Direction selectivity for perceived motion in strabismic and anisometropic amblyopia

Clifton M. Schor and Dennis M. Levi

Interactions between direction-selective mechanisms for motion were examined in strabismic and anisometropic amblyopia. Amblyopes were found to have a marked reduction in sensitivity to flicker or movement when the amblyopic eye was presented with a combination of two gratings drifting in opposite directions at the same velocity (i.e., a counterphase grating). Sensitivity to flicker of the counterphase grating was improved by preadapting the amblyopic eyes to a single grating which was drifting nasalward, but there was no improvement if the drift of the adapting grating was temporalward. Sensitivity to flicker was also improved by reducing field size from 10° to 3°. However, occluding the central 4° of the 10° field did not significantly alter the sensitivity to flicker. These data suggest that inhibition between motion detectors in the parafovea of amblyopic eyes reduces slow-motion perception in both the parafovea and the fovea. The results also demonstrated a reduction in amblyopic eyes of direction selectivity for motion detection.

Key words: amblyopia, strabismus, anisometropia, direction specificity, contrast sensitivity, inhibition, motion/flicker thresholds, motion aftereffect

Amblyopia due to strabismus and/or anisometropia is a sensory motor complex, which is clinically diagnosed on the basis of reduced visual acuity as measured with the high-contrast letters of a Snellen chart. It has recently been shown that the threshold contrast sensitivity of the amblyopic eye is depressed over a wide range of spatial frequencies and that temporal processing of spatial information is also affected.

The degree to which temporal processing of spatial information is impaired has important implications for recent theories of amblyopia. Unfortunately, there is disagreement as to the degree to which pattern and motion (or flicker) perception are affected in amblyopes. For example, Hess et al. compared the contrast sensitivity of an amblyopic observer for detecting stationary and drifting gratings and concluded that only the pattern detecting mechanism was affected. This finding lends support to the hypothesis of Ikeda and Wright that amblyopia results from a defect of the central sustained neurons, i.e., neurons that are considered to be involved in pattern perception. Several other studies have capitalized on the finding of Keesey and Kulikowski and Tolhurst that there are two distinct psychophysical contrast detection thresholds for temporally modulated gratings: one threshold for detection of the spatial pattern and one for the detection of movement or flicker. In these studies a spatiotemporal grating that is flickered in...
counterphase or turned on and off is used to examine movement and pattern sensitivity for the same stimulus. Results of several such studies in amblyopes suggest that both pattern and movement detection thresholds may be elevated in strabismic and anisometropic amblyopic eyes.\textsuperscript{1, 3, 5} At issue is the question of whether the pattern (sustained) or movement (transient) detecting systems are more affected. Several of these studies have indicated that the sustained system is more severely affected in amblyopia than the transient system,\textsuperscript{1, 3, 4} whereas other studies\textsuperscript{6, 7} suggest that the transient system may be equally or even more strongly affected. The differences in the data of these experiments may simply reflect the fact that the consequences of amblyopia are not homogeneous across subjects. However, there is another possible source of variance, and that lies in the nature of the stimuli used in these studies. For example, Brettel et al.\textsuperscript{7} report a marked elevation of contrast thresholds for detecting flicker or movement of high-spatial-frequency counterphase gratings, the contrast of which is reversed sinusoidally at 1.5 Hz. They suggest that their results demonstrate an impairment of the transient system. However, it is not clear that the detection of flicker of a slowly moving high-spatial-frequency grating necessarily reflects transient activity, since the pattern system can signal the presence of slow motion.\textsuperscript{11} Previously we have also shown that amblyopic eyes have substantially decreased contrast sensitivity for detecting drifting gratings of high spatial frequencies and low temporal frequency; however, in the current report we have observed that the loss of contrast sensitivity in the amblyopic eye is far greater for counterphase flickering gratings than would be predicted from contrast sensitivity to single drifting gratings.

The counterphase flickering grating provides a unique stimulus for studying motion sensitivity because although it does not physically move, it is equivalent to the sum of two half-amplitude sinusoidal moving gratings drifting in opposite directions. Thus, if moving gratings of near threshold contrast levels are detected by direction-specific mechanisms which are independent detectors and if each detector is insensitive to movement opposite to its preferred direction, then threshold for a grating moving in one direction should be unaffected by the presence of movement in the opposite direction. A counterphase grating would therefore be detected by whichever direction-selective mechanism is momentarily the more sensitive. When either moving component of the counterphase grating is at threshold, the counterphase grating as a whole will be at threshold. Since the amplitude of the counterphase grating is twice the amplitude of either of its moving components, threshold for detecting the counterphase grating should be twice that for detecting a drifting grating of the same spatial and temporal frequency. Levinson and Sekuler\textsuperscript{12} found that the detection threshold for counterphase gratings was in fact two times greater than threshold for the corresponding drifting grating. The observation has been used as evidence in normal vision for independence between direction-specific mechanisms for detecting movement at threshold.\textsuperscript{12} This interpretation does not take into account probability summation of two independent detectors. If probability summation occurs, the threshold for counterphase gratings should be raised by a factor of slightly less than 2; however, since the threshold elevation is reportedly raised by a factor of 2, some inhibition between motion detectors probably occurs at threshold in normal vision.\textsuperscript{11} If in amblyopia the flicker threshold is elevated by more than a factor of 2, this would certainly demonstrate a lack of independence and possibly inhibition between direction-specific movement detectors. The purpose of the present study was to make direct comparisons of contrast thresholds to drifting and counterphase gratings in a group of strabismic and anisometropic amblyopes. Our results demonstrate a lack of independence between direction-specific motion detectors at threshold in amblyopia. The lack of independence is ascribed to inhibition
Table I. Visual characteristics of observers

<table>
<thead>
<tr>
<th>Subject</th>
<th>Refractive error</th>
<th>Visual acuity</th>
<th>Strabismus</th>
<th>Monocular fixation</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. S.</td>
<td>R: -1.75 - 0.75 ax 180</td>
<td>20/15</td>
<td>None</td>
<td>Central and steady</td>
</tr>
<tr>
<td></td>
<td>L: 1.75 - 0.50 ax 180</td>
<td>20/15</td>
<td></td>
<td>Central and steady</td>
</tr>
<tr>
<td>J. K.</td>
<td>R: -2.25 DS</td>
<td>20/20</td>
<td>8 Δ constant</td>
<td>Central and steady</td>
</tr>
<tr>
<td></td>
<td>L: -1.50 - 0.75 ax 165</td>
<td>20/70</td>
<td>left esotrope</td>
<td>3Δ nasal E.F.</td>
</tr>
<tr>
<td>D. H.</td>
<td>R: +3.00 - 0.50 ax 175</td>
<td>20/60</td>
<td>12Δ constant</td>
<td>1Δ temporal E.F.</td>
</tr>
<tr>
<td></td>
<td>L: plano</td>
<td>20/20</td>
<td>right esotrope</td>
<td>0.5Δ temporal E.F.</td>
</tr>
<tr>
<td>T. M.</td>
<td>R: -1.00 DS</td>
<td>20/15</td>
<td>15Δ constant</td>
<td>Central and steady</td>
</tr>
<tr>
<td></td>
<td>L: -0.50 DS</td>
<td>20/100</td>
<td>left esotrope</td>
<td>3Δ nasal E.F.</td>
</tr>
<tr>
<td>J. R.</td>
<td>R: +1.00 DS</td>
<td>20/20</td>
<td>None</td>
<td>Central and steady</td>
</tr>
<tr>
<td></td>
<td>L: +10.00 - 1.25 ax 90</td>
<td>20/200</td>
<td></td>
<td>Central and unsteady</td>
</tr>
<tr>
<td>C. D.</td>
<td>R: +2.00 DS</td>
<td>20/15</td>
<td>None</td>
<td>Central</td>
</tr>
<tr>
<td></td>
<td>L: +7.50 - 1.25 ax 90</td>
<td>20/270</td>
<td></td>
<td>6Δ nasal E.F.</td>
</tr>
</tbody>
</table>

in the parafovea, which reduces sensitivity to slow movement of fine detail presented to both the parafovea and the fovea.

Comparison of contrast sensitivity to drifting and counterphase patterns

Methods. Vertical sinusoidal gratings with a space average luminance of 4 cd/m² were generated electronically on a CRT (Tektronix 5110BN) with a P31 phosphor by a television technique. The screen of the CRT was at a viewing distance of 75 cm and subtended 8° by 10°. Gratings were caused to drift by triggering the CRT Z axis and time base at slightly different temporal frequencies. The drift rate was equal to the difference between these two frequencies and was monitored continuously via a phase meter. The contrast of gratings was caused to reverse sinusoidally by amplitude modulation of the input to the Z axis with an exact waveform generator (Model 519). Gratings of 6 cycle/degree spatial frequency were drifted or reversed in contrast at temporal frequencies ranging from 1.5 to 12 Hz. Temporal frequencies were presented in a randomized sequence. Contrast thresholds were determined for detecting pattern and movement/flicker of drifting gratings and detecting pattern and movement/flicker of counterphase gratings. The movement/flicker notation indicates that the subject reported whichever of these percepts appeared as contrast of the test grating was increased. Thresholds for both types of gratings were measured in the same session. Each experiment was repeated three times on different occasions in order to determine reliability. Thresholds were determined by a modified method of adjustment, and five settings yielded an S.E.M. of less than 5%. A small fixation point was placed on the center of the CRT to reduce or prevent tracking eye movements or optokinetic nystagmus. Eye movements were recorded via an infrared technique during threshold measurements to confirm eye fixation. The details of our eye-movement recording techniques are provided elsewhere. Objective records of eye movements indicated that fixation movements of normal and amblyopic eyes on the stationary fixation point were unaffected by the presence of threshold drifting or counterphase gratings.

Results. Contrast sensitivity for detecting nasalward and temporalward drifting gratings and sensitivity to pattern and motion are shown in Fig. 1. Sensitivity of the amblyopic eyes of Subjects J. K. and C. D. was equally reduced in response to nasal and temporal target motion. The reduction was greater for the severe amblyope (C. D.) than for the moderate amblyope (J. K.). Reduced sensitivity appears to be greatest at low temporal frequencies (<3 Hz). Responses to nasal and temporal drifting gratings for a normal control subject, C. S., are interesting, since he was slightly more sensitive to temporal than nasal field motion. This slight asymmetry was observed consistently upon repeated measurements. In Fig. 1 is also shown contrast...
sensitivity to flicker and pattern of counterphase gratings. Contrast sensitivity corresponding to the movement/flicker and pattern thresholds were essentially identical across temporal frequency for a normal observer, C. S., and also for the nonamblyopic eyes of J. K. and C. D., not shown in Fig. 1. At low temporal frequencies (<4 Hz) the sensitivity to counterphase gratings for these normal eyes was about one-half (0.3 log unit) that for detecting motion of a single drifting grating. At higher temporal frequencies the sensitivity to counterphase gratings for C. S. was reduced by a factor of 2.5 to 3 from that for detecting motion of drifting gratings. The results for low temporal frequencies are in agreement with the data of Levinson and Sekuler\textsuperscript{12} in normal observers.

The most striking result of this experiment was the finding that the contrast sensitivity of the amblyopic eyes was reduced by significantly more than the predicted factor of 2 for detecting movement/flicker of counterphase gratings compared to motion thresholds of single drifting gratings. The difference was most apparent at low temporal frequencies (Fig. 1). Here, the contrast sensitivity for detecting flicker of the counterphase grating was reduced for J. K. by more than 1 log unit over that for detecting motion of the drifting grating. Other amblyopes such as C. D. also showed abnormally reduced sensitivity to counterphase gratings at medium and high temporal frequencies. The marked reduction in movement/flicker sensitivity only occurred for spatial frequencies greater than 4 cy/deg. Similar effects to those shown in Fig. 1 were also found for vertical movement of horizontal gratings and horizontal counterphase gratings. These differences between drifting and counterphase gratings were noted for all five amblyopic observers, although the magnitude of the effect showed some individual variation. Four of the subjects showed about 1 log unit difference between sensitivity to motion of drifting gratings and sensitivity to movement/flicker of counterphase gratings. The fifth subject (D. H.), who showed the mildest degree of amblyopia, showed a smaller difference (0.5 log unit). These reduc-

![Fig. 1. Contrast sensitivity for drifting and counterphase sinusoidal gratings of 6.0 cy/deg plotted as a function of temporal frequency. Open symbols show the sensitivity for detecting motion; closed symbols show the sensitivity for pattern detection; the single gratings drifted either nasalward (circles) or temporalward (squares); triangles, contrast sensitivity for detecting movement/flicker (open symbols) and pattern (closed symbols) of the counterphase grating. The S.E.M. for each point was less than 5%, so that an S.E. bar would equal the width of the symbol. Functions are illustrated for a moderate (J. K.) and severe amblyope (C. D.) and a normal control subject (C. S.).](image-url)
Fig. 2. Contrast sensitivity to a 6 cy/deg sinusoidal test grating modulated at 1.5 Hz in counterphase plotted for the normal and amblyopic eyes of two observers (J. K. and T. M.) as a function of drift direction (nasal or temporal) of a 6 cy/deg adapting grating. Elevated contrast sensitivity following adaptation to nasal target drift demonstrates a release from inhibition between direction-selective mechanisms. The S.E.M. of three measures on separate occasions was less than 10%.

Influence of adaptation to a drifting grating upon detection of flicker in a contrast reversal grating

Method. Since the ratio of movement sensitivity to drifting and counterphase gratings at low temporal frequencies was much greater than the 2:1 found in normals, we tested for possible inhibitory interactions between direction-selective motion detectors in two amblyopes (J. K. and T. M.) via selective adaptation.14-16 We reasoned that if the 10:1 ratio shown by these observers resulted from inhibition, then by adapting one of the direction-selective mechanisms we could reduce the inhibition and change the ratio. Therefore we adapted the amblyopic eye to a high-contrast (80%) 6 cy/deg grating drifting horizontally at 6 Hz either nasally or temporally for 60 sec. We determined the contrast threshold of the adapted eye for detecting movement/flicker of a 1.5 Hz counterphase pattern of the same spatial frequency. After the drifting grating had been exposed for 60 sec, it was substituted for 5 sec with the counterphase test grating. The adapting grating was then replaced for 30 sec in order to sustain adaptation while the investigator adjusted the contrast of the
test grating, according to a modified staircase technique. Measurements were repeated on three separate occasions.

Results. Fig. 2 shows data for the two amblyopic observers, J. K. and T. M. The horizontal axis shows the direction of motion of the 6 cy/deg adapting grating, and the vertical axis shows contrast sensitivity for detecting movement/flicker of the counter-phase test grating. It is clear that adaptation to nasalward motion significantly enhanced the sensitivity for detecting the movement/flicker in the counterphase gratings for both subjects. The effect was verified on repeated tests. These results suggest that adaptation to nasalward motion results in a release of inhibition between nasalward and temporalward motion detectors. Interestingly, sensitivity to the counterphase gratings was not enhanced following adaptation to temporalward target motion. Such a result was unexpected, since both subjects showed equal sensitivity for detecting individual gratings drifting either nasalward or temporalward. This finding suggests the possibility of a loss of direction specificity for detectors normally sensitive to nasalward target motion. If there was a loss of direction specificity for nasal motion detectors, then adapting to a nasalward drifting grating would still reduce sensitivity to nasal but not temporal target motion. However, adapting to a temporalward drifting grating would reduce sensitivity to both nasal and temporal target motion. An equal reduction of nasal and temporal motion sensitivity would permit continued inhibition between nasal and temporal motion detectors after adapting to the temporalward drifting grating.

We considered the possibility that differences between adaptation to nasalward and temporalward motion might have been influenced by an eye-movement artifact. Amblyopic eyes have been shown to have abnormal monocular fixation control characterized by large saccades and drifts biased in the nasal direction.17 In addition, optokinetic nystagmus (OKN) of amblyopic eyes has abnormally low slow-phase velocities in response to temporal target motion.8 Since the test stimuli used in this study are also strong stimuli for OKN, we used a stationary fixation spot on top of the drifting grating to suppress reflex tracking eye movements. In the first experiment this proved to be an effective means for preventing OKN responses to threshold drifting gratings. The second and third experiments in this study used high-contrast (80%) drifting gratings, which in spite of a fixation spot resulted in increased nasalward drift rate when the adapting grating moved nasalward before the amblyopic eye. The nasalward drift was 1° in amplitude. When adapting gratings drifted temporalward over the stationary fixation spot, there was no directional bias of fixation drift. On the basis of these observations, we anticipated that nasal drift bias would reduce motion adaptation to suprathreshold gratings moving nasalward but not temporalward, since these eye movements reduced retinal image motions. Thus temporalward adapting gratings would have a greater aftereffect than nasalward adapting gratings upon the sensitivity to counterphase test gratings if only ocular motor factors were involved. Our results were opposite to this prediction. Since sensitivity to threshold counterphase gratings was enhanced by preadapting to nasalward but not temporalward target motion, it is unlikely that eye movement artifacts could have influenced our results. If there was a motor influence, it would minimize rather than exaggerate the sensory effects we report.

Direction-specific adaptation to drifting gratings

Method. In order to assess the loss of direction specificity, we examined the direction specificity of nasal and temporal motion detectors in J. K. and C. D. by adapting the amblyopic eye to a high-contrast (80%) 6 cy/deg drifting grating either nasalward or temporalward and then determined the contrast thresholds of the adapted eye for detecting a grating of the same spatial frequency drifting at 1.5 Hz in the same or opposite direction. Preadapted thresholds were also determined for both directions in order to establish a baseline. Eye movements were monitored during the ex-
MOTION OF 6 cpd ADAPTING

Δ NO STIMULUS
○ NASAL MOVEMENT
○ TEMPORAL MOVEMENT

Fig. 3. Contrast sensitivity to a 6 cy/deg grating drifting at 1.5 Hz plotted for the nonamblyopic eyes (A) and amblyopic eyes (B) of a moderate amblyope (J. K.) and a severe amblyope (C. D.) as a function of drift direction of the test grating following adaptation to a high-contrast (80%) grating of 6 cy/deg drifting at 6 Hz in the same or opposite direction. Triangles, Baseline data; circles and squares, contrast sensitivity after adapting to temporal and nasal drift, respectively. Sensitivity for detecting both temporalward and nasalward drift is reduced for the moderate amblyopic eye following adaptation to a grating moving in the temporalward direction. The S.E. of three measures was less than 10% of the mean.

Results. Data for the normal and amblyopic eyes of J. K. and C. D. are shown in Fig. 3. For both subjects, adapting the nonamblyopic eye to a nasalward moving grating reduced the motion sensitivity of that eye for detecting a grating moving in the same direction but not in the opposite direction, and vice versa for a temporal moving grating. For the amblyopic eye of the moderate amblyope (J. K.), thresholds for detecting nasalward drift were elevated by adaptation to either nasal or temporal motion, whereas temporalward drift detection was only im-

experiment to ensure that the same retinal area received the adapting and test gratings. Although the subjects had nasal eccentric fixation, the 10° test field size was large enough to include the fovea.
paired following adaptation to a grating drifting temporally (Figure 3, B, top). The fact that nasal motion detection could be desensitized by adaptation to either nasal or temporal drift was observed in two of the three moderate amblyopes (J. K. and T. M.). The third moderate amblyope (D. H.) retained direction-specific adaptation for both nasal and temporal motion. Interestingly, this subject showed the smallest deficit in sensitivity to low-temporal-frequency counterphase gratings that were studied in the first experiment.

We examined direction specificity to both vertical and horizontal movement for the severe amblyopic eye of Subject C. D. Figure 3, B (bottom) illustrates that for the severe amblyope (C. D.), adaptation to either horizontal direction of drift desensitized both nasal and temporal drift detection at threshold. Similar results were found for vertical movements. Adaptation to either up or downward motion desensitized both vertical directions of drift detection. Direction specificity for vertical motion was not disturbed in the moderate amblyopes J. K. or T. M. These results were verified upon repeated testing. The results suggest that direction-selective mechanisms normally sensitive to nasal target motion at threshold have reduced specificity in moderate amblyopia and that direction-selective mechanisms normally sensitive to nasal, temporal, upward, or downward motion have reduced specificity in severe amblyopia.

We confirmed the loss of nasalward direction specificity for Subjects J. K. and T. M. using a method developed by Levinson and Sekuler (cited in ref. 14) by asking the subjects to report the direction of apparent motion of a 1.5 Hz counterphase grating with a contrast near threshold after they had adapted to a high-contrast grating drifting either nasalward or temporalward. The normal observer and both of the moderate amblyopes reported that after adapting to nasalward drift with their nonamblyopic eyes, the counterphase grating appeared to move temporalward; however, after they had adapted to a temporalward drift, the counterphase grating appeared to be stationary. Thus it appears that temporalward drift desensitizes both nasal and temporal motion detectors in these subjects.

The apparent loss of direction selectivity of nasal motion detectors in amblyopia might be explained if slow movement were normally processed by both directionally selective and also nonselective detectors. Such a coexistence is evidenced in normal vision by the threshold elevation to test patterns moving in both the same and opposite directions as a preadapting pattern.15 16 Direction specificity is evidenced by the large threshold elevation in the same direction, and non-directional selectivity is evidenced by the small threshold elevation in the opposite direction as the adapting stimulus. Additional evidence of coexistence derives from observations that the initial speed and duration of the motion aftereffects are reduced as the contrast of a test grating is increased.18 19 This reduction in the motion aftereffects appears to result from the saturation of directionally selective channels at low-contrast levels19 and the continued operation of nonselective channels16 at higher-contrast levels. In amblyopia nonselective channels may have become manifest at threshold contrast levels because of reduced sensitivity of direction-selective motion detectors. In fact, recent reaction time studies suggest that the low-contrast mechanism responsible for detecting flashed gratings in normal observers may be abnormal or absent in strabismic and anisometropic amblyopes.20

Discussion

The data presented show that amblyopia is a complex process, affecting not only visual acuity and detection of static patterns but also motion sensitivity, particularly for high-spatial-frequency stimuli at slow drift rates. This is consistent with the findings of other experimenters,1–4,7 which suggest that sustained channels may be more affected than...
transient channels. In addition, however, the data presented suggest that in amblyopia, inhibitory interactions may occur at threshold between detectors of opposite directions of motion. This inhibition is found with high-spatial-frequency patterns modulated at low temporal frequencies. Normal observers show a 2:1 ratio of sensitivity between drifting and counterphase detection with similar stimulus parameters, although normal observers do show a greater difference in the detection of motion or flicker in drifting and in counterphase patterns at very high spatial frequencies (above 15 cy/deg) and to a much lesser degree than noted in amblyopic eyes.11 Thus the elevated thresholds to flicker of counterphase gratings seen in amblyopia may be an extension of a normal visual phenomenon to lower spatial frequencies. The 2:1 ratio of sensitivity to drifting and counterphase gratings seen in normal observers has provided strong evidence that, at threshold, opposite directions of movement are detected by independent direction-selective mechanisms.12 We interpret the 10:1 ratio found in amblyopic observers as an inhibition between direction-selective motion detectors at threshold. Another possible interpretation is that reduced sensitivity to counterphase gratings results from an abnormal flicker detection mechanism and that drifting gratings are detected by a separate movement detection mechanism. However, since moderate amblyopes showed greater reductions in sensitivity to horizontal than vertical counterphase gratings, this suggests the involvement of a direction-selective mechanism for detecting motion rather than a non-directional selective mechanism for detecting flicker in counterphase gratings.21,22

We performed an additional experiment to determine whether the inhibitory interactions described above were local or extended across the visual field. Flicker and pattern thresholds were compared for a 1.5 Hz 6 cy/deg counterphase grating in a 10° by 8° field (as in Fig. 1) with a similar grating in a 3° field. These data are shown in Fig. 4 for the moderate amblyope, J. K., who was experienced at maintaining steady fixation during contrast threshold measurements. This subject had 1.5° nasal eccentric fixation, which caused the 3° test grating to be imaged on the nasal half of the fovea. This eccentric point was found to be the retinal locus of peak sensitivity to high spatial frequencies for Subject J. K.'s amblyopic eye (results published elsewhere).5 In Fig. 4 the sensitivity of the amblyopic eye for detecting the flicker and pattern of the counterphase grating in the 3° by 3° field is compared with similar data for the large field replotted from Fig. 1. Note that the flicker sensitivity with the 3° field is higher than the pattern sensitivity across temporal frequency, whereas flicker sensitivity with the 10° field is markedly reduced, particularly at low temporal frequencies (1.5 to 3.0 Hz). This result is paradoxical because in normal observers sensitivity for a 10° field is as high as or higher than for a 3°

![Fig. 4. Contrast sensitivity plotted as a function of temporal frequency for detecting flicker and pattern (open and closed symbols) in a 1.5 Hz counterphase grating of 6 cy/deg by the amblyopic eye of observer J. K. Triangles and circles, Sensitivity to gratings presented in an 8° by 10° field and a 3° by 3° field, respectively. The S.E.M. of each point was less than 5%, so that an S.E. bar equaled the width of a symbol. Sensitivity to flicker of the counterphase grating (open symbols) is higher for the small than for the large test field.

Fig. 4: Contrast sensitivity plotted as a function of temporal frequency for detecting flicker and pattern (open and closed symbols) in a 1.5 Hz counterphase grating of 6 cy/deg by the amblyopic eye of observer J. K. Triangles and circles, Sensitivity to gratings presented in an 8° by 10° field and a 3° by 3° field, respectively. The S.E.M. of each point was less than 5%, so that an S.E. bar equaled the width of a symbol. Sensitivity to flicker of the counterphase grating (open symbols) is higher for the small than for the large test field.
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field; moreover, in the same amblyopic observer (J. K.), this reverse field-size effect is not evident for either static gratings or single gratings drifting to the left or right.

A recent report by Breitmeyer and Valberg describes how peripheral counterphase gratings reduce visibility of a central incremental light flash presented within 1.75° eccentricity of the fovea. This inhibition is thought to result from a combination of (1) the periphery or shift effect, in which remote stimulation outside the boundary of a receptive field increases activity of transient neurons, and (2) inhibition of sustained neurons by neighboring transient neurons. The inhibition of foveal-sustained neurons by transient neurons in the periphery has been suggested as a mechanism for saccadic suppression. This model provides a possible explanation for the reverse field-size effect described above for amblyopic eyes. Excessive inhibition by peripheral transient channels in amblyopic eyes could reduce activity of central sustained channels in the 3° or 4° encompassing the fovea and the eccentric fixation site, which are sensitive to slow movement of fine gratings. Since the activity and density of transient neurons are lower in the central retina than in the periphery, inhibitory interaction between sustained and transient channels would be less with small central than with large peripheral stimuli.

Inhibition of central sustained units in amblyopia is suggested, since the reverse field effect only occurred for slow reversal of high-spatial-frequency counterphase gratings (6 cy/deg). This effect was not seen with faster contrast reversals or with lower spatial frequencies. The association of the inhibitory interaction with counterphase gratings and not drifting gratings may result from the physical equivalence of a counterphase grating with a combination of two gratings moving in opposite directions. At threshold a counterphase grating would drive more direction-selective mechanisms than a grating drifting in one direction. As a consequence, inhibition by transient channels would be more intense with counterphase than with single drifting gratings. This explanation may also account for a recent report that the shift effect in normal vision is produced by a counterphase grating but not by an equivalent drifting grating. An alternative hypothesis suggested earlier is that inhibition occurs between detectors sensitive to different directions of motion and that this inhibitory interaction between motion detectors occurs in the parafovea but not the fovea of the amblyopic eye.

Confirmation of these observations comes from Sokol who reported that in some strabismic amblyopes the visual evoked potential elicited by high-contrast counterphase checkerboard patterns is reduced in amplitude in the amblyopic eye and that the visual-evoked potential of the amblyopic eye derives from the parafovea. He postulated that in amblyopia the parafovea may exert an inhibitory influence on the central retina. When we examined contrast sensitivity to counterphase gratings with the central 4° of a 10° field occluded (i.e., gratings presented in an annulus), the sensitivity of the amblyopic eye was identical to that found when tested with the full field. These results suggest the hypothesis that inhibitory interactions occur between directionally selective mechanisms in the parafovea and, in addition, that inhibition originating in the parafovea may reduce sensitivity to slow motion of fine targets in the central visual field of amblyopic eyes.

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REFERENCES