Saccadic compression can improve detection of Glass patterns

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Abstract

Around the time of saccadic eye movements, briefly presented stimuli are seen to be displaced from their real positions. The direction of the displacement is always towards the saccadic target, resulting in a compression of visual space (Nature 386 (1997) 598). To examine whether the compression may be used by the visual system to aid performance, we measured sensitivity for detecting horizontal and vertical Glass patterns around the time of saccades. Sensitivity to widely spaced horizontal Glass patterns improved slightly during the period just prior to making a horizontal saccade, while sensitivity to vertical patterns was impaired by the saccade. The results provide further evidence for compression in the direction of the saccade at saccadic onset, and show that it does not only affect the apparent position of visual stimuli, but can also improve performance on a visual task. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Saccades are ballistic eye movements that frequently reposition our gaze. Each saccade affects our vision in many ways, producing a transient suppression of low-frequency stimuli and displacements in apparent position (for a recent review see Ross, Morrone, Goldberg, & Burr, 2001). One of the more bizarre and least explicable phenomena is the perceptual compression of visual space at the time of saccades, where briefly flashed stimuli tend to be seen near the saccadic target (Lappe, Awater, & Krekelberg, 2000; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). Compression occurs only in the direction of the saccade, without affecting the positions in the orthogonal direction (Morrone et al., 1997). The compression affects the apparent position of single bars, the relative position of two bars flashed at different times and can even cause multiple bars to merge into one. The effects begin at about 75 ms before saccade onset, reach a peak around onset or just before, and returns to baseline 60–70 ms later. Compression occurs only with real saccadic eye movements, not with saccades simulated with mirror motion (Morrone et al., 1997). Interestingly, it seems to affect perceptual but not motor space, as it does not occur when subjects indicate position of peri-saccadic targets by pointing (Burr, Morrone, & Ross, 2001).

One question raised by the previous studies is whether peri-saccadic compression is simply a perceptual phenomenon, affecting the *appearance* of stimuli, or whether it can actually improve performance on a discrimination task. To this end we investigated whether saccadic compression can improve detection of Glass patterns, moiré patterns constructed from spatially random dots by duplication and displacement (Glass, 1969; see Fig. 1). Single pairs in the Glass pattern are visible only at close inspection, but the global "streakiness" is immediately apparent. Detectability of the global structure depends strongly on the separation of the dot pairs, becoming more difficult with wider dot separation (Dakin, 1997b; Jenkins, 1983; Wagemans, Van Gool, Swinnen, & Van Horebeek, 1993). In this study we measured detectability of Glass patterns with wide dot separation, oriented either in the direction of the saccade or orthogonal to it. The results show that saccades produce a small but consistent improvement in

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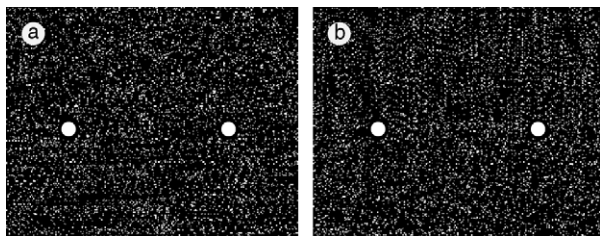*E-mail address:* loredana.santoro@physiol.ox.ac.uk (L. Santoro).

Fig. 1. Examples of the stimuli used in this study. The Glass patterns were confined to the upper or lower half of the screen. Figure (a) shows an example of a horizontal Glass pattern (lower half) with dot spacing 8 pixels (corresponding to 41′ under the viewing conditions of the experiment), and figure (b) vertical pattern (upper half) with dot spacing 8 pixels (44′). The other halves are filled with random noise. The large dots show the fixation and saccade target, turned on and off as described in methods.

detection of parallel Glass patterns, but are detrimental to orthogonal patterns, showing that the compression can affect performance.

2. Methods

2.1. Stimuli

Stimuli were generated on a Barco Calibrator Monitor at 200 frames/s by frame store (Cambridge Research System VSG2/3) under the control of a Pentium III personal computer. The screen resolution was 448 by 310 pixels, subtending $38° × 28°$ from the viewing distance of 57 cm.

The visual stimuli were horizontal or vertical Glass patterns, comprising 100 pairs of random dots, separated either horizontally or vertically by a variable distance (see Fig. 1). If the displacement caused the dots to fall off screen, they were wrapped round to the other side. Each dot subtended 2 pixels (about $10 × 10$ arcmin). To be maximally visible during saccades, the dots were of high contrast, white (70 cd/m²) against a dark (0.06 cd/m²) background. Experiments were performed with dim background room lighting.

2.2. Procedure

We measured detection of both horizontal and vertical Glass patterns during saccadic and normal vision. The Glass pattern was displayed to either the upper or lower half of the screen, with the other half filled with random dots of matched density (Fig. 1).

Observers were required to identify the field containing the pattern by pressing an appropriate response button. Errors were signalled by an audible tone. Prior to collecting data, observers were trained over many sessions to understand well the task, and to asymptote learning effects. Training was also needed to stabilise saccadic latency.
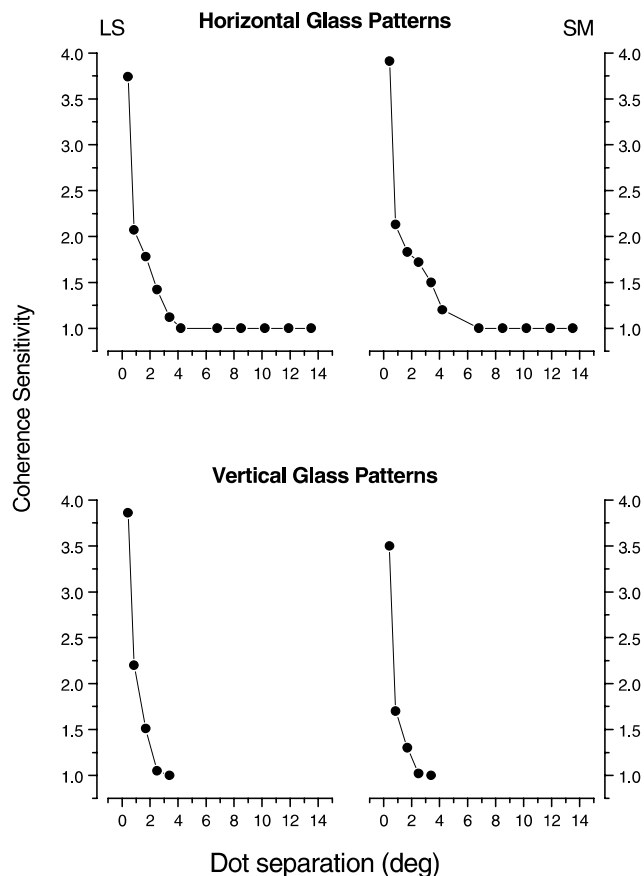

Fig. 2. Coherence sensitivity (inverse of proportion of coherent dots at threshold) for detecting horizontal and vertical Glass patterns, as a function of dot separation, for two observers. For both patterns, sensitivity falls rapidly with dot separation.

For the data of Fig. 2, the coherent Glass pattern was diluted with random dots, maintaining average density. The adaptive QUEST algorithm (Watson & Pelli, 1983) adjusted the coherence ratio after each trial, and the final threshold was estimated by fitting a cumulative Gaussian to the probability of seeing curves. For the data of the other figures, the Glass patterns were totally coherent, and percent correct performance was measured. This was converted to d' from the tables in MacMillan and Creelman (1990).

For each trial a white fixation spot (subtending about 1°) appeared 10° left of centre (9° from the leftward edge of the monitor). After a variable interval (400–650 ms), it was extinguished and a similar white spot, the saccadic target, was displayed 19° to the right for a variable duration. Observers saccaded towards the target, and immediately following the target offset the stimulus (Glass pattern with noise) was displayed for only 5 ms (one video frame) at a variable time before, during or after the saccade.

Eye movements were monitored with an infrared scleral limbus tracker (HVS SP150: 10 kHz), sampled by computer at 1 kHz. At the end of each trial the eye trace

was displayed on the display monitor, so the experimenter (sometimes also the observer) could monitor the quality of the saccade and reject those of insufficient amplitude or precision. For each trial the computer recorded eye latency, saccade duration, time of stimulus presentation and subject's response. After the conclusion of the session, the computer pooled trials into bins of 25 ms width and calculated average percent correct. Each bin contained 154 trials on average, and never less than 100.

2.3. Subjects

Measurements were made on two young female observers, author LS and SM (who was unaware of the goals of the study). Both had corrected to normal vision.

3. Results

Fig. 2 shows measurements of signal to noise sensitivity for detecting the position (upper or lower filed) of briefly presented horizontal and vertical Glass patterns, as a function of dot separation. As previously reported (Dakin, 1997b; Jenkins, 1983; Wagemans et al., 1993) sensitivity falls off sharply with dot separation. Separations greater than 4° required 100% coherence to reach threshold performance, and it was not possible to run the QUEST routine in these conditions. Performance was slightly worse for vertical than horizontal patterns, at all separations.

To test large dot separations during saccades, where compression may be expected to help performance, we used patterns with 100% pattern coherence and measured percent correct performance for each separation, for various times relative to saccadic onset. The percent correct values were converted to d'. Fig. 3 summarises the main results of this study, showing detection performance of Glass patterns as a function of dot separation for fixation (open circles) and for the 25 ms period just prior to making a horizontal saccade (filled circles). The upper curves show performance for horizontal Glass patterns, lower curves for vertical Glass patterns. For the horizontal patterns, saccades improved performance for the wider dot spacings (>5°), while not affecting performance for the closely spaced dots. The average saccadic advantage for the larger dot spacings was about $0.3d'$ for LS and $0.5d'$ for SM. At very large separations, the performance in both conditions fell to chance ($d' = 0$).

The results for the vertical Glass patterns, oriented orthogonally to the saccades, were quite different. For no separation was there an advantage for the peri-saccade condition. At all separations measured (those at which performance was better than chance), perfor-
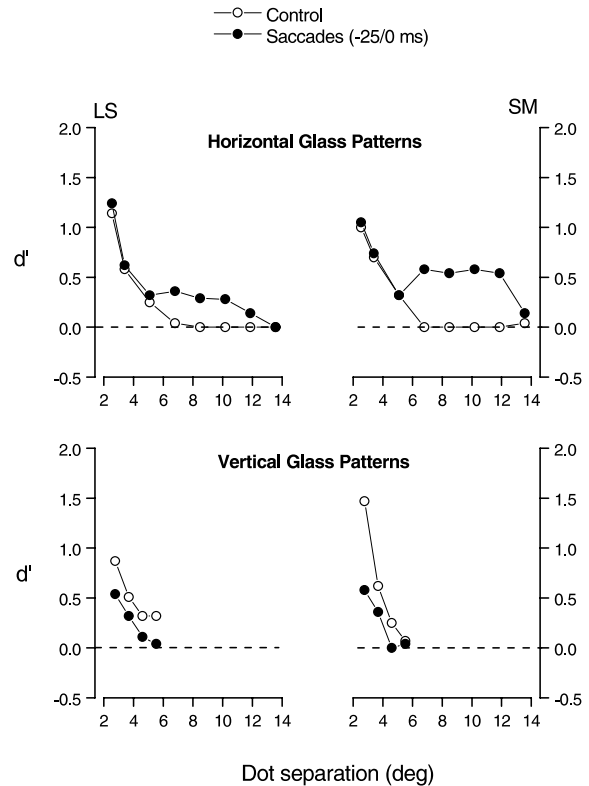

Fig. 3. Sensitivity for detecting horizontal and vertical Glass patterns during fixation (○) and during the 25 ms just prior to saccades (●). The patterns had 100% dot coherence and d' was calculated from the percent correct. Standard errors were about the size of the symbols.

mance was better in the control condition than just before saccades.

Fig. 4 shows detection performance for horizontal and vertical Glass patterns as a function of time relative to saccadic onset (with dashed lines indicating control performance).

As shown in Fig. 3, there is very little pre-saccade advantage for horizontal patterns with dot separation less than 5°. However, for those separations, there was often an advantage sometimes after the saccade. We find difficult to explain why this should occur, but it did seem to be consistent. For the vertical patterns, there was never this advantage.

4. Discussion

This study shows that the perceptual compression that has been reported to occur at the time of saccades not only affects the appearance of visual scenes, but can also improve detection performance for widely spaced horizontal Glass patterns. It is as if the compression "brings the dots closer together" making the task easier. The effect was not large, only $0.3–0.5d'$, but very consistent and specific to horizontal patterns of wide dot

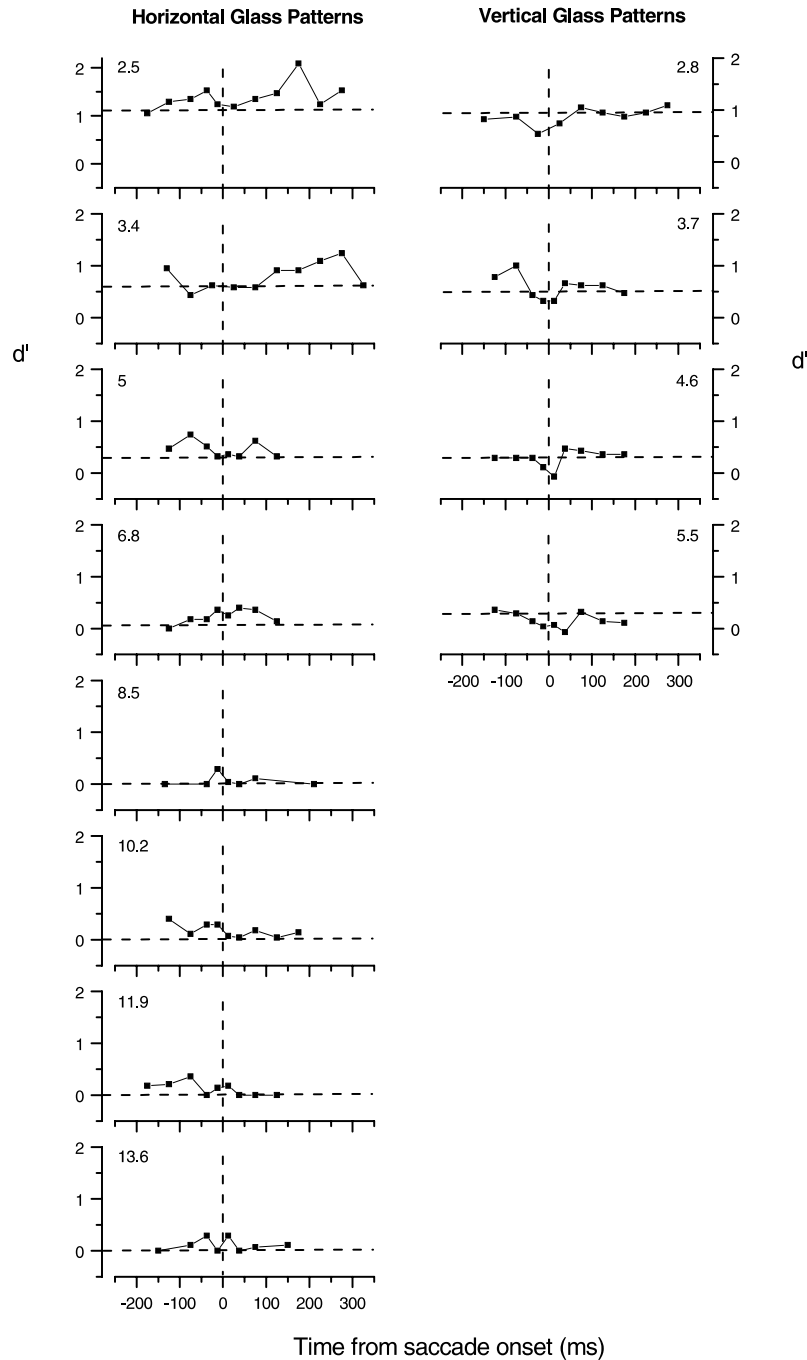**Horizontal Glass Patterns**　　　　　**Vertical Glass Patterns**

Fig. 4. Detection sensitivity for horizontal and vertical Glass patterns for one observer, LS, as a function of time from saccadic onset. The numbers indicate the dot separation (in degrees). The horizontal dashed line refers to sensitivity during fixation.

spacing. The fact that saccades did not facilitate vertical patterns, and indeed hampered their detection, suggests that the results do not merely reflect a generic facilitation of vision, but an improvement specific to widely spaced parallel Glass patterns. This is consistent with the fact that peri-saccadic compression occurs only in the direction of the saccade, not orthogonal to it (Morrone et al., 1997). The slight impairment of performance on

vertical patterns may be a consequence of suppression of low spatial frequencies (Burr, Holt, Johnstone, & Ross, 1982; Burr, Morrone, & Ross, 1994), or may simply result from a generic impairment of vision during saccades, possibly due to the extra attentional load.

One of the questions raised by these results is how the compression may facilitate Glass pattern detection, and at what neural level does the facilitation occur. Informal

observations from our laboratory have suggested that compression acts at a moderately high level. It seems to act after at least some basic image processing has occurred, such as extraction of orientation. For example, if slanting lines are used as stimuli, they do not appear to straighten up during saccades, but are displaced in their entirety towards the saccadic target. Similarly, small circles remain circles (do not become oblongs) and squares do not become rectangles (Matsumiya & Uchikawa, 2001). However, the fact that the compression can assist in the detection of Glass patterns suggests that it should precede the site of processing of Glass patterns.

What neural mechanisms are responsible for the analysis of Glass patterns? At certain spatial frequency bands there is a predominance of contrast energy in Glass patterns in the direction of the perceived streaks. Several studies (e.g. Dakin, 1997a,b) have shown that this energy is used in the detection of Glass patterns, suggesting that low-level orientation-selective mechanisms, such as neurones of V1, could be involved in Glass pattern detection. However, other studies show that early filtering mechanisms are not sufficient to explain all the data on Glass pattern detection. For example, when duel Glass patterns are composed of simultaneous vertical and horizontal displacements of different contrast strength, the most salient structure is determined by pairing of the two low-contrast elements of the pattern, not the high (but slightly different) contrast pairs (Earle, 1999). This and other data (see Stevens & Brookes, 1987) suggests that other, higher-order processes such as "symbol matching" may be involved. Thus it is possible that these higher-order processes may benefit from saccadic compression, not the low-level mechanisms.

Neurophysiological correlates for the psychophysically observed compression have been reported at many neural centres, mainly along the parietal processing stream (see Ross et al., 2001, for review). Duhamel, Colby, and Goldberg (1992) showed that the receptive fields of some, but not all neurones in the lateral intraparietal area (LIP) of monkeys change position before each saccadic eye movement, effectively anticipating its consequences. Other neurones continue to respond to the presaccadic position and some respond to stimuli in both positions. Neurones upstream from LIP (including the frontal eye field and the superior colliculus) might interpret stimuli arising over a large area (comprising pre- and post-saccadic receptive fields) as being in the same position, resulting in compression. A population analysis of neurones in VIP and LIP in response to briefly flashed stimuli at the time of the saccade showed clear compression of the population output (Kubischik & Bremmer, 1999). Neural correlates of peri-saccadic mislocalization have also been observed in MT and MST neurones. Using a Bayesian analysis, Krekelberg, Kubischik, and Bremmer (2000) showed that a population of MT and MST cells can encode veridically the position of briefly flashed bars. However, analysis of the same neurones just prior to a saccade (using the weights derived from free viewing) shows a gross mislocalization in the population response that would cause compression.

A complementary phenomenon takes place in some V4 neurons. There the receptive fields shrink and shift towards the saccadic target just prior the saccade execution onset (Tolias et al., 2001). This change is in the opposite direction from that would produce compression, but could well be related.

At present there is little evidence of what neural mechanisms may be involved with Glass pattern detection. Wilson and Wilkinson (1998) suggested that V4 may be implicated in the detection of radial and circular Glass patterns, on the basis of the receptive field properties of V4 cells (Van Essen, 1985; Van Essen, Anderson, & Felleman, 1992), but there is no firm evidence for this. In a recent fMRI study, Braddick, O'Brien, Wattam-Bell, Atkinson, and Turner (2000) showed that areas differentially activated by global Glass-like patterns (again radial and circular), included regions in the middle occipital gyrus, the ventral occipital surface, the intraparietal sulcus, and the temporal lobe. V1 was not activated by these patterns. However, there have been no studies to date using horizontal or vertical Glass patterns.

So while it is far from clear what neural mechanisms may be responsible for the detection of Glass patterns, and how these may be modified by saccades, it is clear that the perceptual compression caused by saccades can improve detection performance for Glass patterns. Hopefully future studies about the neural mechanisms involved in the detection of Glass patterns and in saccadic compression will help understand how saccades can facilitate the detection of Glass patterns.

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