SELECTIVE DEPRESSION OF MOTION SENSITIVITY DURING SACCADES

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SUMMARY

1. Horizontal gratings flashed for 20 ms were used to compare visual contrast sensitivity during horizontal saccades with sensitivity during normal vision, at three luminance levels, 4×10^2 , 4×10^{-2} , and 4×10^{-4} cd/m².

2. Greatest sensitivity loss during saccades was found at low spatial frequencies. There is little or no loss at high spatial frequencies.

3. As luminance level is decreased there is a decrease in the spatial frequency below which saccadic sensitivity loss occurs. This shift in spatial frequency with luminance level, considered in conjunction with measurements of stationary and drifting gratings, indicates the functional involvement of movement sensitive mechanisms in saccadic sensitivity loss.

4. At the two lower luminance levels $(4 \times 10^{-2} \text{ and } 4 \times 10^{-4} \text{ cd/m}^2)$ sensitivity during saccades is greater than normal at high spatial frequencies. This enhancement of sensitivity was confirmed by forced choice measurements.

5. It was also shown that sensitivity to abrupt changes in the trajectory of moving gratings is lowered during saccades.

6. It is concluded that mechanisms sensitive to movement and transients are damped during saccades, so preventing perception of image motion during saccades and thereby preserving visual stability.

INTRODUCTION

As we look about us our eyes make rapid ballistic eye movements called saccades, some voluntary and some not, which serve to bring a new region of the world onto the foveal field and thus to reposition the visual image on the retina. Students of vision have long sought to explain why we do not notice motion while a saccade is in progress, and why the external scene seems not to have shifted in position after fixation is shifted by a saccade. These two aspects of the question of visual stability have often been confused. Here we deal separately with them, but explain both as consequences of the damping during saccades of mechanisms sensitive to motion.

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Helmholtz was well aware of the difference between the two aspects of the question of visual stability. He believed that we do sense movement of the image during a saccade, but that we do not notice it because it serves to inform us of a change of gaze. 'Movement must be accompanied by a constant system of changes of sensation in the fibres of the optic nerve. Ultimately, we learn to recognize it as being the sensory expression of the ocular movement connected with that particular change of gaze' (Helmholtz, 1866, III, p. 66).

The visual world appears not to have moved after an eye movement, Helmholtz believed, because apparent position in space (visual direction) depends upon our judgement as to the direction of the visual axis, which in turn depends upon sensations during eye movement and upon 'the effort of will involved in trying to alter the adjustment of the eyes' (Helmholtz, 1866; see also Merton, 1964).

Holt (1903) concluded from observations of after-image motion and from the visibility of targets exposed during rapid eye movements that 'voluntary movements of the eyes condition a momentary visual central anaesthesia'. Holt's 'central anaesthesia' has since been renamed 'saccadic suppression' and has been widely invoked to explain why we do not see motion during saccades. Appealing as this explanation is, however, any idea of complete visual anaesthesia cannot be reconciled with subsequent experimental measurements which show at most a 2–3 fold elevation of threshold during saccades (e.g. Volkmann, 1962; Latour, 1962; Zuber & Stark, 1966; Riggs, Merton & Morton, 1974), which is negligible at normal viewing contrasts. In any case, suppression of vision during saccades would not by itself explain the stability of the visual world after the saccade had been completed.

Dodge (1900, 1905) and Woodworth (1906) took a position, directly opposite to Holt's, that 'vision with the rapidly moving eye...does not differ essentially from vision with the resting eye' (Woodworth, 1906, p. 69). Dodge, impressed by the fact that we cannot see our own saccadic eye movements when we look in a mirror (Graefe, 1895 cited in Holt, 1903; Dodge, 1900), argued that image motion during saccades produced no sense of motion because it was too rapid to do so, and reduced the sharper contours of the fixation process to give only faint, blurred stimulation during the saccade. The faint stimulation itself passed unnoticed, Dodge reasoned, because of interference from the sharp image of the preceding and succeeding fixations. This idea has recently been revived by Campbell & Wurtz (1978).

However, the assumption that image motion brought about by saccades is too fast to resolve has recently been proven to be erroneous. Johnstone & Riggs (1979) showed that object movement could be perceived at velocities greater than 1000 deg/s, and Burr (1979) and Burr & Ross (1982) have shown that rapid image motion does not decrease visual sensitivity. Contrast sensitivity functions measured with drifting gratings, at drift speeds of up to 800 deg/s, have much the same height (maximum sensitivity) and width (range of effective spatial frequencies) as curves measured with stationary gratings. Motion merely translates the sensitivity function down the spatial frequency axis, so that the visual system responds to a lower range of spatial frequencies. Thus visual saccades will not, by virtue of their velocity alone, render the visual image a motionless blur. A velocity of say 200 deg/s (a typical saccade: Carpenter, 1977) would certainly blur the higher spatial frequencies, but it would also act to *enhance* sensitivity to the lower spatial frequencies so that, for example, a component of 0.03 c/deg, invisible when stationary, should now be detectable at minimal contrast, 0.2% in daylight.

The problem, therefore, is to explain why very low spatial frequency components, normally not noticeable, do not startle the observer by their sudden appearance during a saccade, and why large objects do not appear to sail across the visual field during saccades. No special mechanism like Holt's central anaesthesia is required to eliminate high spatial frequency components during a saccade: to this extent Dodge (1900, 1905), Woodworth (1906) and Campbell & Wurtz (1978) were correct. But low frequency image components are, on the contrary, made more conspicuous by the image motion, and the problem is to explain why they, and their motion, are not vividly perceptible during saccades.

We report here measurements of contrast sensitivity which show considerable depression of sensitivity during saccades selectively at low spatial frequencies. Further experiments suggest that the loss of sensitivity at low spatial frequencies is a consequence of damping of motion detecting mechanisms during saccades.

METHODS

Some of the measurements were made in Perth, others in Pisa. Two main types of stimuli were used in these experiments: horizontal, sinusoidally modulated gratings, stationary or drifting, and random dot patterns. Both types were generated by computer (PDP-8/E in Perth, PDP-11/03 in Pisa) and displayed on cathode ray oscilloscopes (Joyce Electronics, Cambridge, for gratings, and Tektronix 602 for dot patterns).

The gratings were produced with a standard raster technique (Schade, 1956) at 200 frames/s, 500 lines/frame. The screen was covered with close fitting onion paper, thick enough to diffuse the raster lines. The oscilloscope face was visible within a circular opening 20 cm in diameter cut in a 2 m square featureless screen, floodlit to match mean luminance of the oscilloscope (400 cd/m^2). For measurements of sensitivity within saccades, gratings were displayed for 20 ms (four frames) with the observer 20 cm from the screen (53 deg diameter). Presentation timing, viewing distance, mean luminance, and other experimental details varied for other experiments, and will be stated in the relevant sections.

The dot patterns comprised 800 dots pseudo-randomly positioned within a square field, generated on an oscilloscope face by a computer, which provided X, Y co-ordinates and a 4 μ s unblanking pulse to illuminate each dot. Each dot was cyclically refreshed every 'frame' of 25 ms. Again the oscilloscope face (10 × 10 cm) was surrounded by a 2 m square featureless screen, floodlit, together with the oscilloscope face, to 20 cd/m². The dots were intensified to a contrast of 100 times their visibility threshold, determined by adjusting the intensity control until they appeared at threshold behind a 2 log unit neutral density filter. Viewing distance was 10 cm (correcting refraction with a positive lens), so the screen subtended 53 × 53 deg of visual angle.

Measurements were made both during saccades and in normal viewing, triggering the stimulus or configuration change either from the observer's saccade or from a hand-held electronic switch. In both cases an audible tone confirmed successful triggering. Saccades were always horizontal, being made between two clear fixation marks, 30 deg apart, positioned symmetrically about the centre of the screen.

Saccades were detected by recording the change in electrical potential around the eyes which accompanies eye movements. Two silver electrodes, coated with electrode gel, were positioned near the outer canthus of each eye, and a third reference electrode on the forehead. The potentials were amplified 10,000 times with an a.c. coupled differential amplifier (Tektronix TM504), filtered and read by the computer through an A/D buffer every frame of pattern generation (5 ms for gratings, 25 ms for dot patterns). If a low threshold had been reached, the computer deduced that the observer was making a saccade, and presented or changed the stimulus. It then continued to read the A/D buffer every frame until a high voltage threshold was reached, ensuring that the saccade was sufficiently large, and hence of long enough duration to enclose the stimulus or the change of

the configuration. If the higher threshold was not reached within 100 ms, the trial was aborted and the observer so informed. As a further precaution that the saccade outlasted the stimulus, both saccade and stimulus were monitored visually on a storage oscilloscope. As the stimulus (or time for the stimulus to alter configuration) never exceeded 20 ms, and the saccade typically lasted about 70 ms, the stimulus usually fell well within the saccade.

Measurements were made with the method of adjustment, except for those which employed a forced choice technique. For the contrast sensitivity measurements, contrast was varied by two logarithmic attenuators connected in series. One was under the control of the experimenter, who set it to a random attenuation between 0 and 10 db each trial, and the other under control of the observer, who adjusted it to threshold. This method minimized response stereotyping which sometimes occurs with the method of adjustment. Movement displacement thresholds were also made by the method of adjustment with a hand-held rotary multiswitch, read digitally by the computer. Here the computer provided a random displacement offset for each trial, again minimizing response stereotyping. The forced choice measurements were made entirely under computer control: the computer set the contrast (by means of an analogue multiplier driven by a D/A), detected and controlled the adequacy of saccades, randomized and presented the trials, and registered and scored observer responses.

All viewing was monocular, with the left eye shielded. We report results for two observers (two of the authors), but have confirmed all major results on colleagues, both in Perth and in Pisa.

RESULTS

Sensitivity to the contrast of horizontal grating was first measured at high photopic luminance (400 cd/m^2) , during saccades and in normal viewing. Gratings were displayed for 20 ms, triggered by either a 30 deg horizontal saccade or a button held by the observer. For each spatial frequency, five separate settings were made for both saccadic and normal viewing, alternating randomly between the two conditions. Viewing was monocular from a distance of 20 cm, providing a 53 deg diameter screen. Since both gratings and saccades were horizontal, and the grating extended well beyond the fixation marks, the saccade introduced no change in the image falling on the foveal and parafoveal region of the retina.

Results for the two observers are shown in Fig. 1*A*. In normal viewing sensitivity is high at all spatial frequencies, up to the point at which the high frequency cut begins (about 1.0 c/deg for D.B. and 0.3 c/deg for J.R.).

Sensitivity during saccades is little impaired at the high end of the spatial frequency range. D.B.'s curves almost converge at the point at which the high frequency cut begins to appear, and J.R.'s run parallel beyond this point. There is substantial and progressively greater impairment of sensitivity during saccades as spatial frequency falls (in agreement with Volkmann, Riggs, White & Moore, 1978). This loss of sensitivity is found precisely in that part of the spatial frequency range which, in normal vision, is highlighted by motion at saccadic velocities.

Higher spatial frequencies, above 1 c/deg, are not measurable with our techniques. The experimental method relies on the fact that saccades parallel to the grating stimulus will cause no smearing of the stimulus, which would reduce visibility by optical means (Campbell & Wurtz, 1978). However, the trajectory of visual saccades is not perfectly linear, but tends to oscillate somewhat (Dodge & Cline, 1901). Furthermore, they are not perfectly accurate, but typically fall as far as 30 min from their target (Lennie & Sidwell, 1978). Both these factors introduce a vertical velocity component into the saccadic trajectory, which will have negligible effects at the lower spatial frequencies but will introduce significant blur above 1 c/deg.



Fig. 1. Normal (O) and saccadic (\bigcirc) contrast sensitivity functions at three different luminance levels, 400 cd/m² (A); 4×10^{-2} cd/m² (B); and 4×10^{-4} cd/m² (C). B and C are discussed at a later stage.

Detection of flashed gratings

We were obliged to use a brief stimulus to ensure that it fell comfortably within a saccade. The stimulus itself was not moved during the saccade: however, its transient nature gives it a wide spread of energy in the temporal frequency domain, making it an effective stimulus for movement-dependent as well as movementindependent visual mechanisms (e.g. Tolhurst, 1973; Kulikowski & Tolhurst, 1973; Arend, 1976).

In order to understand more fully the means by which briefly flashed gratings are detected, we measured sensitivity for gratings of 20 ms duration, and compared this with sensitivity to continuously displayed stationary gratings and to drifting gratings. The drift speed was set at 5 Hz, so as to enhance sensitivity for the lower

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spatial frequencies over a wide luminance range (e.g. Robson, 1966; Van Nes, Koenderink, Nas & Bouman, 1967). To avoid problems of probability summation, which favours grating with many cycles visible (Sachs, Nachmias & Robson, 1971), the display screen always showed four cycles of grating, and spatial frequency was varied by varying viewing distance, from 10 cm to 100 m. Measurements were made at three luminance levels, 400 cd/m^2 , $4 \times 10^{-2} \text{ cd/m}^2$, and $4 \times 10^{-4} \text{ cd/m}^2$, the observer wearing neutral density filter goggles of 4 and 6 logarithmic units for the lower two luminances.



Fig. 2. Contrast sensitivity functions for the resting eye obtained at three different luminance levels, under three different conditions: stationary gratings continuously in view (\bigcirc); gratings drifting at 5 Hz, continuously in view (\blacksquare); and gratings flashed for 20 ms (\blacktriangle). The luminance levels were 400 cd/m² (A), 4×10^{-2} cd/m² (B), and 4×10^{-4} cd/m² (C). The gratings all had a spatial frequency of 0.2 c/cm, thus displaying 4 cycles on the 20 cm screen. Field size, and hence spatial frequency in c/deg, was varied by varying viewing distance, from 10 cm to 100 m. The arrows indicate the points at which the low frequency cut for the curves for stationary gratings begins (see text).

Results for two observers are shown in Fig. 2. Consider first the results for the highest level of luminance (Fig. 2A). Stationary gratings are best seen at a spatial frequency of 3.0 c/deg for D.B. and 1.0 c/deg for J.R. Below this peak, sensitivity rolls off in proportion to spatial frequency (low frequency cut) and above it, at the higher spatial frequency end, sensitivity cuts out sharply (high frequency cut). Moving gratings show a similar high frequency cut, but no low frequency cut: sensitivity is virtually identical at all low spatial frequencies. The sensitivity curve for flashed gratings lies below and roughly parallel to the curve for moving gratings, converging slightly toward it at the higher frequencies.

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A similar pattern is evident at the two lower luminance levels (Fig. 2B and C). Once again the curve for stationary gratings shows a sensitivity peak, but the peaks occur at lower spatial frequencies: 0.7 and 0.4 c/deg at 4×10^{-2} cd/m² (for D.B. and J.R. respectively), and 0.25 and 0.2 c/deg at 4×10^{-4} cd/m². The curves for the moving and flashed gratings preserve their shape (high, but no low frequency cut) and their relationship, the flashed curve running under the normal curve and parallel to it. The high frequency cut, like that for the stationary gratings, occurs at a lower spatial frequency at the lower luminance levels.

A briefly flashed grating contains a wide spread of temporal frequencies, encompassing a range from 0 to over 50 Hz, and thus may be expected to excite visual mechanisms tuned to both low and high temporal frequencies. This is reflected in the results. The curve for the flashed gratings tends to follow that for the moving gratings in the low frequency range (where sensitivity is higher for moving gratings) and that of the stationary gratings in the high frequency range (where sensitivity is higher for stationary gratings). Sensitivity to a 20 ms grating may be expected to be less than that for continuously presented gratings, by a factor of 5 or 6, given the time constants of visual temporal summation for moving and stationary gratings (Burr, 1981). This is about the amount shown in Fig. 2.

It will be noted that the curves of Fig. 2 are slightly different from other published data (such as Campbell & Green, 1965; Robson, 1966) and indeed from our own measurements for normal viewing of Fig. 1. These small discrepancies can probably all be put down to spatial probability summation (Sachs *et al.* 1971). Usually, screen size is kept constant so that the number of visible cycles varies with spatial frequency, which depresses the lower end of the curve where there are fewer cycles, and elevates the higher end where there are more. The results of Fig. 2, which were obtained with a constant number of cycles at all spatial frequencies, are free from this effect.

Saccadic sensitivity at low luminances

The results of the previous section show that, at low spatial frequencies, drifting and stationary gratings are detected differently. Sensitivity to stationary gratings falls rapidly below a certain peak frequency, while that for drifting gratings remains constant over this range, the point of divergence being lower at lower luminances. Flashed grating sensitivity follows the curve for moving gratings in the lower frequency range. Measurements at 400 cd/m² showed that sensitivity to gratings flashed during a saccade steadily declines with spatial frequency below a certain peak value. In this section we examine the effect of luminance on saccadic sensitivity to see whether there is a change with luminance in the frequency at which saccadic and normal sensitivity converge.

Saccadic sensitivity was measured as before, but with the subject wearing tightly fitting goggles, with one eye shielded, and a neutral density filter (4 or 6 log units) in front of the other.

Results for measurements at 4×10^{-2} and 4×10^{-4} cd/m² are shown in Fig. 1*B* and *C*. The results clearly show that the point of convergence of the saccadic and normal curves shifts to a lower frequency at lower luminances. At 400 cd/m² (Fig. 1*A*) the curves converge at 3.0 and 1.0 c/deg (for D.B. and J.R. respectively), at 4×10^{-2} (Fig. 1*B*) at 0.7 and 0.4 c/deg, and at 4×10^{-4} cd/m² (Fig. 1*C*) at 0.25 and 0.2 c/deg. It may be noted that these frequencies match closely those at which the curves for

the stationary and drifting gratings of Fig. 2 converge. This point, and its significance, will be discussed in more detail later.

The results of the measurements of saccadic sensitivity loss are summarized in Fig. 3, which reports the ratios of saccadic to normal thresholds at the three luminance levels. At each luminance level the ratio, which indicates the amount of depression of sensitivity in saccades, rises steadily as spatial frequency decreases below an appropriate peak, to a value of more than 1 log unit at the highest luminance for both D.B. and J.R. Above this peak, the ratio of saccadic to normal thresholds seems to be constant. At the lowest luminance levels, this constant ratio is less than 1, indicating enhanced sensitivity during saccades.



Fig. 3. Saccadic suppression, the ratio of saccadic to normal thresholds, as a function of spatial frequency, for three different luminance levels: $400 \text{ cd/m}^2(\triangle)$, $4 \times 10^{-2} \text{ cd/m}^2(\bigcirc)$ and $4 \times 10^{-4} \text{ cd/m}^2(\blacksquare)$.

Saccadic enhancement

One of the more surprising results of the previous section is that at the lower luminance levels saccadic sensitivity actually climbs above that for normal viewing, implying saccadic enhancement. At 4×10^{-4} cd/m², both D.B. and J.R. show greater sensitivity during saccades than in normal vision above about 0.2 c/deg (Figs. 1*C* and 3). In order to be certain that this enhancement during saccades is real, and not merely a result of criterion change or some other artifact, we re-measured one point (0.3 c/deg, 4×10^{-4} cd/m²) with a forced choice technique.

On a signal derived either from a saccade or button (depending on the session), a grating appeared either above or below the fixation marks. Observers were required to indicate, by pressing one of two hand held buttons, which half of the screen contained the grating. Contrast (in the vertical dimension) was shaped within a 'raised cosine' envelope (to minimize the spread of spatial frequencies), centred 7.5 deg above or below the fixation marks, and extended over 30 deg. The computer randomized the presentation order and presented the stimuli, controlled for the adequacy of the saccades and registered, scored and averaged the responses. Measurements were collected over ten sessions, five for saccadic and five for normal viewing (arranged in random order), each session lasting about five minutes.

The results, set out in Fig. 4, show unambiguously that at low luminance levels gratings of 0.3 c/deg are visible during saccades at lower contrast than in normal viewing, confirming the results of Fig. 1 obtained by the method of adjustment.



Fig. 4. Percentage of trials on which the observer correctly identified which half of the screen contained the grating, both during saccades (\bigcirc) and for normal viewing (\bigcirc). The grating had a spatial frequency of 0.3 c/deg and a mean luminance of 4×10^{-4} cd/m². The results clearly show that the grating is more visible during saccades than in normal vision. For both observers, the visibility thresholds (taken as the 75% point) are about 0.1 log unit (2 db) higher in normal viewing than in saccades.

Sensitivity to interrupted motion

The results of the previous sections suggest, for reasons elaborated later in the discussion, that mechanisms which detect motion are selectively silenced or reduced during saccades. However, because the stimulus must necessarily be brief to ensure it falls within the saccade, this hypothesis could not be directly tested by comparing sensitivity for moving and stationary stimuli. Briefly exposed stimuli, even when stationary, have a temporal frequency spectrum extending well into the range optimal for motion detection, and will therefore excite the same mechanisms as drifting flashed stimuli (see also Burr, 1981). Therefore, instead of measuring sensitivity thresholds, we chose another index of motion sensitivity, namely the ability to perceive an abrupt change in the motion trajectory of a continuously moving stimulus.

Again horizontal gratings drifting vertically were chosen as the stimulus, because of their one-dimensionality and their periodic repetition. On a signal, either from the observer's saccade or from the response button, the drifting grating jumped backwards and then continued at its original velocity (see inset to Fig. 5). The observer adjusted the distance of the backwards jump with a hand-held rotary switch until he could just notice the displacement in the motion trajectory. Measurements were made for a 0.1 c/deg grating (of large enough cycle width to allow large displacements) over a velocity range from 0 to 300 deg/s. Threshold was taken as the average of five settings, randomly alternating saccadic and normal measurements.

Fig. 5 shows the results. For both saccadic and normal viewing threshold displacement increases roughly in proportion to velocity. However, at all velocities the threshold during saccades is about three times as great as that for normal viewing. Furthermore, there is a pronounced qualitative difference between the two conditions.



Fig. 5. Normal (\bigcirc) and saccadic (\bigcirc) thresholds for detecting the backward displacement ($\triangle x$) of the trajectory of a drifting 0.1 c/deg horizontal grating, as a function of its drift velocity (v). The inset shows the motion trajectory of the stimulus. Both normal and saccadic displacement thresholds increase in proportion to drift velocity, with saccadic thresholds always about three times as high as those for normal viewing.

Motion is clearly seen to be disrupted when a suprathreshold displacement occurs in normal viewing. However, during saccades the motion appears to have proceeded smoothly before, during, and after the displacement with no sense of disruption. The observer has only a vague sense that an untoward event occurred, sufficient for psychophysical detection, but insufficient to perturb his sense of smooth motion.

Sensitivity to change

What is an observer's reaction to a change of scene during a saccade ? Random dot triplets, designed to give an appearance of whole field striation were rapidly swung through 90°, by switching X and Y, on a signal from a saccade or a response button. When the switch was triggered by hand, observers reported a compelling sensation of *change*, as if the display had rotated physically from one orientation to another. No such change was sensed if the switch occurred during a saccade. The observer was aware intellectually that a change of orientation had occurred, but it did not catch his attention.

Other changes of scene, including displacements of random dot fields, the replacement of one field of random dots by another, and the sudden displacement of a projected landscape (Turner, 1805–1810) could also be detected with scrutiny, but failed to startle the observer or even to be noticed without close attention when they occurred during saccades. Similarly, McConkie and Zola (1979) report that readers fail to detect exchanges of upper for lower case type face if they occur during the reader's saccade, although they are obvious to an onlooker.

DISCUSSION

We conclude that our failure to notice image motion brought about by saccadic eye movements in free natural viewing is brought about by a neural damping of the mechanisms by which we normally detect motion and change. The grounds for this conclusion are as follows.

There is convincing evidence, from studies of the effects of adaptation, for the existence of movement-dependent as distinct from movement-independent mechanisms of vision (Tolhurst, 1973; Kulikowski & Tolhurst, 1973). The motion-dependent channels, sometimes termed 'transient' channels, respond best to stimuli of high temporal and low spatial frequency (see also Burr, 1981; Burr & Ross, 1982): when visual sensitivity is measured with gratings caused to reverse in phase or to drift at a temporal frequency of 5–10 Hz, there is no loss of sensitivity at low spatial frequencies (e.g. Robson, 1966; Van Nes *et al.* 1967; Kelly, 1971, 1979) whereas stationary gratings produce a low frequency cut with a unit slope (Campbell & Green, 1965; Campbell, Johnstone, & Ross, 1981). It seems that it is the movement dependent or transient mechanisms which detect moving and counterphasing gratings over the whole of the low frequency range (Burr & Ross, 1982).

The motionless grating used to measure sensitivity during saccades is necessarily brief, since saccades last no longer than 100 ms, and often less (Yarbus, 1967; Robinson, 1968). A brief stimulus of this kind has a wide spread of temporal frequency components, and may be expected to stimulate both motion-independent and motion-dependent mechanisms. At low spatial frequencies, this stimulus is presumably detected by the more sensitive mechanisms, the motion channels. The results of Fig. 2, showing that sensitivity for flashed stimuli parallels that for moving stimuli at the low end of the spatial frequency scale, supports this contention (see also Arend, 1976).

If motion-dependent mechanisms were rendered ineffectual during saccades we should expect to find, as we do in Figs. 1 and 3, that a progressive loss of sensitivity begins to appear immediately below the frequency at which the motion-dependent mechanisms are required to support it. The position of this point changes with mean luminance, shifting to a lower spatial frequency as luminance is lowered (Fig. 2; see also Van Nes *et al.* 1967). Fig. 3 shows that at each of the three luminance levels, a progressive loss of sensitivity during saccades begins to emerge for both observers precisely at the point where Fig. 2 shows that motion is required to support sensitivity.

Two aspects of the curves of Fig. 3 require further discussion. Were the loss of motion-dependent sensitivity complete, all curves should have unit slope where

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sensitivity begins to fall, as do the curves for stationary gratings of Fig. 2. Some curves do, but others do not, indicating that the damping of motion sensitivity is not always complete. Secondly, unless other factors come into play, saccadic sensitivity should be identical to normal sensitivity in the spatial frequency region above the point of saccadic loss. The facts are that saccadic sensitivity above this point remains inferior to normal by about $\frac{1}{2}$ log unit at the highest luminance level, but is superior to normal at the two lower luminance levels. The inferiority at the highest luminance level is probably due to smearing of images of horizontal gratings by vertical components in horizontal saccades (Lennie & Sidwell, 1978; Bahill & Stark, 1979). This effect is significant only at high spatial frequencies which are visible only at high luminances.

Enhanced sensitivity during saccades at lower luminances probably results from an increase of sensitivity of motion-independent mechanisms. This would be expected were we to assume that the motion-dependent mechanisms exert a cross inhibition on motion-independent mechanisms.

That motion sensitivity is impaired during saccades is confirmed by the fact that thresholds for detecting interruption of motion of a smoothly moving, high contrast grating are much higher during saccades than in normal viewing (Fig. 5). Furthermore, dot patterns and natural scenes caused to move or change configuration abruptly during a saccade fail to elicit the startling sensation of change that they do in normal viewing. Decrease in sensitivity to image motion has previously been reported also by Beeler (1967), Bridgeman, Hendry & Stark (1975) and Stark, Kong, Schartz, Hendry & Bridgeman (1976).

So far we have dealt with one aspect of the question of visual stability, why motion is not noticed during saccades. We now consider the other aspect, why the world seems not to have shifted after its image has been repositioned on the retinae. Motion can be sensed only by a mechanism capable of comparing events which occur at different times; that is to say a mechanism with memory, if only brief (see for example Reichardt, 1961; Barlow & Levick, 1965). The connexion between the detection of change and the detection of motion is obscure, but it can be offered as a working hypothesis that a sudden shift of position is signalled by the same mechanisms that detect motion. A corollary to this hypothesis is that change will go unnoticed except by mechanisms which rely upon longer term memory if motion mechanisms fail to detect it. For example, a slowly rotating grating of high spatial frequency is not seen to move, but on careful inspection can be noticed to have changed orientation (Campbell & Maffei, 1979). The reason, presumably, is that the fine grating is outside the frequency range of the motion-dependent mechanisms (cf. Tolhurst, 1973; Kulikowski & Tolhurst, 1973), and therefore escapes their detection.

The same argument can be applied to perception during saccades. No motion signal is received (this time because the motion mechanisms are actively depressed), so the visual system registers no motion, and no sensation of change, despite the rapid movement of the image across the retina and the image displacement resulting from this movement. Damping of the motion system has three consequences: it suppresses the rapid image motion during a saccade, the transients which occur when the sharp image disappears and then reappears after the saccade, and also the 'stroboscopic' or 'beta' motion which the successive clear images may be expected to elicit.

Helmholtz's (1866) remarks on visual stability have been taken to mean that he

believed (although careful reading of his works suggests that he probably did not) in a continuous translation of the visual frame of reference, coincident with each saccade, which precisely annulled its effects. This idea of 'vectorial cancellation' during saccades has been stated explicitly by Sperry (1950) and, independently, by Holst & Mittelstadt (1950) – see also Holst (1954) and Johnstone & Mark (1971). However, if this idea were correct, an observer should be disconcerted by image shifts and changes in image content which would not be the result of his saccade. Observations with random dot patterns and natural viewing scenes displaced during saccades clearly show that he is not.

It has been argued by Richards (1968, 1969) that lowered sensitivity during saccades may be due, at least in part, to shearing forces on the retina which misalign receptors, so that sensitivity is lowered by virtue of the Stiles-Crawford effect (Stiles & Crawford, 1933). If this was correct, one would expect sensitivity to be lowered equally at all spatial frequencies. We find, however, that the suppression is spatial frequency dependent, and that there can even be an enhancement of sensitivity at higher spatial frequencies.

Disabling, or at least muting, the mechanisms which signal motion neatly solves all the problems posed for the visual system by saccades. No image motion is perceived, because no image motion is signalled. Large objects do not become startlingly conspicuous, as they do when the image is moved at saccadic speeds across the resting retina (Burr & Ross, 1982), because these stimuli are detected by motion-dependent mechanisms, disabled during saccades. And the rapid changes in image position caused by saccades pass unnoticed because the mechanisms which serve to bring these changes to attention are linked to motion-dependent mechanisms, and therefore are also silenced during saccades.

This notion is supported by neurophysiological evidence. Robinson & Wurtz (1976) show that 61 % of cells in the superior colliculus of monkeys, capable of responding at saccadic velocities, fail to do so during a saccade. Zaretsky & Rowell (1979) show that in the locust, only movement detector neurones are silenced during saccadic head turning movements. Neither Robinson & Wurtz nor Zaretsky & Rowell find any comparable inhibition when the visual field is moved at saccadic velocities. Some supportive evidence is also available from cat studies (e.g. Noda, 1975; Wolf, Hauske & Lupp, 1978; Kimura, Komatsu & Toyama, 1981), although some caution is required in their interpretation, particularly in the light of the work of Lennie (1980) and others which casts some doubt on the conjecture that the Y- and complex cells of the cat are motion detecting cells.

The visual system does not work normally during saccades, in the sense that all mechanisms continue to perform as they usually do, as proposed by Dodge (1900, 1905) and Woodworth (1906) and more recently by MacKay (1970, 1973) and Campbell & Wurtz (1978). However, neither does it perform abnormal feats of calculation as proposed by Holst & Mittlestadt (1950). There is no need. Once the motion mechanisms are silenced, there is no longer a problem of maintaining visual stability.

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