Saccadic suppression precedes visual motion analysis

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There is now good evidence that perception of motion is strongly suppressed during saccades (rapid shifts of gaze), presumably to blunt the disturbing sense of motion that saccades would otherwise elicit. Other aspects of vision, such as contrast detection of high-frequency or equiluminant gratings, are virtually unaffected by saccades [1–5]. This has led to the suggestion that saccades may suppress selectively the magnocellular pathway (which is strongly implicated in motion perception), leaving the parvocellular pathway unaffected [5,6]. Here, we investigate the neural level at which perception of motion is suppressed. We used a simple technique in which an impression of motion is generated from only two frames, allowing precise control over the stimulus [7,8]. One frame has a certain fixed contrast, whereas the contrast of the other (the test frame) is varied to determine the threshold for motion discrimination (that is, the lowest test-frame contrast level at which the direction of motion can be correctly guessed). Contrast thresholds of the test depended strongly and non-monotonically on the contrast of the fixed-contrast frame, with a minimum at medium contrast. To study the effect of saccadic suppression, we triggered the two-frame sequence by a voluntary saccade. Thresholds during saccades increased in a way that suggested that saccadic suppression precedes motion analysis: when the test frame was first in the motion sequence there was a general depression of sensitivity, whereas when it was second, the contrast response curve was shifted to a higher contrast range, sometimes even resulting in higher sensitivity than without a saccade. The dependence on presentation order suggests that saccadic suppression occurs at an early stage of visual processing, on the single frames themselves rather than on the combined motion signal. As motion detection itself is thought to occur at an early stage, saccadic suppression must take place at a very early phenomenon.

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Results and discussion

The experimental procedure is illustrated and described in Figure 1. Observers saw a motion sequence comprising two frames of horizontal sinusoidal gratings, 90° out of phase with each other, and reported whether the motion seemed to be upwards or downwards (guessing when unsure). During normal viewing, they initiated the trials by pressing a button; during saccadic viewing, by a voluntary 20° rightward saccade.

The results are all shown in Figure 2, separately for the three subjects. The green circles refer to sensitivity measurements during normal viewing, blue triangles to sensitivity during saccades; sensitivity is the inverse of threshold. The graphs on the left refer to the condition when the test frame was presented first, those on the right when it was presented second. Under normal viewing conditions when the subjects fixed a fixation spot, the sensitivity was maximal when the fixed-frame contrast was around 0.01 (5–10 times threshold), but decreased at higher and lower contrasts. Under the conditions of this experiment, the order of presentation made very little difference to the pattern of results (as observed in some previous studies [7] but not others [8], where the spatial frequency of the stimuli was quite different). The horizontal lines show the results for a specific test condition when the contrasts of the two frames were yoked together, in other words when they were both able to vary but were kept the same as each other. Sensitivity can greatly exceed this value, reinforcing previous results showing that motion can be seen, even when the test frame would be invisible if presented alone [8]. Extra contrast in one of the single frames can facilitate motion sensitivity, even though it does not add to the motion signal, presumably by some form of summation process [8].

Saccades affected the two sets of graphs in different ways, depending on whether the test frame was presented before or after the fixed-contrast frame. The graphs in which the test frame was second in the sequence show less saccadic suppression, particularly at high stimulus contrasts of the fixed-contrast frame. Indeed, at some high contrasts, sensitivity was actually higher during saccades than in normal viewing.

This result is consistent with saccadic suppression occurring early in visual processing. Saccadic suppression is maximal at the onset of a saccade, decreasing monotonically with time for about 100 milliseconds [5,9]. The first frame of the motion sequence should therefore be suppressed more strongly than the second frame: when the test frame is first, the test frame will be more strongly
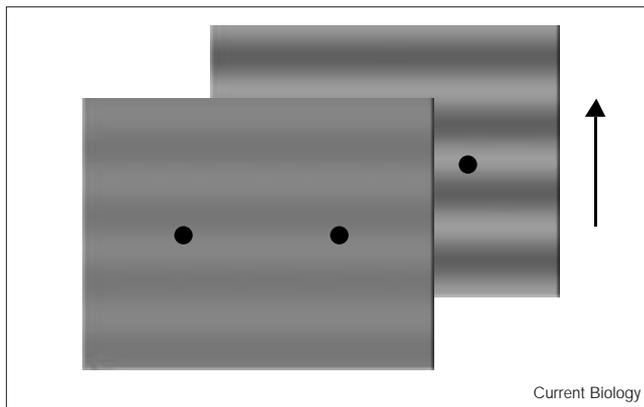
Figure 1

Illustration of the stimuli used in this experiment. The motion sequence comprised two frames, each four cycles of horizontal sinusoidal gratings of 0.1 cycles per degree, subtending $60 \times 40°$ when viewed from 30 cm away. The gratings were displayed on a monitor (Barco Calibrator), surrounded by white card (100×150 cm) floodlit to a similar mean luminance as the display screen. The grating was displayed for 100 msec in a given random chosen phase, then for another 100 msec with phase displaced $\pm 90°$ (100 msec was chosen because it gives a very strong motion signal). Subjects were required to report whether the motion was upward or downward. One frame (presented either first or second) had a fixed contrast throughout the experimental session (fixed-contrast frame), while the contrast of the other (the test frame) varied. Threshold was measured using the QUEST procedure to vary contrast over the region near threshold, then calculating threshold as the contrast at which 75% of responses were correct [14]. Thresholds were determined by fitting cumulative Gaussian functions to the percentage correct results. Stimuli were generated by a framestore under computer control (Cambridge Research Systems, VSG) and displayed on a Barco Calibrator monitor at 200 frames/sec, with mean luminance 20 cd/m². During 'normal' conditions, observers initiated the motion sequence by pressing a button. For the saccadic conditions, observers saccaded from the fixation target on the left to a spot that was turned on 20° to the right. The eye movements were recorded by a computer-monitored infrared recorder (HVS Image), and used to trigger the motion sequence (in practice 10–15 msec after saccade initiation). After each trial, the saccade was displayed on the same monitor to the observer, together with the time of initiation of the motion sequence. If the saccade was not adequate (if it was of insufficient amplitude, it included a 'corrective saccade' or the stimulus was triggered too late) the observer aborted that trial.

suppressed, whereas when the test frame is second, the fixed-contrast frame will be more strongly suppressed. Suppression of the test frame should cause an overall decrease in sensitivity, shifting the curves downwards by a fixed amount on logarithmic axes, corresponding to a multiplicative scaling: the test frame needs a higher contrast to compensate for its suppression. By a similar argument, suppression of the fixed-contrast frame should move the curves to the right, as more contrast of the fixed-contrast frame is required to compensate for its suppression.

These predictions can be made more quantitative. The blue curves are predictions from the data in normal viewing conditions, assuming that saccadic suppression

Figure 2
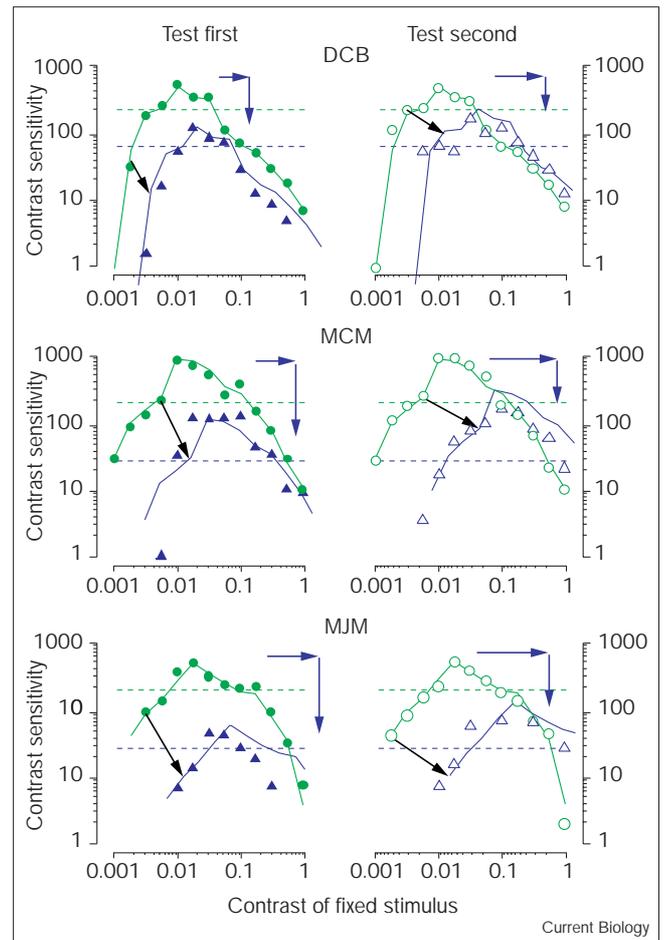
Contrast sensitivity (inverse of contrast thresholds) for discriminating the direction of a two-frame motion sequence as a function of the contrast of the fixed frame. Green circles refer to measurements under normal viewing conditions, blue triangles to those during saccades. Graphs are shown for each observer (DCB, MCM and MJM). The graphs on the left (filled symbols) depict results for motion sequences in which the test frame was presented first, those on the right (open symbols) for when it was second. The green curves are the geometric means of these two conditions in normal viewing. The fact that the curve passes very near the data points in both conditions shows that thresholds were very similar under normal viewing whether the test frame was first or second. During saccades, however, the graphs were very different for the two conditions. Sensitivity was much higher for when the test frame was presented second than when it was presented first, particularly at high contrasts. At some contrasts, sensitivity was sometimes higher during saccadic than normal viewing for this condition. The blue curves are saccadic sensitivities that are predicted if the first and second stimuli were suppressed independently of each other. These curves were derived from the average normal sensitivity estimates by displacing the green data points along both logarithmic axes, illustrated by the blue arrows (corresponding to a multiplicative scaling). The resultant displacement vector is illustrated by the black arrows. The multiplicative values (horizontal and vertical, respectively) of saccadic suppression used for the displacements were: DCB 4.0, 2.1; MCM 8.1, 2.9; MJM 9.0, 4.0. The dashed green and blue horizontal lines show contrast sensitivity when the contrast of the two frames was yoked.

precedes the site of motion analysis and acts independently on the two single frames. We first measured the detectability of single frames of the motion sequence, presented either at saccadic onset or 100 milliseconds later (mimicking the two separate motion frames). As previously observed (for example [5]), the suppression is strongest immediately after the saccade and diminishes with duration. Thus, the suppression for the first frame was greater than that for the second (see legend to Figure 2 for precise values of the multiplicative suppression). To generate the predictions, these values were used to displace the average thresholds under normal viewing (green curves) along both axes (corresponding to a multiplicative scaling of contrast of each stimulus). When the fixed-contrast stimulus was first, it was scaled by the larger factor, and sensitivity scaled by the smaller factor; when it was second, the reverse held. The predictions are not perfect, but adequate.

Previous studies of motion under normal conditions have suggested that two-frame motion sequences excite a local motion detector that multiplies the contrast signals of the two frames after one of them is appropriately delayed (commonly referred to as a 'Reichardt detector' after its originator [10]). The rising part of the curve reflects contrast summation between the two stimuli within the Reichardt detector; the falling part a contrast gain control mechanism, that normalises for contrast [8]. If the saccadic suppression were acting on the output of a Reichardt detector (or other neural device that combined the motion sequence), then it would be indifferent to presentation order, suppressing sensitivity by an equal amount for both orders of motion sequence. The fact that the suppression clearly depends on presentation order shows that saccades must act, at least in part, on the input to the Reichardt detector. It is conceivable that it interacts with the detector itself, but it must act before the delay line that equates the two stimuli in time: if it occurred after the delay line, the results would not be dependent on the sequence of the stimuli.

A common question about saccadic suppression is whether it results from an extra-retinal signal accompanying each saccade or whether it is the retinal motion caused by the eye motion that is responsible for the suppression in a form of masking [11]. Although we attempted to minimise the effects of image motion by making the saccades run parallel to the grating bars and surrounding the screen with a uniform field of similar luminance some image motion will remain, and this may in fact cause the suppression. However, it is unlikely to be the sole cause. In other experiments, we have shown that under many experimental conditions, saccadic-like motion may have very little effect on sensitivity [12]. Saccadic-like motion may well contribute to the suppression under some conditions, but is very unlikely to be the whole explanation.

Indeed, in this experiment we made some measurements with simulated motion and found the effects to be smaller than those with the real saccades, particularly at low fixed-frame contrasts. But irrespective of whether the suppression has a retinal or extra-retinal origin, or a combination of both, it must act at a very early stage.

An interesting aspect of the data is the paradoxical increase in sensitivity during saccades at high contrasts. This 'saccadic facilitation' is predictable from a recent model by Morgan and Chubb [8]: over the high-contrast range, the fixed-contrast frame acts to regulate the gain of the test frame, or 'mask' it, reducing sensitivity. If the contrast of the fixed-contrast frame is reduced, so is its masking effect, and sensitivity improves as a result of the 'de-masking'. Our data indicate that saccadic suppression does act at a very early stage of visual processing, possibly as early as the lateral geniculate body. One possibility previously mooted is that saccadic suppression acts through contrast gain mechanisms [6,12,13]. If this idea is correct, then the gain mechanisms themselves must act on the input to Reichardt-like motion detectors, consistent with Morgan and Chubb's suggestion [8].

Acknowledgements

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