Blurring by Fixational Eye Movements

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A complete description of the loss of contrast sensitivity at high spatial frequencies requires an estimate of the role of eye movements, which could blur fine detail. We describe a new technique to isolate their effect. Observers viewed either a 100 c/deg interference fringe, which the cone mosaic aliased to a low frequency zebra stripe, or an artificial zebra stripe. The real and artificial zebra stripes have similar spatial patterns, but differ in the temporal modulation produced by eye movements. Contrast threshold was measured as a function of duration for both stimuli flashed in the dark. The ratio of the contrast thresholds for the real and artificial zebra stripes with long durations, when eye movements could have a differential effect, is always within a factor of two or so of the ratio for 1 msec flashes, when eye movements are eliminated. These results support the view that eye movements are only a minor source of image degradation even at very high spatial frequencies, and provide no support for the view that they improve high resolution tasks.

Acuity   Contrast sensitivity   Fixation   Eye movements   Aliasing   Cone mosaic   Spatial vision

INTRODUCTION

The effects of eye movements on contrast sensitivity appear to be mediated by different mechanisms at different spatial frequencies. At spatial frequencies below 2–10 cycles/degree (c/deg), the retinal image motion produced by eye movements is beneficial for normal vision (cf. Steinman, Levinson, Collewijn & van der Steen, 1985; Arend, 1976; Van Nes, 1968). This paper examines the role of eye movements at spatial frequencies above the peak of the contrast sensitivity function. In this frequency range, eye movements could theoretically either improve or degrade contrast sensitivity. If successive images could be combined, resolution might be improved. Otherwise, the sluggish temporal response of the visual system would cause blurring, in the same way that the image of a moving object recorded on film is blurred if the camera shutter is open too long.

Spatial contrast sensitivity for sinusoidal gratings presented in the fovea decreases from a peak at 4 c/deg to a cut-off frequency of 50–60 c/deg (e.g. Schade, 1956; Campbell & Robson, 1968). Even after eliminating optical blurring with interference fringes, contrast sensitivity at 60 c/deg is still 0.8 log units below peak sensitivity (Williams, 1985a, b). One possible source of additional loss is blurring by eye movements. Even during fixation, the eyes are in constant motion (Ratliff & Riggs, 1950; Ditchburn & Foley-Fischer, 1967; Steinman, Haddad, Skavenski & Wyman, 1973; Eizenman, Hallet & Frecker, 1985) causing the retina to move with respect to the retinal image.

On the other hand, several theories of spatial vision have hypothesized a beneficial role for eye movements (for a review see Steinman & Levinson, 1990). Averil and Weymouth (1925) and Marshall and Talbot (1942) suggested that successive stimulus presentations between fixational eye movements might be combined to improve spatial vision. More recent theorizing from Bryngdahl (1961) and Arend (1973) postulated that the temporal variation in visual stimulation provided by eye movements was critical for spatial vision. Most recently, Maloney (1989) described how the visual system might combine information from several glances that are closely spaced in time, effectively increasing the number of photoreceptors sampling the retinal image. However, none of these theories has been satisfactorily validated by experimental data, in some cases because the theory was never precisely stated.

Empirically, the effects of retinal image motion on acuity have been measured using a number of techniques and stimuli (Riggs, Ratliff, Cornsweet & Cornsweet, 1953; Kahneman, 1964, 1966; Baron & Westheimer, 1973; Tulunay-Keesey, 1960; Ratliff, 1952; Westheimer & McKee, 1975). Most of these studies concluded that acuity was little affected by fixational eye movements. The effects of retinal image motion on contrast sensitivity have also been measured under similarly diverse conditions (Schober & Hilz, 1965; Nachmias, 1967; Tulunay-Keesey & Jones, 1976; Kelly, 1979; Robson, 1966; Van Nes, 1968; Kulikowski, 1971; Arend, 1976; Steinman et al., 1985). Studies in which stimulus duration was varied reported higher thresholds for very short stimulus durations, probably due to temporal integration rather than degradation by retinal image motion. Studies which introduced retinal image motion

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report an average loss of contrast sensitivity for spatial frequencies above 2–10 c/deg of about 0.3 log units. Thus, although contrast sensitivity at high spatial frequencies can be reduced by moving the retinal image across the retina at velocities similar to those found during fixation, the effects are modest in size and involve retinal image motion rather different from fixational eye movements. In short, how we are able to tolerate appreciable retinal image motion during fixation without suffering large losses in sensitivity at high spatial frequencies remains unanswered.

In order to address this issue, we have used a combination of new and old techniques to examine the effects of eye movements on contrast sensitivity at spatial frequencies above the peak of the contrast sensitivity function. Optical blur was minimized by using a laser interferometer to form sinusoidal interference fringes directly on the retina (Williams, 1985a), allowing the use of high spatial frequencies of high contrast. Although many studies have controlled for the effects of fixational eye movements by measuring and compensating for them, stabilization is difficult to achieve and to verify. All of the methods used to compensate retinal image motion have been the subject of intense scrutiny (Barlow, 1963; Arend & Timberlake, 1986, 1987; Ditchburn, 1987; Steinman & Levinson, 1990).

In order to sidestep the uncertainties inherent in monitoring eye position, we controlled for the effects of eye movements by varying stimulus duration. This is an old idea, but the standard stimulus configuration includes a uniform field before and after the stimulus to keep the state of adaptation constant. A serious side effect of this procedure is a reduction in effective contrast when a stimulus shorter than the integration time of the visual system is integrated with the uniform fields that precede and follow it. Indeed, in preliminary experiments using this technique, we were unable to detect gratings presented for the very short durations required to freeze the eye. This also probably explains the higher contrast thresholds for short presentations reported by previous studies. One of these studies, Tulunay-Keesey and Jones (1976), reported higher thresholds for the short duration stimuli both when the retinal image was stabilized and when it was not, suggesting that the higher thresholds were not due to eye movements. To avoid these reductions in effective contrast, we flashed our test fields in the dark. In the first experiment, we examined the effect of eye movements on acuity. In a second experiment, we measured contrast thresholds for low spatial frequencies, for spatial frequencies near the acuity limit, and for very high spatial frequencies that are particularly susceptible to blurring by eye movements.

A general problem with duration experiments is that stimuli of different durations or spatial characteristics may be detected by different neural mechanisms with different temporal properties. Such spatial and temporal interactions (for a review see Watson, 1986) during neural processing can be confounded with effects due to eye movements. One of the main goals of these experiments was to control for this possibility. Therefore, in a third experiment, we used a new method based on aliasing to control for differential neural blurring of stimuli presented for different durations. These techniques allowed us to measure the true effects of eye movements on the detection of contrast at high spatial frequencies.

GENERAL METHODS

All of the experiments used a laser interferometer to produce sinusoidally modulated gratings on the retina (Williams, 1985a, 1988). In brief, two beams from a single 632.8 nm laser were spatially filtered, expanded to a diameter of several centimeters, and brought to a focus at the front of the cornea. Light diverging from the corneal point sources interfered on the retina, producing the grating. Spatial frequency and orientation were controlled by varying the separation and orientation of the two point sources. Contrast was controlled by chopping the two beams into 1 msec pulses and varying the amount of temporal overlap. Head position was stabilized by a bite bar. The subject moved the bite bar fore and aft to focus the two point sources in the plane of the entrance pupil and left, right, up and down to center the two beams around the Stiles–Crawford maximum.

For most of the experiments, a 1.5 deg circular test field was flashed in the dark for a duration ranging from 1 msec, which is too short to allow appreciable image motion due to eye movements, up to 2 sec, which allows a full range of eye movements. Based on Riggs, Armington and Ratliff's (1954) measurements of the amplitudes of eye movements as a function of stimulus duration, we calculated that a 1 msec duration is short enough to restrict average image translation to about one-thirtieth of a photoreceptor width. Each stimulus delivered a similar number of quanta since retinal illuminance and duration were inversely varied, although control experiments done under conditions of constant luminance produced similar results. Finally, stimuli were flashed at a steady rate to keep the long term adaptation state of the observer as constant as possible.

EXPERIMENT 1:
EFFECTS OF FIXATIONAL EYE MOVEMENTS ON ACUITY

In the first experiment, we measured the effects of normal fixational eye movements on acuity for interference fringes, using methods that preserve the contrast of briefly presented stimuli and do not require the stabilization of eye movements.

Methods

Both subjects were experienced psychophysical observers with normal vision. To aid fixation and accommodation, a dim red annulus slightly larger than the stimulus was constantly visible. In order to prevent the iris from occluding the laser beams at high spatial frequencies, tropicamide (0.5%, Alcon, 1 drop) was used
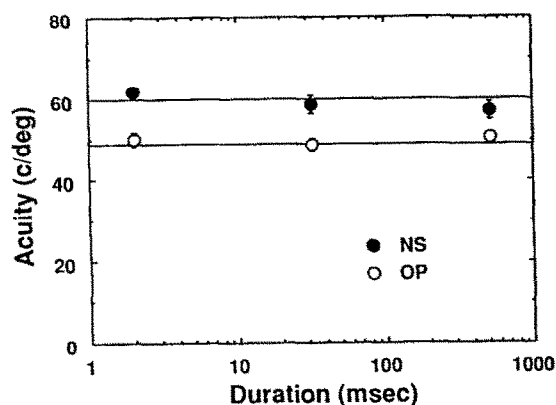
FIGURE 1. Acuity measured with interference fringes plotted as a function of duration in msec for observers OP and NS. Error bars are ± 1 SD and where not visible are smaller than the symbol.

to dilate the pupil. The subject's task was to adjust the spatial frequency of the fringe, until its orientation was just discriminable. The subject was given unlimited time and asked to approach threshold from both above and below before making a final setting. Fringe contrast was set to 100% and fringe duration to 1, 32, or 512 msec. The total length of each trial was 3 sec. The retinal illuminance of the unattenuated beam used for the 1 msec stimulus was 4.7 log td. Neutral density filters kept total luminous flux constant at all durations. The three durations were presented in random order. This procedure was replicated 7 times for each observer.

Results

Acuity is independent of pulse duration (Fig. 1). Subjects OP and NS have acuities near 50 and 60 c/deg respectively. Neither subject shows any consistent differences as a function of duration. Thus, acuity under conditions where eye movements are effectively eliminated is the same as acuity measured under conditions allowing fixational eye movements, confirming previous studies. These data do not exhibit the decrement of performance at short durations shown by other studies (cf. Tulunay-Keesey & Jones, 1976), presumably because flashing the stimuli in the dark eliminates contrast reductions within the integration time of the visual system.

EXPERIMENT 2:
EFFECTS OF FIXATIONAL EYE MOVEMENTS ON CONTRAST SENSITIVITY

In the second experiment, we extended the acuity measurements to contrast sensitivity, first measuring contrast sensitivities to low frequency fringes, and then extending the measurements to spatial frequencies above 60 c/deg. Blur due to eye movements should increase with spatial frequency because an eye movement of a given size causes a larger phase shift for high than for low spatial frequencies. Thus, interferometry allows a sensitive test of blurring by eye movements by permitting the use of spatial frequencies higher than those normally present in the retinal image.

Methods

Stimulus gratings were produced with the interferometer described above. Contrast threshold was measured as a function of duration for 10, 50, and 100 c/deg fringes. Stimulus durations ranged, in powers of two, from 1 to 2048 msec. Initially, the subject used method of adjustment to estimate thresholds for a two alternative forced choice experiment using the Quest algorithm (Watson & Pelli, 1983). Ten 50-trial thresholds were set for each duration in two separate experimental sessions performed on different days. Durations and spatial frequencies were randomly presented. The retinal illuminance of the shortest stimulus was 4.7 log td. The illuminances of the longer stimuli were reduced by neutral density filters so that the total energy remained constant. The total length of each trial was 3 sec. Zero contrast stimuli continued to occur with the same timing until the subject responded, holding the long term adaptation state of the observer as constant as possible.

Results

Figure 2 shows contrast thresholds for 10, 50, and 100 c/deg fringes plotted as a function of stimulus duration for observers OP and NS. Raw data from a third observer (DRW) were similar for the 100 c/deg condition. Contrast threshold for the 10 c/deg grating is 5% for the 1 msec stimulus, decreasing to 3% for the 2048 msec stimulus. The 50 c/deg grating had a threshold of 20% for the 1 msec pulse. OP has a slightly lower contrast threshold for the 2048 msec duration compared to the 1 msec duration, while NS has the reverse. For 100 c/deg fringes, both observer's thresholds were lower
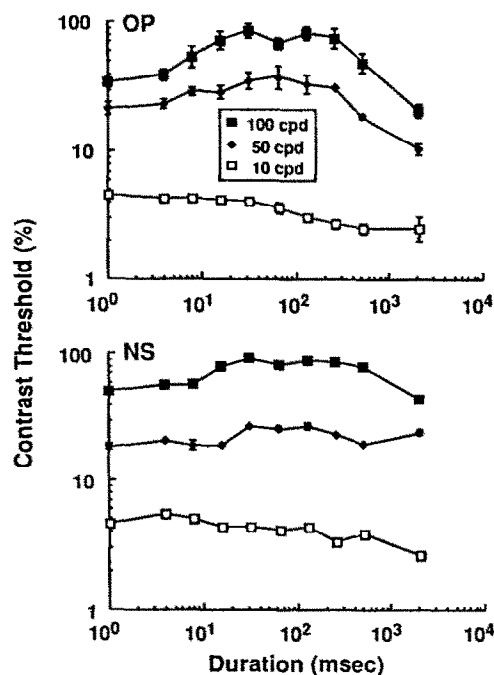

FIGURE 2. Contrast thresholds as a function of stimulus duration in msec for observers OP (top) and NS (bottom). Thresholds are shown for 10, 50, and 100 c/deg fringes. Error bars are ± 1 SEM and where not visible are smaller than the symbol.

for the 2048 msec stimulus than for the 1 msec stimulus, but the difference was never greater than 0.3 log units.

There is also a tendency for stimuli of intermediate length to have higher thresholds than stimuli of either the shortest or the longest durations. This is true for OP at 50 c/deg and for both observers at 100 c/deg. At 100 c/deg, contrast thresholds for 32 msec pulses are 0.3 (NS) and 0.45 (OP) log units higher than thresholds for 1 msec pulses. These differences, though small, were reliably seen in each experimental session.

The following analysis shows why these data, taken by themselves, fail to provide us with clear information about the blurring effects of eye movements, and led us to perform the control experiment described in the next section. Consider first the factors that are responsible for the difference in log contrast threshold for the 10 and 100 c/deg data at each duration. The difference in log contrast threshold can be attributed to two kinds of factors, which we will call eye movement and non-eye movement factors. When the duration is 1 msec, the presentation is so brief that the eye is essentially stationary for both spatial frequencies. Eye movements can not account for the threshold difference. Now consider the contrast threshold difference for the same two spatial frequencies when stimulus duration is 2 sec. In this case, there are non-eye movement factors that are responsible as before, but in addition, the stimulus is long enough that eye movement blurring could also play a role.

If the difference in contrast threshold caused by non-eye movement factors were exactly the same in the 1 msec and 2 sec conditions, then the difference in contrast sensitivity attributable to eye movement blurring for 10 and 100 c/deg fringes could be calculated. After normalizing the 10 and 100 c/deg curves by the contrast threshold values at 1 msec, any remaining threshold differences between the two curves at longer durations would then be attributable to blurring by eye movements. But this analysis rests on the assumption that the non-eye movement factors change in the same way for both spatial frequencies with increasing stimulus duration. Unfortunately, this assumption need not be true.

Indeed, we know from other studies (for a review see Watson, 1986) that contrast threshold can depend on both temporal and spatial frequency. For example, when gratings are introduced into fields of the same space-averaged luminance, threshold continues to drop for high spatial frequencies at longer durations than for low spatial frequency gratings. This is illustrated by Baron and Westheimer's (1973) finding that thresholds for detecting a Landolt C asymptote at shorter exposure durations than do thresholds for resolving the position of the gap. Presumably, detection is mediated by low spatial frequencies to which the visual system is most sensitive, while gap resolution requires the detection of higher spatial frequencies.

So the response of the visual system to stimuli of different durations depends on the spatial frequency content of the stimulus. In the present case, the 10 and

the 100 c/deg fringes could in principle be tapping different neural mechanisms with different temporal properties because they have different spatial frequency content: the 10 c/deg fringe is a sinusoidal grating whereas the 100 c/deg fringe is aliased by the cone mosaic into a Moire pattern of scintillating wavy stripes. Thus, we performed an additional experiment, to confirm that the temporal properties of the neural mechanisms that detect 10 and 100 c/deg were in fact quite similar. This result will allow us to make inferences about the role of eye movements alone.

EXPERIMENT 3:
ARTIFICIAL ZEBRA STRIPES

This control experiment capitalizes on the fact that we can create an artificial zebra stripe with a spatial frequency content similar to the alias of a 100 c/deg grating, but on which eye movements should have little effect. The artificial zebra stripe is formed when an artificial cone mosaic undersamples a high frequency sinusoidal grating. When there are too few sensors to adequately sample a grating, its spatial frequency is misinterpreted as a lower spatial frequency. The temporal spectrum, on the other hand, remains the same (Coletta, Williams & Tiana, 1990). Because we constructed the artificial cone mosaic using cone position data from a real mosaic, the artificial zebra stripe and the real zebra stripe look very similar to each other. The critical difference between them is that they differ in their susceptibility to blurring by eye movements. Real zebra stripes are affected because the fine fringe that generates them is moving relative to the retina, while the artificial zebra stripe is generated by an artificial photoreceptor mosaic that is stationary with respect to the fringe. When the artificial zebra stripe is imaged on the moving retina, only low spatial frequencies remain in the image, and they are relatively unblurred by eye movements. Thus, both stimuli have very similar spatial spectra, but different susceptibilities to blurring by eye movements. We would therefore expect differences in their contrast thresholds to reflect only differences in their susceptibility to eye movements.

Methods

The observer viewed either a high frequency interference fringe which his own cone mosaic aliased to a low frequency zebra stripe, or an artificial zebra stripe, produced by imaging the same fringe on an artificial cone mosaic. Any remaining high spatial frequencies were removed by a spatial filter.

Real zebra stripes were produced with the interferometer described above. Artificial zebra stripes were generated as shown in Fig. 3. A 632.8 nm helium neon laser beam was spatially filtered (SF) and collimated (L1). The collimated beam passed through a pair of crossed Ronchi rulings (RR) in rotating mounts. The rulings diffracted the beam into a grid of point sources which were focused on a slit (S) by lens L2. The slit (S) was positioned to pass the central zero-order beam and
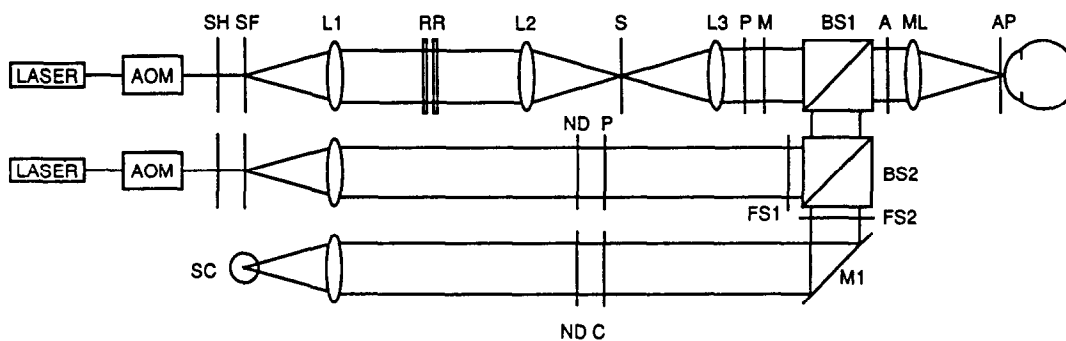
FIGURE 3. Schematic diagram of the interferometer used to generate the artificial zebra stripes. Not drawn to scale. See text for description.

a pair of first-order beams flanking it. Only the zero-order beam is shown. Rotating a single ruling changed the separation between the first-order beams, varying the spatial frequency of the fringe. Rotating both rulings together changed the orientation of the point sources and the resulting fringe. The point sources were recollimated by lens (L3). The fringe was then sampled by an artificial cone mosaic (M), made by digitizing the locations of the centers of the cones from a photomicrograph of a monkey fovea and making an opaque mask (Kodak Technical Pan film) with a hole at the location of each cone. The cone spacing of the image of the artificial cone mosaic was adjusted to be the same as the cone spacing of the real mosaic. The laser beams were brought to a focus at the front of the observer's cornea by the Maxwellian lens (ML).

The contrast of the artificial zebra stripes was controlled by adding uniform coherent light from a second channel. The two channels were combined by beam-splitters (BS1, BS2). The relative intensity of the two channels was adjusted by orthogonally polarizing them (P), adjusting them to the same intensity with a neutral density wedge (ND), and then rotating an analyzer (A) behind the Maxwellian lens. Pulse duration was controlled with an acousto-optic modulator (AOM) and a shutter (SH) in each channel. The field stop (FS2) of a third channel provided a dim red fixation annulus. Field size was 40' of arc and was controlled by field stops in the plane of the artificial mosaic (M) and in the background channel (FS1). A 2 mm artificial pupil (AP)

removed any remaining high spatial frequencies before the artificial zebra stripes were imaged on the retina.

The observer rotated the analyzer to change artificial zebra stripe contrast and find the detection threshold. Each observer set two thresholds starting from above threshold and two thresholds starting from below threshold. This was repeated 5 times for a total of 20 settings.

Results

Figure 4 shows contrast thresholds as a function of duration for both the artificial zebra stripes and for the 10 c/deg grating of the previous experiment. Thresholds are somewhat higher for the artificial zebra stripes than for the 10 c/deg grating, possibly because some of the energy in the high frequency grating is dispersed by the irregularity in the artificial photoreceptor mosaic (Yellott, 1982). Nevertheless, the shape of the two curves is similar and both show a tendency for lower thresholds
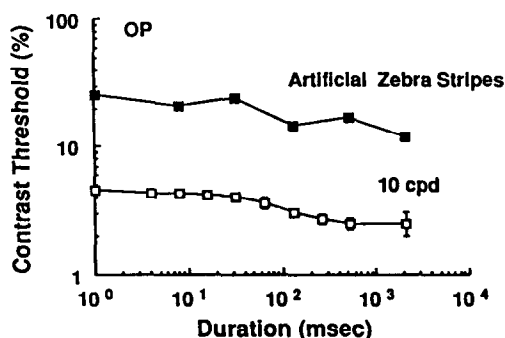

FIGURE 4. Contrast thresholds as a function of stimulus duration for observer OP. The black squares represent thresholds measured for the artificial zebra stripes. The open squares represent thresholds measured for a 10 c/deg grating. Error bars are ± 1 SEM.
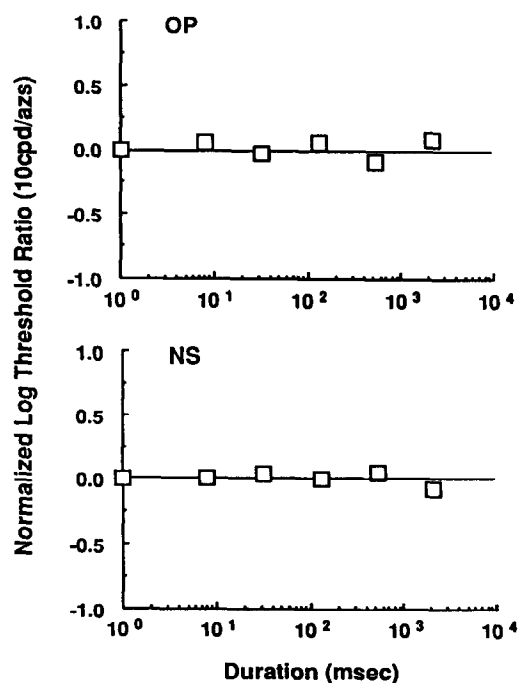

FIGURE 5. The log of the threshold ratio for the 10 c/deg grating and the artificial zebra stripes as a function of stimulus duration. The two curves were set to the same value at a duration of 1 msec before taking the ratio. Data are for observers OP (top) and NS (bottom).
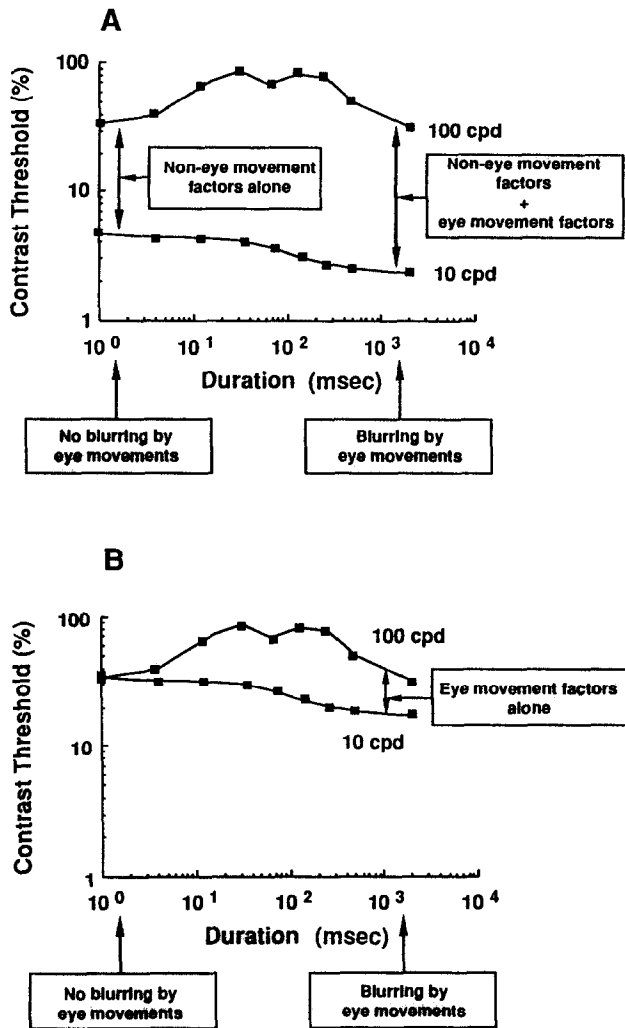
FIGURE 6. Contrast threshold as a function of duration for 10 and 100 c/deg gratings at a series of durations annotated to show our interpretation of the threshold differences. See text for explanation.
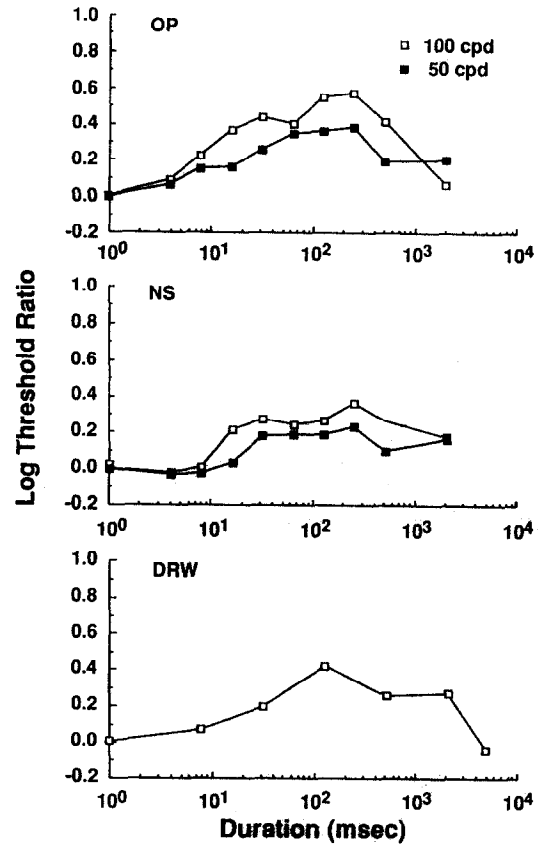

FIGURE 7. The log of the threshold ratio for the 10 c/deg grating and the 100 c/deg grating (open symbols) and the 10 c/deg grating and the 50 c/deg grating (solid symbols) as a function of stimulus duration for observers OP (top) and NS (middle). The log ratio was calculated after sliding the 10 c/deg curve of Fig. 2 vertically until the threshold at a duration of 1 msec was equal to that of the 100 or 50 c/deg curve. For observer DRW (bottom), the log ratio was calculated for the artificial zebra stripes and the 100 c/deg grating. One SEM is about the same size as the symbol.

with increasing duration. Raw data from a second observer (NS) were similar.

In order to compare the differences between the two curves, we set the two curves to the same value at a duration of 1 msec, and plotted the log of the ratio at each duration (Fig. 5). If the temporal effects of duration are equal for the 10 c/deg grating and the artificial zebra stripe, then the log threshold ratio would be 0. For both observers OP (top) and NS (bottom), the effects of stimulus duration on eye movements were similar for both stimuli at all durations.

INTERPRETING THE EFFECTS OF EYE MOVEMENTS ON CONTRAST SENSITIVITY

Figure 5 shows that the 10 c/deg grating and the artificial zebra stripe are processed by neural machinery with similar temporal properties. Furthermore, the spatial spectrum of the artificial zebra stripe and the 100 c/deg grating are similar. Therefore, we have a way of looking at eye movements uncontaminated by other factors (Fig. 6).

The 10 and 100 c/deg curves [Fig. 6(A)] are replotted from Fig. 3. Since eye movements are effectively elimi-

nated for a 1 msec presentation, differences in threshold between the two spatial frequencies represent differences in neural processing not related to eye movements or differential attenuation by the cone aperture. For a long duration, the difference between the two curves represents differences in neural processing not related to eye movements plus the effects of eye movements. Thus, neural effects not related to eye movements can be factored out by normalizing the two spatial frequencies at a duration of 1 msec [Fig. 6(B)]. The remaining difference between the two curves represents the effects of eye movements alone, and can be calculated by taking the log of the ratio for each duration (Fig. 7, open symbols).

When viewing a 100 c/deg grating (Fig. 7, open symbols), the difference in contrast thresholds between the shortest and longest stimuli is small. Observers OP and NS are 0.1 and 0.15 log units more sensitive to the shortest stimuli, while DRW is 0.08 log units more sensitive to the longest stimuli. Of course we are not normally able to view 100 c/deg stimuli, so of more relevance to normal vision are the effects of eye movements on spatial frequencies of 60 c/deg or less. The log threshold ratio for the 10 and 50 c/deg gratings (Fig. 7,

solid symbols) shows a similar result. OP and NS are 0.2 and 0.15 log units more sensitive to the shortest stimuli.

A tendency for higher thresholds at intermediate stimulus durations was also evident. The maximum threshold increase occurred at 128 or 256 msec and was 0.6, 0.4 and 0.45 log units for OP, NS, and DRW respectively. Thus, at the high spatial frequencies possible with the interferometer, there is a small range of stimulus durations that appear to be slightly blurred by fixational eye movements. At lower spatial frequencies, eye movements ought to be less deleterious. We confirmed this by calculating the log threshold ratio for the 10 and 50 c/deg gratings (Fig. 7, solid symbols) for two observers. In both cases, the shape of this function was similar to the comparison between 10 and 100 c/deg gratings but the contrast reductions at intermediate durations were less.

Thus, at spatial frequencies near the maximum normally imaged on the retina, blurring by eye movements reduces contrast by less than 0.2 log units for prolonged viewing and by only slightly larger amounts even at the intermediate durations that are most strongly blurred.

DISCUSSION

In these experiments, we used a new technique that allowed us to control for neural blurring not related to eye movements, while at the same time using stimuli of high spatial frequencies that ought to have been very sensitive to blurring by eye movements. Even using stimuli of higher spatial frequency (100 c/deg) than are normally imaged on the retina, contrast thresholds were similar for both the shortest and the longest stimulus durations. Thus, the visual system seems to be remarkably resistant to blurring by the small eye movements that occur during normal fixation.

To understand why, it is helpful to consider stimulus appearance as a function of duration when stimulus contrast is set slightly above threshold. For very short durations of 1–4 msec, stimuli appear to be of consistently high contrast from trial to trial. However, at durations exceeding 512 msec, perceived contrast waxes and wanes during the trial, producing a scintillating quality quite different than stimulus appearance at short durations even though thresholds are similar.

These observations are consistent with a hypothesis that detection occurs during moments when the eye is stationary. At the very shortest durations, the effects of eye movements are effectively eliminated, stimulus contrast is not reduced by blurring, and detection thresholds are low. At long durations, the probability increases that the eye will be stationary for an interval long enough to mediate detection, reducing the thresholds to values similar to those obtained for very short presentations.

This observation is consistent with the linear filter model of temporal sensitivity proposed by Watson (1986). Our simple adaptation of this model can be expressed symbolically as:

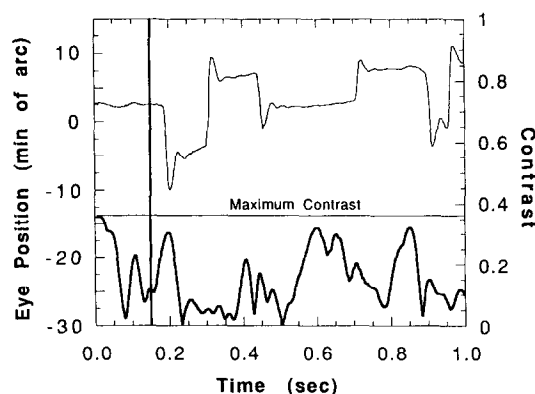$$o(x, t) = g(x) \cdot m(x, t) * h(t) \qquad (1)$$

FIGURE 8. A simple linear filter model of temporal sensitivity. The upper trace is an eye movement record from Eizenman et al. (1985). The size of the eye movement is shown on the left ordinate. The lower trace is the contrast predicted by the model. Contrast is shown on the right ordinate. The maximum contrast at 100 c/deg is 0.36 due to filtering by the cone aperture. The linear filter is from Watson (1986) and has a transience of 0, a time constant of 4.94 msec, and 9 stages. The vertical line shows maximum extent of influence from stimulus onset.

where the calculated contrast of the waveform, $o(x, t)$, produced when a sine wave grating, $g(x)$, is phase shifted by one-dimensional eye movements, $m(x, t)$, depends only on the characteristics of a linear temporal filter, $h(t)$. See figure legend for parameters.

The filter acts as a moving averaging window. Short stimuli always have a high calculated contrast, because at stimulus onset, the averaging window barely overlaps the stimulus, causing little averaging of peaks and troughs, and little loss of contrast. This onset pulse is over by 150 msec. A similar effect occurs after stimulus offset. However, long stimuli also show later periods of high contrast. Figure 8 shows predicted contrast for a 100 c/deg grating jittered by one particular eye movement record. The upper trace is the eye movement record and the lower trace is predicted contrast. Even ignoring the onset peak, there are 3 contrast peaks within 0.1 log units of the maximum contrast during the 1 sec duration of the stimulus. This suggests that even at high spatial frequencies, there are stationary moments that allow detection. The fact that thresholds for long duration stimuli were the same even when a constant luminance was present before and after the stimulus to suppress the onset and offset transients, suggests that these intermediate periods of high contrast play an important role in detection. Thus, a simple linear filter model is consistent with low thresholds for both very short and very long stimuli.

Although the model predicts similar thresholds for short and long stimuli, the small increase in thresholds for stimuli of intermediate durations are not quantitatively predicted. Nevertheless, we have an idea that might explain intermediate duration thresholds. Unlike very short and very long stimuli whose contrast is similar from trial to trial, the contrast of stimuli of intermediate durations is more variable. For identical trials, perceived contrast is high on a few trials, but is low on most of the others. This suggests that as stimulus duration increases,

eye movements may begin to blur the retinal image. However (Fig. 8, lower trace), there are moments when the eye is stationary enough to avoid blurring, so detection depends on the probability that the stimulus occurs during one of these intervals. The probability of this happening increases with stimulus duration. If this explanation is correct, the slopes of the psychometric functions at both short and long durations should be steeper than the psychometric functions for stimuli of intermediate duration. It will be interesting to see if this turns out to be the case.

In summary, eye movements could either increase the spatial sampling rate if the integration time of the visual system was short or cause blurring if the integration time was long. An extreme example of a visual system seemingly designed according to the former principle is Copilia, a tiny creature equipped with a single ommatidium-like structure that it scans across the image produced by its lens (Exner, 1891). Although nature has implemented scanning in this case, we have found no evidence that the human visual system is able to use small eye movements to scan the retinal image in any similar manner. On the other hand, although the visual system is relatively sluggish, fixational eye movements produce only minor blurring, at least at high light levels when temporal integration is relatively short. These results are consistent with a range of previous studies (cf. Steinman & Levinson, 1990) showing that although small eye movements may be necessary to maintain a visual response and may even improve the detection of low spatial frequencies, the visual system is remarkably resistant to their blurring effects. Our calculations suggest that similar contrast thresholds for the shortest and longest stimuli are consistent with a simple model of temporal vision in which a linear filter acts on fixational eye movements that contain occasional static moments. By eliminating the need to monitor eye movements, avoiding contrast losses due to temporal integration, and carefully distinguishing neural blurring from the temporal configuration of the stimulus, this study reinforces the view that fixational eye movements are not an important source of retinal image blur.

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