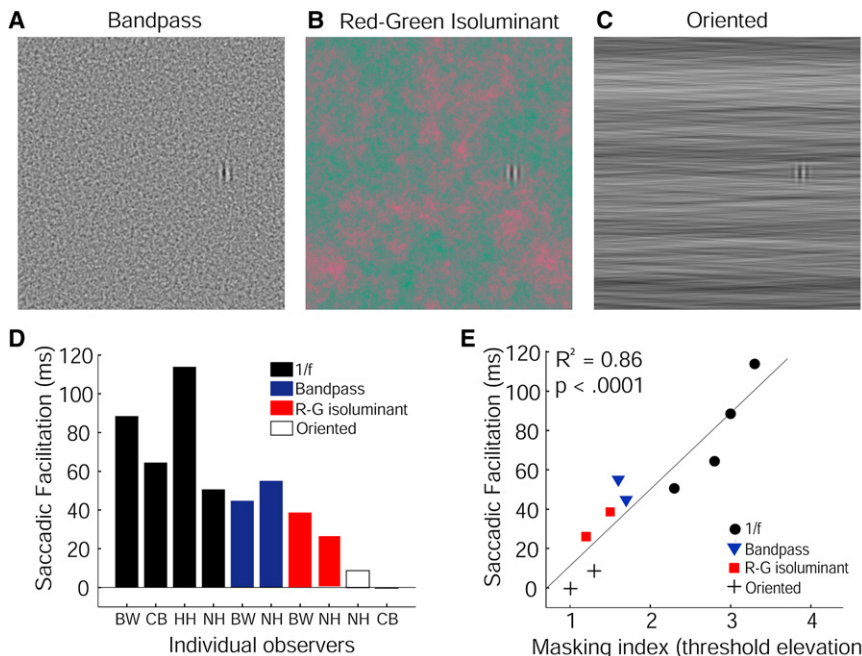

Figure 4. Structured Backgrounds Designed to Minimize the Degree of Masking

(A) Band-pass filtered texture with a center spatial frequency of 3.5 cpd.

(B) Isoluminant 1/f noise modulated along the cardinal red-green axis in the DKL color space.

(C) Horizontally oriented noise with its dominant energy orthogonal to the target. The target was always vertically oriented at 1 cpd.

(D) Saccadic facilitation (see Experimental Procedures) in milliseconds for each background type across individual observers and (E) as a function of masking (multiples of threshold elevation for targets in the structured—relative to uniform—backgrounds).

must then influence the saccade circuitry directly by preactivating the same neurons that respond to the target.

In sum, our results were not adequately explained by a speed-accuracy tradeoff, faster sensory integration, or an *unspecific* preactivation of the saccade system. The fact that the saccadic response is not entirely dependent upon the SNR disagrees with bottom-up saliency-based models of visual attention [30, 31]. However, when target uncertainty is high, salience may be a less important factor driving the saccadic response [32, 33]. We also found the same results under conditions of high target spatial uncertainty (Supplemental Data). The results might involve a top-down component, whereby knowledge of the target is integrated with visual signals conveyed by a background containing similar visual structure [34]. For example, a representation of the target is believed to be held in working memory (e.g., prefrontal cortex) [35], and signals from prefrontal cortex are also believed to bias visual processing for features similar to the target [36, 37]. When the SNR is low, visual signals from a structured background that resemble a target template may activate the same population of neurons that would normally respond to the target alone [34], resulting in advanced motor-preparatory activity that can reduce latencies [38, 39]. This would not be possible for a background absent of visual structure. While our results do not rule out the contribution of top-down signals, any such effects would however be specific to the presence of the structured background that must nevertheless influence the saccade circuitry independent of perceptual processing.

In conclusion, these results highlight a major difference in measuring eye movements under naturalistic contexts: saccade latency is not locked to the SNR. Instead, the saccadic system is able to compensate for the masking produced by natural scenes, which can ensure a fast reaction to potentially critical stimuli that may be camouflaged by their surroundings.

Experimental Procedures

Observers
Two to six observers took part in each experiment. With the exception of the first author, all observers were naive to the nature of the study. All observers had normal or corrected to normal visual acuity, and ranged from 20 to 37 years of age.

Visual Stimuli
Stimuli were displayed on a 21 inch CRT monitor driven by an ASUS V8170 GeForce 4 MX440 graphics board at a refresh of 100 Hz (noninterlaced). The resolution was 1280 × 1024 pixels (37 cm × 29.6 cm). At a viewing distance of 47 cm, the display extended 45° horizontally and 36° vertically. Eye movements were measured using EyeLink II system (SR Research, Ontario, Canada) at a sample rate of 250 Hz.

The target was a stationary, vertically oriented Gabor patch (SD = 0.7°). Tests were performed using targets of either a low (1 cpd) or high (8 cpd) spatial frequency, which appeared either 8° randomly left or right of the central fixation (primary experiment). The fixation stimulus was a black spot ~0.2° in diameter.

The primary backgrounds were uniform gray and luminance-based 1/f or "pink" noise textures whose amplitude spectra fall as a function of 1 over the spatial frequency. Three additional noise textures were used for subsequent control experiments: (1) a band-pass noise texture (Figure 4A) with its dominant spatial frequency at 126 c/image or 3.5 cpd, (2) a 1/f texture modulated along the R-G isoluminant axis in the DKL color space (Figure 4B), and (3) a horizontally oriented 1/f texture with spatial frequencies greater than ±5° about the horizon removed (Figure 4C). An additional test was carried out with targets embedded in real natural images consisting of natural landscapes, rocks, trees, and water, with no man-made objects, humans, or animals (Figure 3A). Note that on a given trial of a given experiment each structured background (noise texture or natural image) was randomly selected from a sample of 100 images of each background type. These backgrounds extended 1024 × 1024 pixels (36° × 36°) and were presented at an average luminance of 32 cd/m (as with the uniform gray background). The noise textures were generated off-line using Matlab. With the exception of the red-green isoluminant backgrounds, which were presented at 70% of the maximum contrast possible on our equipment, all structured backgrounds were presented at 50% contrast. Despite the greater contrast value for the isoluminant backgrounds, actual cone contrast was only about 15% of that of the luminance-based 1/f textures, due to the overlap in spectral sensitivities of the L and M cones.

Tasks
The primary experiments consisted of two separate tasks: a *detection task* and a *saccade task*. First, detection thresholds were determined for each observer to targets at 8° right or left of a central fixation spot on the uniform and structured backgrounds. During this procedure, observers maintained fixation on a central black spot (0.2° in diameter), which remained present throughout the trial. Eye movements were controlled with the eye tracker. Observers had to fixate the central fixation stimulus and then initiate the trial by pressing a key on a game-pad (note that the intertrial background color was uniform gray). If fixation was not accurate within 1°, an error tone was presented, and the trial had to be reinitiated. As soon as the trial started, a randomly selected structured background appeared or the screen remained uniform gray (with an equal probability of either background on each trial). A saccade greater than 1° during a trial resulted in a visual warning. After a random period of 1000–1400 ms, the target appeared randomly left or right of fixation. Observers simply made a two-alternative forced choice as to the location of the target by pressing the appropriate key (left or right arrow keys). Target contrast was varied, and all conditions were randomly interleaved. For comparisons with natural images, we used threshold values from the 1/f textures for a given observer. In this case, targets were presented at detection threshold only for each condition.

During the saccade task of the primary experiments, the visual display was identical to the threshold procedure except observers were instructed to make a saccade to the target as quickly and accurately as possible without making saccade direction errors. After a trial was initiated, a randomly selected structured background appeared or the screen remained uniform gray. This was followed by an 800–1200 ms random period, then a 200 ms gap (fixation spot removed), after which the target appeared for 1000 ms. Observers were encouraged to make a saccade on every trial (and did so on 98% of trials), resulting in at least 32 trials per condition for each observer. Eye traces and event data were recorded, and analyses were done off-line.

Analyses
Latency was the time between target onset and the onset of the first saccade, which was based on a velocity threshold of 30°/s and an acceleration threshold of 8000°/s^2. All mean latencies are based on correct saccades only. Saccadic facilitation was the average difference (latency$_{structured}$ − latency$_{uniform}$) between several interpolated points along the latency/multiples of threshold curves and was restricted to points along the curves where the proportion of correctly directed saccades was significantly above chance.

Supplemental Data
The Supplemental Data for this article can be found online at http://www.current-biology.com/cgi/content/full/18/2/124/DC1/.

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