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SACCADIC SUPPRESSION OF LOW-LEVEL MOTION

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Abstract—We measured the detection of motion before, during and after a saccade to explore the effects of a saccade on motion perception. To isolate the low-level motion mechanism, the stimulus was a random-dot field displaced by small distance (0.3 deg) within a stationary frame. The displacement signaled motion clearly if eyes were fixated, but for the displacement during a saccade, motion was not detected whether the displacement was defined in spatial coordinates (expt 1) or in retinal coordinates (expt 2). Since motion could be seen with ISIs longer than the duration of a saccade (expt 3), the suppression cannot be attributed to visual loss during the saccade. Experiment 3 also showed that motion was never seen for a displacement that occurred during a saccade, even though the random dots were replaced by a uniform field during the eye movement thereby eliminating any masking effect of the sweep of the image across the retina. The purpose of the saccadic suppression of motion may be to block out unreliable motion signals that would be produced by a saccade. Since saccade distances are very often greater than the maximum distance over which the low-level motion mechanism can produce accurate direction discrimination for fine textures, motion signals would generally indicate false directions if they were not suppressed.

Saccadic suppression Low-level motion Spatial coordinates Retinal coordinates $D_{\max}$ ISI

INTRODUCTION

The elevation of threshold for detecting a brief flash of light while a saccade is in progress is well documented and is known as saccade suppression (see reviews by Matin, 1974; and Volkmann, 1986). Degraded performance during saccades has been reported for other visual tasks as well, such as contrast sensitivity (e.g. Volkmann, Riggs, White & Moore, 1978).

The effect of saccades on the visibility of image displacement has also been explored (Bridgemann, Hendry & Stark, 1975; Bridgeman & Stark, 1979; Goto & Ikeda, 1981; Heywood & Churcher, 1981; Mack, 1970; Stark, Kong, Schwartz, Hendry & Bridgeman, 1976; Whipple & Wallach, 1978). Stark et al. (1976) displaced a stimulus in a one-dimensional Ganzfeld and found that small displacements during a saccade were not noticed, even though observers could detect these displacements if their eyes were steady. Their results imply that mechanisms which detect displacement do not work during a saccade in the same way as they do when the eyes are fixated. However it is not clear from previous research which mechanisms were used to detect the displacement during steady viewing. There were two possible cues: perceiving the movement of the stimulus or noticing the change in its location. Either or both of these mechanisms may have mediated performance during steady viewing and, therefore, either or both of them may be suppressed by saccades. The present report isolates motion mechanisms in order to study the influence of saccades specifically on motion perception in the absence of other cues for detecting the displacement of images, such as the position of a target relative to the surround or to the observer's head position.

To isolate motion independently of position change, we used random-dot patterns as our stimulus. The displacement of random-dot patterns stimulates a motion process that occurs at an early stage in the visual system—the so-called low-level or short-range motion mechanism (Braddick, 1974) that is distinguished from higher-level processes (form-based or long-range motion processes) by Anstis (1980) and Braddick (1980). Random-dot patterns are appropriate to isolated low-level motion, since they have few identifiable forms whose displacement can be noticed. Although Stark et al. (1976) also displaced a random-dot pattern, the edges of the pattern moved with the dots, so that the detection of the displacement could be due to detection of the position changes of the entire patch of dots.

EXPERIMENT 1. DISPLACEMENT LESS THAN D_{max} IN SPATIAL COORDINATES

The stimulus displacement was chosen to be less than D_{max} so that all the dots were seen as moving in the same direction (i.e. coherent motion) with fixated eyes; D_{max} is the maximum distance of displacement over which coherent motion can be seen (Braddick, 1974). There are two coordinate systems that can be used to describe the displacement of an image presented to the visual system: viewer-centered coordinates to describe the displacement independent of eye position and retinal coordinates to describe the displacement on the retina. In the first experiment, stimuli were displaced a small distance in spatial coordinates. We also examined the interaction between the direction of the dot displacement and that of the saccade.

Methods

Observers. Two male observers participated in the experiment. Both had normal or corrected-to-normal acuity.

Stimuli and apparatus. Random-dot fields were generated by a computer (PDP-11/23) and displayed by a image processor (Grinnell GMR 270) on a CRT in a dim room. The size of the random-dot field was 30 × 30 deg and the field was composed of a square matrix of 128 × 128 dots, each dot approx. 0.23 deg arc square. Half of the dots were black (1 cd/m^2) and the other half were white (30 cd/m^2). Two random-dot patterns were used for a trial: the first pattern was generated arbitrarily and then shifted 0.3 deg horizontally or vertically to make the second. The shift direction was either left or right in the horizontal displacement condition and either up or down in the vertical displacement condition. Since the edges of the display were stationary, some dots disappeared at one edge of the screen in the second pattern, and others appeared at the opposite edge. Two circular spots of different colours (one blue and one red) served as fixation points. These were positioned on a white horizontal bar (1.3 deg high × 30 deg wide) which divided the random-dot field at the center. These two spots were always located equal distances to the right and left of the center of the screen and were used to indicate the required direction and distance of a saccade. In both the horizontal and the vertical displacement conditions, two saccade distances, 15 and 3.8 deg were investigated.

The horizontal component of the movement of the observer's right eye was monitored by detecting light reflected from their sclera with infrared-sensitive photocells mounted on spectacle frames (Biometrics Inc., Model SGH/V-2). Eye movement signals from the photocells were fed to a microcomputer (Apple II) which sampled them every 8 msec. The spatial resolution of the measurement of the eye position was limited to 0.12 deg as a result of the 8-bit sampling used by the microcomputer. The observers viewed the display with their right eye and their left eye was covered.

The microcomputer sent signals to the host processor (PDP-11/23) to control the display sequence: the onset of the first pattern, the exchange of the first and the second patterns and the offset of the second pattern. The timing of the exchange of the patterns was synchronized to occur at the beginning of the image processor's vertical refresh cycle. As there was no feedback to the microcomputer from the image processor which exchanged the patterns, the exchange could occur up to 16.7 msec (1 frame of the display) after the signal from the microcomputer.

Procedure. The experimental sequence of a trial was as follows. The observer first fixated the red spot, and pushed a button when he was ready for the trial. The signal from the button initiated the display of the first random-dot pattern. A warning tone sounded 500 msec after the onset of the first pattern. This was the signal for the observer to make a horizontal saccade to the blue spot. After a randomly determined interval from the tone (duration of between 100 and 300 msec with 8 msec steps), the first pattern was replaced by the second pattern with no ISI (other than the 16.7 msec of refresh time on the screen). The trial finished 2 sec after the onset of the first pattern, with the offset of the second pattern. The variable interval between the tone and the exchange of patterns determined whether the exchange was more likely to occur before, during or after a saccade. After the end of the trial, the observer identified the direction of motion of the random-dot field in a two-alternative forced choice. The observer had to respond either left or right in the horizontal condition and up or down in the vertical condition. After each trial the experimenter checked the record of the observer's eye movements and discarded trials in which eye blinks occurred.

For one half of the trials the red spot was to the right of the center of the screen, and for the other half it was to the left. Thus, half the saccades were from right to left, while the other half of the trials were in the opposite direction. The direction of the displacement was also randomly determined from trial to trial independently of the direction of the saccade. The saccade distance and the axis of the displacement were constant throughout a session. Each session comprised 200 trials. One observer, SS, completed 4 sessions and the other observer, PF, completed 2 sessions for each of four combinations of two saccade sizes (15 and 3.8 deg) and two displacement axes (horizontal and vertical).

The eye tracker was calibrated prior to each session. While the observer alternated fixation between two spots separated by either 15 or 3.8 deg, depending on condition, the experimenter adjusted the calibration constants until a marker that indicated measured eye position fell on each fixation spot in turn. The marker position moved with a minimum step of 0.23 deg on the screen. Prior to each trial, the alignment between the marker and fixation spots was verified while the observer was fixating the first fixating spot (red one). When the experimenter found the misalignment that exceeded two units of the marker step (0.46 deg), the calibration constants were adjusted again. The maximum error of the eye-position measurement was, therefore, within ±0.5 deg throughout a session.

Since we used eye movement monitoring only to identify the onset and offset of saccades in this experiment, we were interested only in the velocity of eye movements. The velocity of eye movements was measured as the difference between sequential two readings of the eye position. A saccade was defined as being in progress when the velocity of an eye movement exceeded 50 deg/sec. When the velocity of an eye movement exceeded 50 deg/sec for the first time in a trial, the time of the first reading of the sequential two that provided the velocity was adopted as the time of the beginning of a saccade. Similarly, the time of the end of the saccade was defined as the time of the second reading for which the velocity became less than 50 deg/sec after the beginning of the saccade.

Results and discussion

The measured time offset between the exchange of the two patterns to the beginning of a saccade was, on average, somewhat shorter than the true offset because of the delay while the host computer waited for the beginning of the next screen refresh cycle of the image processor before exchanging the images. The time offsets have therefore been modified by adding 8.4 msec, half of the maximum delay of 16.7 msec.

Since the delay of displacement from the tone was determined randomly and since the saccadic latency of the observers varied, the time offset between the saccade and the displacement also varied from trial to trial. Time offsets were pooled in 10 msec bins and the percentage of detections of displacement direction was calculated for each of these discrete intervals. Each point was derived from 30 trials on average with a minimum of 10 trials for SS and 10 trials with a minimum of 5 trials for PF.

Figure 1 shows the percentage of correct responses for the horizontal displacement condition. The average saccadic duration is also shown along with the standard deviation in each panel as the horizontal line at the top. The percentage of correct responses began to fall around 20 msec before the beginning of a saccade for SS, or 40 msec before the beginning of a saccade for PF, and then reached chance levels (50%) about 10 msec before the beginning of a saccade for both observers. The percentage of correct responses remained at chance levels during the saccade but recovered quickly at the end of the saccade. Almost all displacements which occurred only 20 msec after the completion of a saccade were correctly identified. This occurred for both the 15 and 3.8 deg saccades. These results suggest that saccades suppress the low-level motion process.

Figure 2 shows results of the vertical displacement condition for two observers. The percentage of correct responses for the vertical displacement shows a similar time course to that for the horizontal displacement in both the 15 and 3.8 deg saccade sizes. Nevertheless, a small difference in the onset of saccadic suppression can be seen between the horizontal and vertical conditions. In the vertical displacement condition, suppression began around 10 msec before the beginning of the saccade for SS and 20 msec before for PF, whereas it began 20 or 40 msec before the saccade in the horizontal displacement condition.

The response was at chance level for both horizontal and vertical displacements during saccades, suggesting that the suppression of motion detection does not depend on the relationship between the direction of the displacement and the saccade, agreeing with Stark et

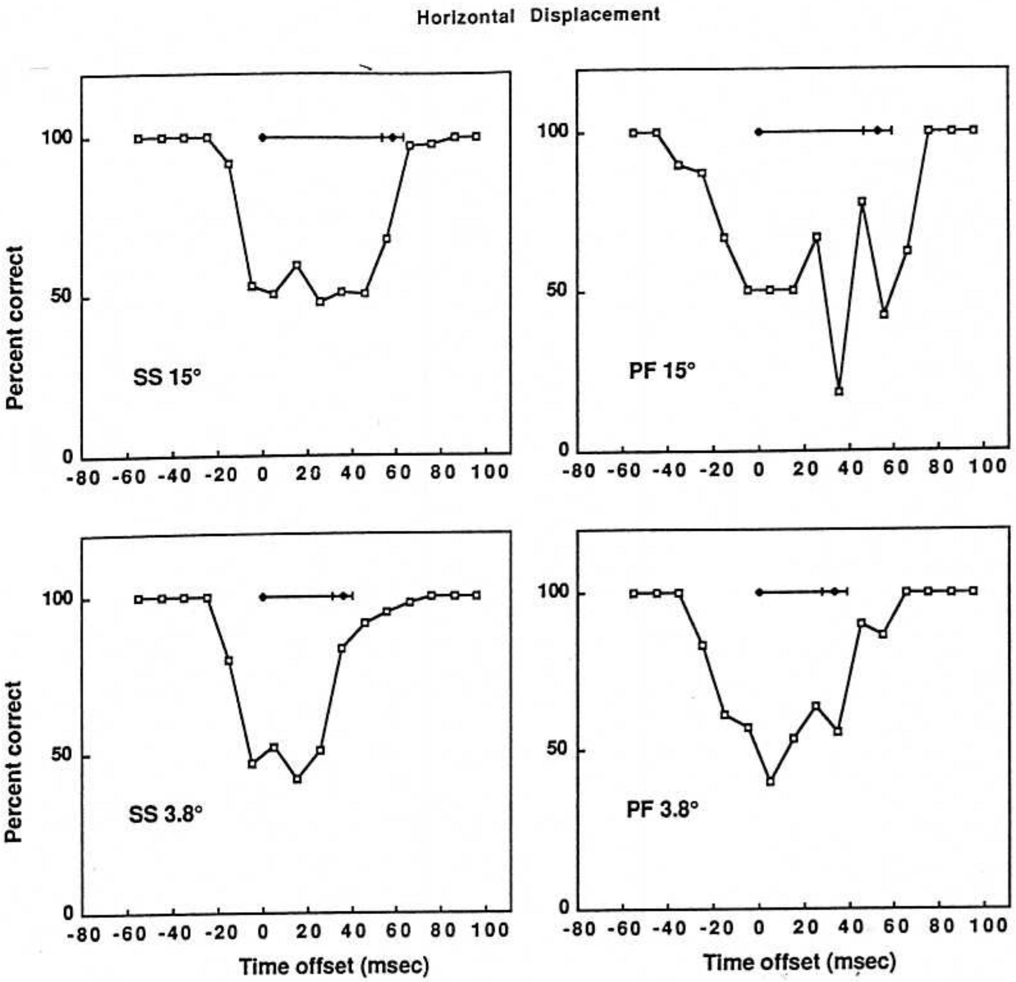

Fig. 1. Percent correct direction discrimination as a function of the time offset between the displacement and the *beginning* of a saccade for horizontal displacement conditions. Both displacement directions (right and left) are pooled together. Left panels, observer SS. Right panels, observer PF. Top: for 15 deg horizontal saccades. Bottom: for 3.8 deg horizontal saccades. Each point was derived from 30 trials on average for SS and 10 trials for PF; the mimimum number of trials of a point was 10 for SS and 5 for PF. The length of the horizontal solid line with filled diamonds shows the average saccade duration for each condition. The standard deviation of the saccade duration is shown at the righthand end of the line by an error bar.

al. (1976). On the other hand, the source of reported effects of displacement direction (Heywood & Churcher, 1981; Whipple & Wallach, 1978) may have been the slight difference in the onset of suppression between the horizontal displacement and vertical displacement that we found here.

The ±8.4 msec of our temporal uncertainty introduced into the time offset measure by the asynchronous operation of our two computers has the effect of blurring any sharp transient in performance. The results nevertheless showed quite steep changes in percentage of correct responses with time offset, steeper, in fact, than those seen in many previous reports of saccadic suppression (e.g. see figures in the review by Volkmann, 1986).

Although random-dot fields were used to isolate the low-level motion mechanism, it is possible that identifiable clusters of dots may have been used as visible markers in order to notice the displacement. However, the observers claimed that they based their responses on a perception of motion without noticing the displacement of any structure of random dots.

The break down of motion perception due to a saccade indicates that a saccade may have effects that extend well beyond its duration. Motion can be perceived accurately even when a dark interval (ISI) up to 100 msec is inserted between two displaced random-dot patterns (Baker & Braddick, 1985; Braddick, 1973; Lappin & Bell, 1976). The saccadic duration in our experiment was only 60 msec for a 15 deg sac-

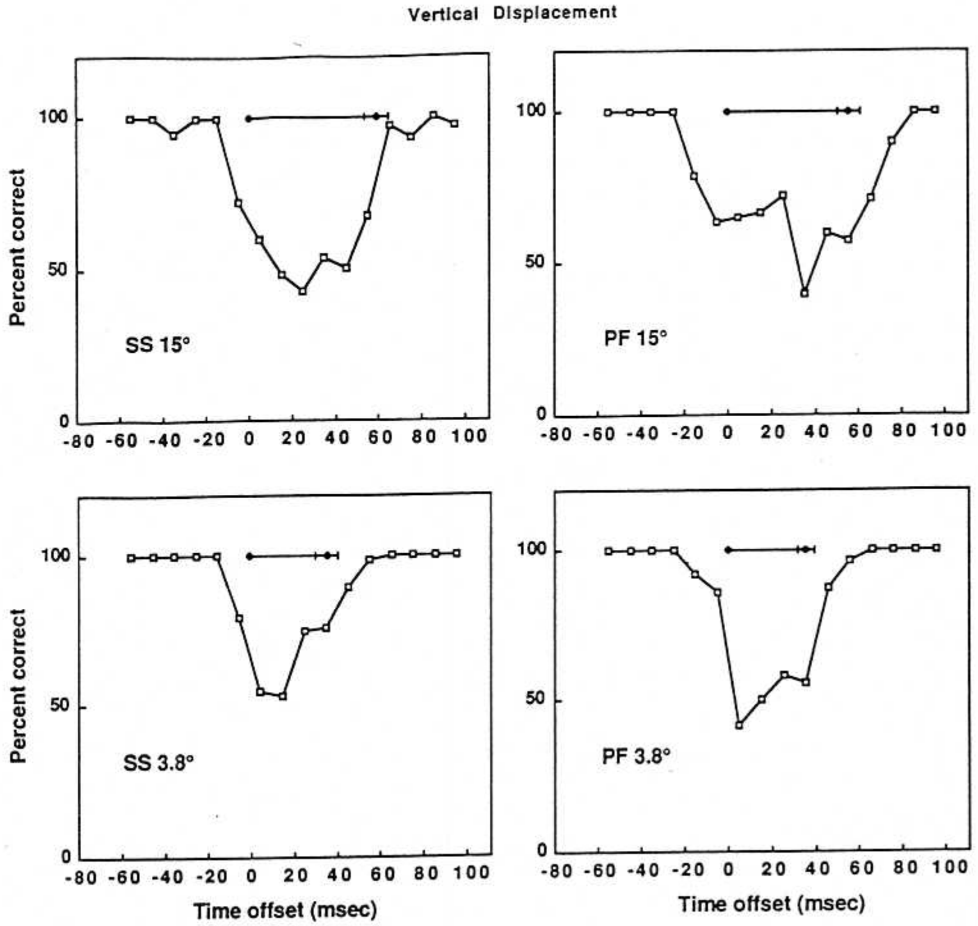

Fig. 2. The same figures as Fig. 1 but for vertical displacements of the stimulus with horizontal saccades.

cade and 35 msec for a 3.8 deg saccade. Our results, therefore, suggest not only that the low-level motion process is suppressed during the saccade but also that processes which could normally integrate over even longer periods must be suppressed as well. It should be noted, however, that the retinal image during a saccade cannot be simply regarded as a dark field. The image is degraded by a rapid eye movement that sweeps the display over the retina and this may in some way mask the perception of motion. This issue will be discussed in more detail in expt 3, in which only a uniform field was present during a saccade on some trials.

In expt 1, stimulus displacements were 0.3 deg in spatial coordinates so that the spatial displacements of the stimuli were small enough to signal coherent motion. However, on trials where the stimulus was displaced during a saccade, the resulting displacements on the retina were greater than 3 deg; for example, the retinal displacement was 4.1 deg when eyes moved 3.8 deg horizontally in the opposite direction to the stimulus (which itself moved 0.3 deg). Although $D_{\max}$ seems to vary with experimental conditions, it is not greater than 3 deg for the random-dot fields used here. If the low-level motion process only works for displacements smaller than $D_{\max}$ on the retina, coherent motion could not be seen with the retinal displacement which occurred during a saccade in expt 1. The failure to detect the direction of displacement during a saccade may therefore have resulted from the large displacement of the stimulus in retinal coordinates. To address this issue, the second experiment used stimulus displacements smaller than $D_{\max}$ in retinal coordinates.

EXPERIMENT 2. DISPLACEMENT LESS THAN $D_{\max}$ IN RETINAL COORDINATES

To calculate the image displacements in retinal coordinates, the spatial coordinates were adjusted to take account of the saccade size. The displacement in spatial coordinates was 3.5 deg for the 3.8 deg saccade, so that the position of the dot pattern on the retina before the saccade differed from its position after the saccade by 0.3 deg, the same size as the spatial displacement in expt 1.

We have labelled the retinal displacement 0.3 deg but because of the inaccuracies of saccades, this will only be the mean value of the retinal displacement. Since the standard deviation of saccades is about 10% of saccade distance when the target is within 5 deg of fixation (see Findlay, 1982; Hallett, 1978; Henson, 1979; Kapoula, 1985; and Kapoula & Robinson, 1986), the variability of the saccades in our experiment will be about the same magnitude (±0.4 deg) as the retinal displacement that we are trying to produce. We can therefore expect that the actual retinal displacement will occasionally be in the direction opposite to that intended. Since we could not identify these trials precisely (our position accuracy was ±0.5 deg and as a result we did not attempt to measure saccade distance during a trial, nor did we evaluate saccade variability) we asked observers not to indicate the direction of motion but whether or not any motion was seen on the display. "Any motion" included global motion of all the dots moving coherently or local motion of individual dots. The "no motion" response indicated that no motion of any kind was seen anywhere in the display. As a control, on one half of the trials, there was no displacement of the pattern on the display while the other half of the pattern was displaced 3.5 deg spatially.

The possible effects of inaccuracy in the saccade were examined by first assuming that the saccade size was normally distributed with a mean of 3.8 deg along the horizontal axis and a standard deviation of 0.4 deg (the standard deviation of 0.4 deg was used symmetrically for all direction in two-dimensional space, although the landing points of saccades seem to scatter along the axis of the saccade direction more than others as can be seen in the plots in Ottes, Van Gisbergen & Eggermont, 1984, 1985). Figure 3 depicts the profile of the assumed two-dimensional distribution function along the horizontal axis. A preliminary experiment showed that perfect detection of motion direction was possible for spatial displacement sizes between 0.06 deg (the minimum displacement possible on the screen) and 0.82 deg, when the eyes were fixated. Using the values of 0.82 and 0.06 deg as D_{max} and D_{min} (the minimal displacement with which motion can be seen), the probability of occurence of trials on which the retinal displacement would be larger than D_{max} or less than D_{min} was statistically evaluated. This informal analysis predicted that for the trials where the displacement occurred during a saccade, 79.7% would produce retinal displacements greater than D_{min} but less than D_{max}; 19.7% larger than D_{max}, either leftward or rightward (grey areas on left and right tails of the distribution in Fig. 3), and 0.6% would be smaller than D_{min} (slanted part in Fig. 3). A second analysis considered the tendency of saccades to undershoot by about 10% and used a mean saccade size of 3.4 deg rather than 3.8 deg. In this case, 83.8% of trials with displacements occurring during a saccade produced retinal displacements greater than D_{min} and less than D_{max}; 15.5% were greater than D_{max} and 0.7 deg were less than D_{min}.

If we assume that these retinal displacements occurring during a saccade produce the same effects as they would if they occurred while the eyes were fixated, then we would predict that over 99% of these trials would produce reports of motion: between 79% and 84% of them because of coherent motion either to the left or to the right and the remainder because of incoherent local motion (displacements larger than D_{max}). Responses of "no motion" due to displacements less than D_{min} (our liberal estimate of it) should occur on less than 1% of the trials.

On the other hand, on trials where the displacement occurred before or after the saccade, the retinal displacement was always greater than D_{max} and should produce a perception of incoherent local motion. "Motion" responses should therefore occur on 100% of the trials.

Clearly, if the proportion of correct responses is near 100% for displacements occurring both within and outside the saccade, our data will not enable us to identify the type of motion percept occurring during the saccade. However, the results will show that no motion percept whatsoever occurred during the saccade, so this problem does not arise.

Method

The procedure used in expt 2 was similar to that in expt 1. One difference was that the size of the displacement in spatial coordinates was defined by subtracting the desired displacement distance on the retina from the expected size of a saccade. The distance between two spots for fixation was 3.8 deg and the stimulus was displaced 3.5 deg in the same direction as a saccade

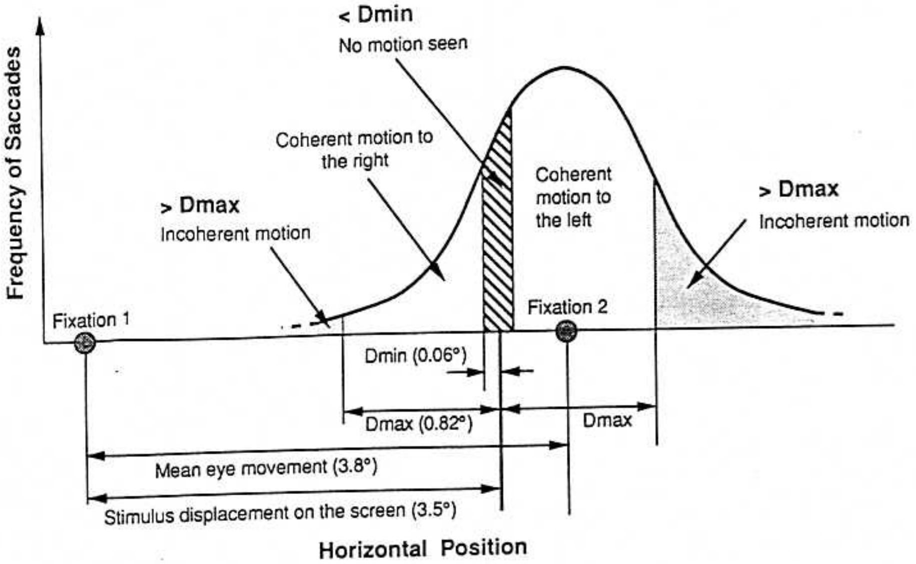

Fig. 3. Schematic view of the distribution of saccade size when the observer makes a saccade to Fixation 2 from Fixation 1 in expt 2. The figure also shows the motion that would be seen for these retinal displacements if they had occurred with the eyes fixated. The distribution is assumed to be a two-dimensional, normal distribution with a mean of 3.8 deg and a standard deviation of 0.4 deg. The areas filled in grey indicate the regions where the retinal displacement will be more than D_{max} (0.82 deg) and the slanted area indicates where the displacement will be less than D_{min} (0.06 deg). Note that this figure is the profile of the two-dimensional distribution along the horizontal axis.

so that the size of retinal displacement would be 0.3 deg in the opposite direction to that of the saccade if the stimulus was displaced during the saccade. Incoherent random motion was seen when the displacement occurred while the eyes were fixated since the stimulus was displaced more than D_{max} in spatial and retinal coordinates (3.5 deg in both coordinates). The displacement in this experiment is therefore a retinal displacement less than D_{max} only when it occurred during a saccade. The second difference was that the stimulus was displaced on one half of the trials and there was no displacement on the other half. The observers were instructed to indicate whether they saw motion or no motion in the display.

The trials in which corrective saccades (small saccades that automatically follow saccades that have failed to land accurately) occurred were discarded in addition to those in which blinks were observed. A corrective saccade was identified as any eye movement larger than 0.5 deg that was found within 150 msec after the end of the first saccade. Approximately 2.5% of all trials were discarded by this criterion. The elimination of trials with corrective saccades helped to reduce the number of the trials on which the retinal displacement might have been larger than D_{max}. The same two observers participated in this experiment: SS completed four session and PF three sessions.

Results and discussion

Figure 4 shows the percentages of trials in which the observers detected the movement of the pattern as a function of time offset for displacement trials for both observers. The percentages of correct responses for no-displacement trials (*No-d*) are shown by the small cross next to the ordinate. Since the trials in the no-displacement condition differed only in the point at which the saccade occurred during the 2-sec static display, they were identical for the purpose of the analysis and were pooled together for the analysis. Each datum point for the displacement conditions was derived from an average of 15 trials (with a minimum of 7) for SS and average of 9 trials (with a minimum of 5) for PF. The mean saccade duration is shown by the length of the horizontal line at the top of each panel.

For both observers the percentage of correct responses for displacement trials began to decrease approx 20 msec before a saccade began and again reached 100% correct around 20 msec after a saccade was completed. When the displacement occurred during a saccade, observers consistently responded "no motion".

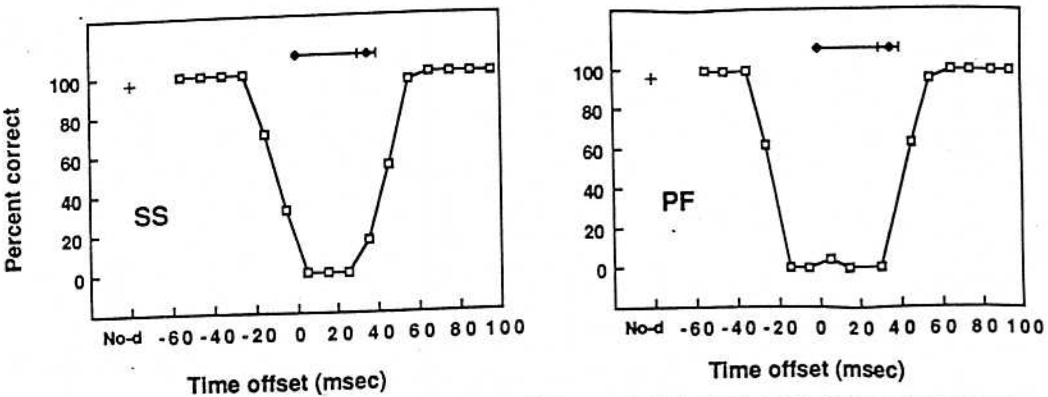

Fig. 4. Percentage of correct motion responses on displacement trials as a function of time offset in expt 2. The left panel for SS; the right panel for PF. The data at *No-d* (+) represent percent correct responses on no-displacement trials. These values were obtained by pooling responses over all no-displacement trials. Each point for displacement trials was derived from 15 trials on average for SS and 9 trials for PF, and the point for no-displacement was derived from 257 trials for SS and 203 trials for PF. The minimum number of trials of a point was 7 for SS and 5 for PF. The length of the horizontal solid line with filled diamonds shows average saccade duration for each condition. The standard deviation of the saccade duration is shown at the righthand end of the line by an error bar.

In fact, the observers reported that no change whatsoever was evident on these trials which appeared phenomenologically identical to the no-displacement trials. In contrast, almost all of the no-displacement trials were reported as "no motion", showing that a saccade that occurred while the image was static in spatial coordinates did not produce any impression of motion. These results indicate that no low-level motion was seen for images displaced during saccades, including those instances for which the image displacement was less than $D_{\max}$ on the retina. Note that the observers never saw coherent motion in any stimulus, only incoherent motion was seen in trials where the displacement occurred when the eyes were fixated (before or after a saccade).

In the discussion above, we have not considered the possibility that the degraded image, swept across the retina during a saccade, may mask the detection of the motion. Experiment 3 was conducted to address this issue. In addition, expt 3 explored the effect of inter-stimulus-interval (ISI) on motion perception while the eyes were fixated, in order to determine whether motion can be seen with an ISI which is longer than the saccadic duration.

EXPERIMENT 3. REMOVAL OF RANDOM DOTS DURING SACCADES AND THE EFFECT OF ISI

Although expts 1 and 2 suggest that the low-level motion system does not operate either during or across a saccade, there are two aspects of the saccade that may have indirectly suppressed the visibility of the motion. First, the random dots on the screen during a saccade are swept rapidly across the retina and this may mask the stimulus motion. In this third experiment, we therefore explored the influence on motion detection of ISIs that were longer than the saccade and were positioned so that the saccade could fall either before, after or *totally within* the ISI. Note that a saccade that occurs within an ISI does not produce any rapid motion of dots on the retina so that any masking effect of the dots is eliminated.

Second, rather than the visibility of the dots during the saccade being a problem, it may have been their invisibility. We argued previously that the duration of the saccade was less than the maximum ISI for which motion can be seen. Since the dots were physically absent during an ISI, the possibility that a saccade also renders the dots invisible should not be a critical factor. However, the previous values (Baker & Braddick, 1985; Braddick, 1973; Lappin & Bell, 1976) were measured with different stimuli. So, we evaluated the effect of ISI using two conditions: a spatial displacement condition (0.3 deg in spatial coordinates) and a retinal displacement condition (3.8 deg in spatial coordinates, 0.3 deg in retinal coordinates).

Method

To eliminate the spatial pattern on the screen during a saccade, an ISI which was longer the duration of a saccade (as measured for 3.8 deg saccades in expts 1 and 2) was interposed between the first and the second random-dot fields, using the procedure used in expts 1 and 2. The time course of the trial was as follows: the onset of the first pattern, the exchange of the first pattern and the ISI field, the exchange of the ISI field and the second pattern and the offset of the second pattern. By varying the interval from the tone (the signal for observers to make saccade) to the exchange of the first pattern and the ISI field, a saccade would occasionally be embedded in the ISI so that no image fell on the retina during the saccade. We labelled these trials embedded-saccade displacements (ESD) trials.

Two conditions were run in expt 3. One was the spatial displacement condition, in which displacement was 0.3 deg in spatial coordinates (thus, automatically retinal displacement was also 0.3 deg when a stimulus displaced during fixation, as was in expt 1). The other was the retinal displacement condition, in which the displacement was 0.3 deg on the retina across a saccade when it occurred during a saccade (as in expt 2).

Procedure. The same procedure used in expt 2 was used, including the saccade size (3.8 deg). The only differences were a 50 msec ISI interposed between the first and the second patterns and the two displacement conditions, spatial and retinal. During the ISI the random-dot pattern was replaced by a uniform field, which had the same average luminance as the random-dot patterns. Observers indicated whether any motion (global and coherent or local and incoherent) was seen by responding "motion" or "no motion". On one half of the trials the random dots were displaced while on the other half there was no displacement of random dots (in spatial coordinates). The ISI was interposed for *both* displacement and no displacement trials.

The 50 msec ISI was longer than the saccade duration obtained for 3.8 deg saccades in expts 1 and 2, which was approx. 35 msec. Thus the 50 msec ISI would cover the whole of a saccade period if a displacement started just before the saccade started, provided that the start of a displacement was defined by replacing the first pattern by the uniform field of the ISI. On such a trial (an ESD trial), the retina was exposed to the uniform field during a saccade and the random-dot pattern was seen only while the eyes were fixated.

Prior to the experiment, one observer, SS was tested to determine whether he could discriminate the displacement trial and the no-displacement trial with 50 msec ISI during steady fixation, varying the displacement size. More than 75% correct responses were obtained when the displacement size was within the range of 0.06 and 0.82 deg. These values were the same as those evaluated for displacements which produced clear motion without ISI in expt 2. If D_{max} and D_{min} for the displacement with 50 msec ISI are therefore assumed to be 0.82 and 0.06 deg, then the retinal displacement should be more than D_{max} on 19.7% of trials where the displacement occurs during a saccade and less than D_{min} on 0.6%, as described in expt 2 (see Fig. 3).

Based on the eye movement records, trials were discarded in the same manner as in expt 2 (about 1.5% of trials were discarded because correct saccades followed the first saccades). The same two observers were used. SS completed four sessions and PF completed three sessions.

Results and discussion

Figure 5 shows the percentage of correct responses as a function of the time offset between the beginning of a saccade and the offset of the first pattern for each observer in both the spatial and retinal conditions. The data for displacement and no-displacement conditions are shown separately in each panel. Although time offsets are pooled in 10 msec bins at between −50 and 60 and in 20 msec at others, for PF 30 or 40 msec intervals were occasionally used so that no datum point was derived from less than 5 trials. On average, each point was derived from 17 trials for SS and 11 trials for PF. The data for all trials with time offsets less than −110 msec are plotted together as well as time offsets greater than 130 msec. Filled ellipses indicate the ESD (embedded-saccade displacement) trials—those trials for which the saccade fell entirely within the ISI. Only trials with time offset between −10 and 0 msec were regarded as ESD trials. Since saccade duration was 35 msec on average, the 50 msec of ISI which started between 10 and 0 msec before the beginning of a saccade ended between 5 and 15 msec after the saccade had terminated, thus presenting only a uniform field on the retina during a saccade (an exception in classifying ESD trials was made for the spatial displacement condition of PF, where trials with time offset between −20

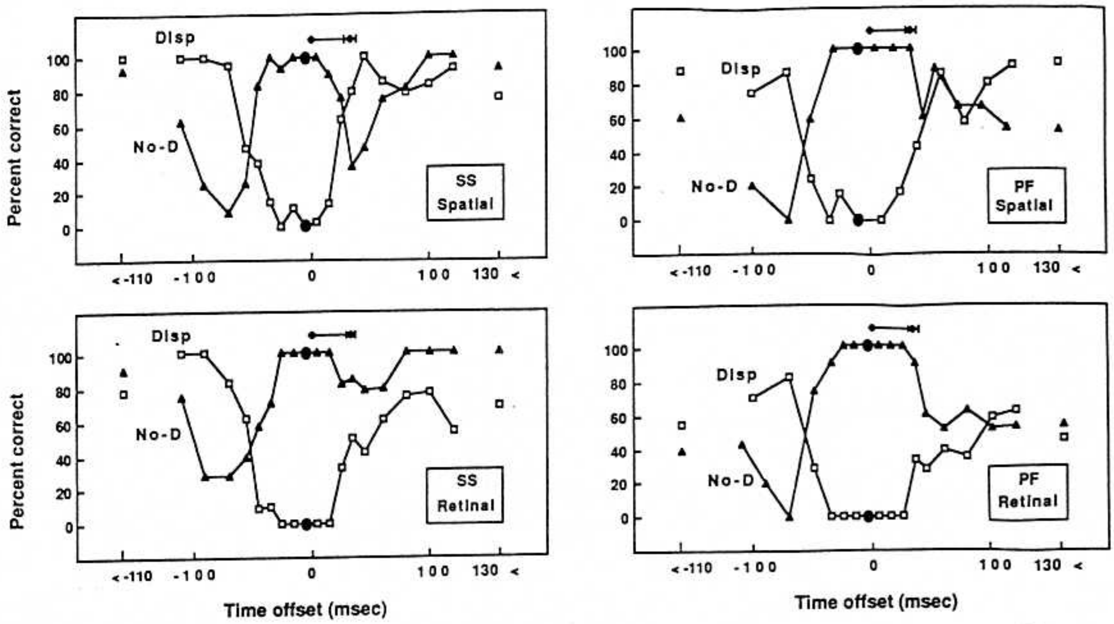

Fig. 5. Percent correct responses as a function of time offset in expt 3. Results of displacement trials (square) and non-displacement trials (triangles) are shown separately in each panel. Data points all time offsets less than −110 msec are pooled as are data for all trials with time offset larger than 130 msec. Filled ellipses represent ESD trials. Top two figures are for the 0.3 deg spatial displacement, and bottom two figures are for the 0.3 deg retinal displacement (3.5 deg spatial displacement). The left panels are for SS; the right panels for PF. Each point was derived from 17 trials on average for SS and 11 trials for PF; the minimum number of trials of a point was 6 for SS and 5 for PF. The average number of trials for the data points of ESD trials is 19 trials for SS and 11 trial for PF. The length of the horizontal solid line with filled diamonds shows average saccade duration for each condition. The standard deviation of the saccade duration is shown at the righthand end of the line by an error bar.

and 0 msec were pooled together as ESD trials). Mean saccadic durations are shown in each panel.

For the spatial displacement condition (0.3 deg displacement, top panels in Fig. 5), SS failed to detect motion for almost all trials when the displacement occurred between approx. from −40 to 20 msec of time offset and PF saw no motion for almost all trials which time offset was from −50 to 35 msec. ESD trials (time offsets between −10 and 0 msec) are included in these period. The results for no-displacement trials in the spatial displacement condition show that the percentages of correct responses ("no motion") are almost 100% in the same period for which correct responses ("motion") for displacement trials are almost 0%. The observers always responded no motion for the trials in that period, whether or not the stimulus was displaced, and reported that they could not discriminate the displacement from the no-displacement trials. Especially for ESD trials, the observers reported that the stimulus appeared to be stationary whether or not dots were displaced and sometimes appeared completely unchanged as if even the perception of the ISI field had been suppressed.

If the ISI occurred while the eyes were fixated, the observers always saw the dots disappear and then return and their responses were based on whether they saw coherent global motion (on displacement trials) or saw the dots flashed at the same spatial location (on no-displacement trials). The percentages of correct responses for both displacement and no-displacement trials were higher than chance level if the ISI occurred while the eyes were fixated. Although "motion" responses to no-displacement trials were obtained in some cases, the percentage of correct responses calculated from all trials on which the time offset was either less than −100 msec or more than 100 msec is 92.2% for SS and 72.2% for PF. These results suggest that the low-level motion mechanism can operate with a 50 msec ISI, when the eyes are fixated.

Similar results were obtained in the retinal displacement condition (3.5 deg displacement, bottom panels in Fig. 5). For time offsets between −50 and 20 msec, almost all responses were no motion responses including those for ESD trials; for displacement trials, the percentage of correct responses is approx. 0%, and it is 100% for no-displacement trials in that period. The results of ESD trials suggest that motion cannot be seen across a saccade even when there is only a uniform field on the retina during the saccade. For ESD trials, the observers always responded "no motion" since the stimulus appeared to be stationary whether or not dots were displaced. When the ISI occurred during fixation the observers' responses were based on whether they saw incoherent local motion (on displacement trials) or identified the dots flashed at the same spatial location (on no-displacement trials).

How effective was the ISI at removing the visual stimulus from the retina during a saccade? For ESD trials, the temporal uncertainty of ±8.4 msec implies that dots may have been presented on the retina in the duration of 8.4 msec at a maximum for trials in which the measured time offset was 0 and 3.4 msec for −10 msec time offset. However, even in these cases, the retina was exposed to the uniform ISI field during more than three quarters of the saccade duration, and the masking effect of the image during a saccade, if any, would be reduced proportionately. Moreover, the percentage of correct responses is very similar (i.e. approx. 0% for displacement trials and 100% for no-displacement trials, Fig. 5) across the larger range of −50 and 20 msec time offsets, indicating that the presence or absence of the stimulus on the retina during the saccade had little effect.

Two conditions in particular are very similar in terms of retinal stimulation: the displacement trials in the spatial displacement condition where the saccade occurred long before or after the displacement (offset less than −110 msec or greater than 130 msec, top panels in Fig. 5) and in the ESD trials of the retinal displacement condition (filled ellipses, bottom panels in Fig. 5). In both cases, the random-dot fields were displaced a small distance on the retina with a 50 msec ISI between the first and the second fields. The difference between these situations was the presence or absence of a saccade during the ISI. This comparison is free from the masking effects of the stimulus on the retina during the eye movements and includes an equivalent interval between the first and the second patterns. Motion was seen for trials in the spatial displacement during steady fixation but not on the ESD trials. Therefore the failure to detect motion on the ESD trials of the retinal displacement must be attributed to the presence of a saccade, and not to the indirect effects of the saccade on retinal stimulation.

GENERAL DISCUSSION

The first experiment showed that the direction of the displacement could not be detected when a random-dot field was displaced during a saccade even though the same displacement was detected if it occurred during steady fixation. In the second experiment, we found that no motion was seen if the displacement occurred during a saccade even when the displacement was smaller than $D_{\max}$ in retinal coordinates. Experiment 3 showed that the replacement of the random dots by a uniform field during a saccade did not change the finding that no impression of motion was produced for a displacement that occurred during a saccade. Experiment 3 also demonstrated that the motion process could operate on images separated by a 50 msec presentation of a uniform field when viewed with the eyes fixated.

These results lead us to claim that the loss of motion perception during a saccade is a consequence of a suppression mechanism specific to saccade. We feel that this suppression is required to eliminate unreliable motion signals that would otherwise result from the large displacement of the retinal image. Before discussing the possible mechanisms of this suppression, we will first consider aspects of the saccade that may have indirectly interfered with the perception of motion.

First, the difficulty in perceiving motion during a saccade might be a result of the loss of visibility of patterns during the saccade. Furthermore, this degradation of detecting images during a saccade may be caused primarily by masking effects of images seen at fixations before and after the saccade (Campbell & Wurtz, 1978; MacKay, 1970; Matin, Clymer & Matin, 1972). Campbell and Wurtz (1978) showed that the smeared image during a saccade could be seen if no images fell on the retina after the saccade, suggesting that no special mechanism which works during saccades is required to interpret the visual loss during saccades. Such masking effects could explain the suppression of motion during a saccade if it is the case that motion cannot be seen when the patterns are not visible during the saccade. However, this hypothesis can be rejected since motion can be seen when a blank ISI is inserted between the two patterns even if the ISI duration is larger than the duration of a saccade, as long as the eyes are fixated. Therefore, the loss of visibility during a saccade cannot explain the loss of motion perception.

Second, the sweep of the pattern across the retina due to rapid eye movement may play a role in suppressing motion perception. It has been shown that the low-level motion mechanism is more deteriorated when a patterned image is presented during ISI than when a uniform field is used (Braddick, 1973). However, expt 3 of this report showed that motion suppression was present even when there was no pattern on the retina during a saccade (results of ESD trials). Our results therefore suggest that, in addition to possible visual loss during a saccade and possible masking effect of the image swept across the retina by the saccade, there must be another factor that degrades the detection of motion.

There are two possible interpretations of the saccadic suppression of low-level motion found in our experiments. First, as Burr, Holt, Johnstone and Ross (1982) claimed, the transient mechanism seems to be suppressed selectively during a saccade. Their claim was based on the results of two experiments which addressed the difference in threshold during a saccade and while the eyes were fixated. In one experiment, contrast sensitivities were measured as a function of spatial frequency. The results showed that contrast sensitivity for low spatial frequencies was selectively reduced during a saccade in comparison with during steady fixation. Since the transient process is most sensitive to low spatial frequencies, these data are consistent with their claim. In their other experiment, they examined whether a momentary reversal in motion direction of moving gratings was detected during a saccade. The performance to detect the reversal was degraded during a saccade, and the observers reported that they saw the motion reversal if it occurred during steady viewing but they had only a vague sense of a disruption when they could detect the reversal that occurred during a saccade. Since the transient process is primarily sensitive to moving stimuli, this also suggests that the transient mechanism is selectively suppressed.

Our results agree with those of Burr et al. (1982). The idea that the transient mechanism is suppressed by a saccade is supported by observers' report in expt 3 that was mentioned above. That is, they sometimes saw nothing changed in ESD trials (where the saccade occurred totally within the ISI period), implying that they did not notice the offset of the first pattern, the onset of the second pattern and the uniform field during the ISI period. All of these events were visible when the displacement occurred while the eyes were fixated. These transient changes in a stimulus may be an important trigger for the low-level motion mechanism.

The other interpretation of our results is based on the appearance of the stimuli. In our experiment, there was always a stationary frame within which random dots moved, and the frame (and other things which surrounded observers outside the frame in the dimly lit experimental room) was perceived as stationary even when the eyes moved, agreeing with observations common in ordinary viewing. Ramachandran and Cavanagh (1987) showed that the displacement of a random-dot pattern is captured by the displacement of a low spatial frequency sinewave grating superimposed on the random dots. That is, the actual motion of the dots is not perceived and they are seen to move with the sinewave grating as if glued on to it. The motion of the stationary frame may as well capture the motion of random dots when the random dots are displaced during a saccade in a stationary frame, and both are attributed to the eye movement thus producing no perception of motion.

The effect of frame displacement during a saccade on the detection of target displacement has been explored by Goto and Ikeda (1981). They found that the displacement of a frame affects detection of the displacement of a light spot. They displaced not only a target, but also an inducing frame which was a set of two vertical lines located 26.7 deg apart. The target was displaced around the center of two inducing lines during a saccade. Their results showed that the target displacement was sometimes not seen when the inducing frame displaced the same distance as the displacement of the target during a saccade, while the target displacement was always detected when there was no displacement of the inducing frame. This suggests that the motion of a frame during a saccade can influence the detection of target displacement, although their results may be based on a process that notices changes in relative position rather than one that produces subjective motion perception.

Since our results suggest that there is a suppression of motion detection during a saccade, it may be the case that saccadic suppression of image displacement reported by Goto and Ikeda (1981) as well as others (Bridgeman et al., 1975; Bridgeman & Stark, 1979; Heywood & Churcher, 1981; Mack, 1970; Stark et al., 1976; Whipple & Wallach, 1978) was also due to the suppression of motion mechanisms, and not to the suppression of processes that detect change in position of stimulus. The influence of a saccade on the mechanisms that detect change in position has not yet been explored independently from motion detection. The fact that the displacement during a saccade was detected when it was large enough (e.g. Bridgeman et al., 1975; Bridgeman & Stark, 1979) may be the result of detecting change in position of the stimulus, and the mechanism that detects such a change may be involved in the integration of visual information before and after a saccade.

CONCLUSION

Observers could not identify the direction of motion of random dots moved within a stationary frame if the displacement occurred during a saccade. The suppression was also observed when the displacement of the random dots was less than $D_{\max}$ in retinal coordinates and even when the saccade was embedded in a slightly longer blank ISI. In all cases, the discrimination of the direction or presence of the same displacement was possible if the eyes were fixated. These results suggest that the low-level motion mechanism is not only suppressed during a saccade, but is also prevented from integrating pre- and post-saccade images in order to produce motion information. Since motion perception is possible with ISIs larger than the durations of the saccade in our experiments, we conclude that this motion suppression does not represent a loss of signal but an active suppression.

The purpose of this suppression may be to block out unreliable motion signals produced by a saccade. Since saccade distance is generally greater than the maximum distance over which the low-level motion mechanism can produce accurate direction discrimination for fine textures, these signals would generally indicate false directions. The visual system can simplify its task of extracting a stable visual world during saccades if it totally ignores motion information from finer image details. Whether or not motion information from larger scale image features are analyzed remains to be determined.

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