Contrast-coding in amblyopia

I. Differences in the neural basis of human amblyopia

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To shed light on the basis of normal contrast perception in general and its susceptibility during early visual development in particular the contrast-coding deficit of amblyopic eyes was investigated. This was accomplished by using two different but complementary paradigms, one involving equating the contrast sensations between the amblyopic and normal fellow eye and the other involving the assessment of incremental sensitivity at different contrast levels. Since human amblyopia is known to have three different forms, representatives of each were tested. These include strabismics, anisometropes and astigmats. The results of the contrast-matching approach suggest that (i) strabismic and anisometropic (including meridional) amblyopes show important differences in supra-threshold contrast matching (this difference, which occurs across different spatial frequencies, at different luminances and for different field sizes, suggests a different neural basis for the two main forms of human amblyopia); (ii) all forms of amblyopia share one common feature, that of large threshold losses relative to the extent of the suprathreshold anomaly; (iii) the accelerating growth in subjective contrast above the raised threshold shown by the matching procedure is not evident in the assessment of incremental contrast sensitivity. From these results it is argued that, although contrast perception (in the low contrast range) is disturbed in amblyopia, amblyopia cannot be adequately understood in these terms alone. This raises important questions for our understanding of the physiological basis of contrast-coding in normal vision and its perceptual importance.

Introduction

Although our understanding of normal visual function has been greatly facilitated by the measurement of contrast thresholds for stimuli of different size (Campbell & Green 1965, Campbell & Robson 1968), we are still very ignorant of visual processing for stimuli whose contrast is substantially above threshold. Yet this is obviously of fundamental concern, because most everyday images are made up of such suprathreshold contrasts. This lack of understanding of suprathreshold processes is even more acutely seen in terms of our approach to the developmental
disorders of vision (amblyopias). Our understanding of these and of visual development in general is in threshold terms only. In this study we investigate the suprathreshold function of representatives from the developmental disorders of vision to address two questions. First, are the classifications and models of amblyopia that have been proposed from threshold experimentation (Mitchell et al. 1973, Levi & Harwerth 1977, Rentschler et al. 1978, Hess et al. 1980) also true for suprathreshold stimuli? Secondly, what are the developmental susceptibility and adaptive properties of the mechanisms underlying suprathreshold contrast-processing in normals? The second question bears upon the two opposing models put forward by Georgeson & Sullivan (1975) and Kulikowski (1976) to account for some of the observed discrepancies found with threshold and suprathreshold stimuli in normals.

Traditionally, there have been two psychophysical techniques available for examining the suprathreshold response of a sensory system. The first is to evaluate the resultant sensory magnitude for a given stimulus magnitude (Stevens 1951). Several methods have developed to estimate sensory magnitude: varying one stimulus magnitude until it appears to have the same sensory magnitude as a second, standard stimulus (matching method); stimulus doubling; and simply attaching some arbitrary scale to the sensory magnitude. The second technique very commonly used is that developed by Bouguer (1760), Weber (1834) and Fechner (1838). This method examines the change in stimulus magnitude necessary to elicit a just-noticeable sensory difference as a function of stimulus magnitude.

Both types of method have been adopted in the present study to examine suprathreshold processing of contrast in both strabismic and anisometropic amblyopes. The results indicate that, contrary to what one might expect, the suprathreshold contrast-matching and discrimination bear no simple relation to the accompanying threshold deficit. In the accompanying paper (Hess 1982) the possible neural substrate of this threshold—suprathreshold dissociation in amblyopia is evaluated. The results suggest indirectly that normal vision may be subserved by more than one 'contrast channel' and that in amblyopia the more sensitive channel (or channels) is selectively affected.

**Methods**

**Apparatus**

Vertical sinewave gratings (temporal frequency 0 Hz) were generated analogically or digitally and displayed on each half of a specially constructed 20 cm x 30 cm video display ($^{31P}$ phosphor). The spatial frequency and contrast of each of these waveforms could be independently varied. Contrast was linear up to 90%. The mean luminance of each was equal and set to 200 cd/m². The subject viewed these gratings from a distance of 114 cm (10° field size) such that, by the use of a partition, the gratings were seen dichoptically. A slowly rotating sectored disc alternately occluded one eye and simultaneously presented a grating to the other eye every $\frac{1}{2}$ s. Furthermore, the gratings were presented for an 8 s interval every 20 s in this mode. This switching from grating to mean luminance was used to avoid differential adaptation effects at higher contrasts (Blakemore & Campbell 1969).
The subject made a series of either threshold setting or suprathreshold matches during these exposures. A tone signalled the beginning of the 8 s test period. For one series of experiments two matched displays were used so that each eye could view a grating of different orientation.

Contrast matching

The method of adjustment \((N = 5)\) was used for all matches. At first the subject was carefully refracted for ametropia and viewing distance. The spatial frequencies were then subjectively matched for normal and amblyopic eyes. Contrast thresholds were measured under the stimulus conditions already discussed and contrast matches at 3 dB steps were then made up to 90% contrast for the two objectively equal spatial frequencies. The standard was always set before the amblyopic eye. Recalibrated Kodak neutral density filters in goggles were used to reduce the luminance (of both fields) and field size was varied by changing distance. All results on amblyopes were checked on at least one subsequent occasion. Amblyopes were divided into four groups: strabismics with and without threshold anomalies and anisometropes with spherical and with meridional (astigmatic) errors of refraction. Three subjects were tested in the first category and five in each of the remaining three categories. The results for only some of these are displayed.

Contrast discrimination experiments

These experiments involved a successive, two-alternative forced-choice procedure for measurement of both the contrast threshold and the contrast necessary to determine that two suprathreshold gratings were different in contrast. In the first procedure the subject was presented (threshold) with two intervals, each of 500 ms duration\(^\dagger\), one of which contained a sinewave grating. The Quest psychophysical procedure was used (Watson & Pelli 1979) that involves a staircase method driven from maximum likelihood estimates. Sixty trials were run for each condition.

In the contrast discrimination experiments the same procedure was used except that two gratings of the same spatial frequency were presented and the task was to choose which interval contained the higher contrast grating. A minimum of 60 trials were run for each condition. A PDP 11/20 computer presented the stimuli and collected responses. The normal and fellow amblyopic eyes were always alternately tested at each condition. The experiments were always repeated on another occasion.

Magnitude estimation procedure

Two different procedures were adopted, each of which involved the normal and fellow amblyopic eye. In the first procedure, referred to as the external-reference procedure, the subject (normal eye and then amblyopic eye tested separately) was presented with a standard grating set to each of a number of contrast levels above the amblyopic eye's threshold. The task consisted of setting an adjacent test pattern (of the same spatial frequency) to double the contrast of the standard. In the second method, referred to as the internal-reference procedure, no standard

\(^\dagger\) The duration is defined as the time over which the gaussian envelope falls from 1 to 1/e.
or reference was shown. The task consisted of setting the contrast of the pattern (for each of a number of base contrasts) to double its initial value. In each procedure the base contrast levels were randomized, the patterns were stationary and the viewing time was unrestricted. Each contrast was shown ten times on two separate occasions. The subjects used were experienced at threshold and suprathreshold measurements and no prior training or subsequent feedback was given for this specific task.

Noise-masking experiments

In these experiments contrast thresholds were determined for stimuli embedded in notch filtered spatial noise having an approximate gaussian amplitude probability distribution. The slope of the notch roll-off was 96 dB per octave; it also exhibited a gradual high frequency roll-off whose 3 dB point was 40 kHz. The noise was produced from a white-noise generator. The notch-filtering was achieved by two parallel channels of kemo filters (each of two filters in series with 48 dB per octave). The method of adjustment was used for threshold settings and for suprathreshold matches. The ‘notch’ was positioned on the test frequency and matches were repeated ten times on two separate occasions. The test signals were stationary and the noise was dynamic (flat temporal spectrum).

For the suprathreshold experiments involving noise-masking two separate procedures were used. In the first procedure, referred to as the constant noise amplitude method, the standard or reference grating was embedded in notch filter noise having a constant noise amplitude, whatever the contrast of the reference. In the second method, referred to as the constant signal:noise ratio method, the amplitude of the notch filtered noise was increased in proportion to the contrast of the reference grating.

Results

Contrast perception

Normal subjects and strabismics with normal contrast thresholds

Figure 1 illustrates the accuracy with which a normal inexperienced subject can match the contrast of two gratings of the same spatial frequency using the technique previously outlined. The results are plotted on logarithmic—logarithmic axes and the equivalence line is indicated. Standard deviations are displayed for each group of settings \((N = 10)\) over a wide frequency range. It can be seen that the accuracy is independent of logarithm of contrast and does not vary systematically with spatial frequency. The threshold points are indicated by half-filled symbols.

Figure 2a, b represents similar results for two strabismic amblyopes who exhibit normal thresholds (half-filled symbols). In this and subsequent experiments the standard contrast was always shown to the amblyopic eye. These two strabismics differ in one very important aspect. Amblyope T.G. exhibited abnormal letter acuity and reported distortions in her perception of medium to high frequency gratings of suprathreshold contrast (Hess et al. 1978). For each subject the threshold contrast sensitivity results are also illustrated (see inset). The contrast
range over which gratings were seen as distorted is also indicated, as well as an illustration of the type of perceptual distortion. Over a substantial contrast range the amblyopic eye of T.G. perceived contrast inappropriately. The overestimation of contrast by the amblyopic eye is a small but consistent and repeatable effect. All of these overestimated dichoptic settings were rejected by the amblyope when the two fields were viewed monocularly by either the normal or the amblyopic eye.

Figure 1. Contrast-matching results are displayed for a normal observer (D.A.) for a range of spatial frequencies. A standard contrast was presented to the right eye and matched by varying the contrast of an identical pattern shown to the left eye. For normal eyes in optimal focus, contrast can be matched accurately. Vertical bars indicate ±1 standard deviation.

Hence, this behaviour is not due to either subject inaccuracy or instrumental artefact. The form of this over-compensation also seems to vary (as the distortions do) with spatial frequency (see inset). A similar but more exaggerated form of overcompensation was also noted in some amblyopes with raised thresholds. In these cases, over-compensation only occurred for frequencies whose thresholds were raised.

Strabismic amblyopes with raised contrast thresholds

In figure 2c, d the contrast-matching results of two strabismic amblyopes are illustrated. The threshold readings form the lowest data points on these functions (half-filled symbols joined by discontinuous lines). In all of these diagrams ±1 standard deviation is indicated as well as the veridical matching line. It is obvious from these two examples that the threshold contrast deficit is not present to any great extent above threshold. These two cases differ dramatically in the extent of the threshold deficit (see insets) but differ very little in the suprathreshold range. In the milder case (figure 2d) suprathreshold contrasts are enhanced by the amblyopic eye as they were for the strabismic without a threshold deficit (figure 2b), whereas for the more severe case (figure 2c) a residual, constant deficit remains at suprathreshold levels. These suprathreshold differences are slight compared with the more severe threshold deficits.
Contrast of variable (good eye)

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Figure 2. (a, b) Contrast was equated between the amblyopic (standard) and normal (variable) eye of two strabismic amblyopes for different spatial frequencies. Amblyopes (a) N.A. and (b) T.G. exhibit anomalous letter acuity but normal contrast thresholds. They perceived contrast above threshold normally. They differ in the fact that T.G. also reports perceptual distortions for grating patterns, the contrast range over which this occurs is indicated.

(c, d) Contrast-matching results for two strabismic amblyopes, (c) S.C. and (d) D.B., who exhibit raised contrast thresholds for grating patterns. In each case, although the threshold defect differs, contrast is correctly matched above threshold. The threshold data (half-filled symbols) are joined by dashed lines to the suprathreshold matches which fall on or close to the normal matching line. Plots of threshold against spatial frequency are displayed in the insets.

Anisometropes with raised contrast thresholds

Figure 3a, b represents contrast-matching results between the normal and fellow amblyopic eye for two representative anisometropic amblyopes. Although the experimental conditions were identical for the strabismics and anisometropes, the results differ. For anisometropes, contrast perception is also more affected at threshold than above threshold, yet this is not as dramatic as it is for the strabismics. The contrast abnormality, which is maximal at threshold, returns...
Figure 3. (a, b) Contrast-matching results for two representative anisometropic amblyopes, (a) S.C.A. and (b) A.C., for a range of spatial frequencies for which thresholds were raised (see inset). In each case the contrast thresholds for the normal and amblyopic eye are plotted as half-filled symbols joined by dashed lines to the suprathreshold matches. In both examples contrast perception gradually returns to normal or near normal (matching line) in the suprathreshold domain. (c, d) Contrast-matching results at and above threshold for two meridional amblyopes, (c) P.S. and (d) N.N., for a range of spatial frequencies for which thresholds were raised. Contrast thresholds are displayed as half-filled symbols and the form of the threshold loss across spatial frequency is inset together with their refractive correction. As with spherical anisometropes, contrast perception gradually returns to normal or near normal above the raised threshold.

more slowly to normal as contrast is made more suprathreshold. The contrast range over which the abnormality occurs depends upon the initial threshold deficit and the contrast range available at that frequency. In some cases, if the threshold deficit is sufficiently large, the contrast deficit may be reduced for higher contrast stimuli but may never disappear altogether. For example, for anisometrope A.C. (figure 3b) the threshold deficit at 2 and 3 c/deg† is similar but because of the remaining contrast range available 3 c/deg is seen at a reduced contrast at all suprathreshold levels. Similar results are obtained for anisometrope S.C.A.

† In this and the following paper the symbol c stands for cycle.
(figure 3a) for 15 and 20 c/deg. For these anisometropes (and others who were tested and not reported here) there was no evidence of the over-compensation at high contrasts that was constantly and repeatably exhibited by some strabismics with similarly raised thresholds.

**Meridional amblyopes with raised thresholds**

The threshold and suprathreshold contrast functions of two meridional amblyopes are displayed in figures 3 and 4. In figure 3c subject P.S. exhibited a combination of spherical and cylindrical anisometropia. By using a vertically orientated grating and a dichoptic method as before it was possible to test the amblyopic meridian and the corresponding meridian of the normal eye. The contrast-matching function for this meridional anisometrope is very similar to that of the anisometropic amblyopes of figure 3a, b. The deficit at threshold is not seen for suprathreshold stimuli; contrast perception is normal above 1% contrast for 1.6 c/deg and above 10% contrast for 10 c/deg. Figure 3d displays the dichoptic matching results for a uniocular meridional amblyope (N.N.) who exhibited plano astigmatism only in the ametropic eye. That is, the refractive correction of one eye was zero whereas the other eye exhibited astigmatism at 180° (plano/−3.00 × 180). This allows the opportunity to compare meridional amblyopia within one eye as well as between eyes. In this way it may be possible to dissociate monocular from binocular influences. In figure 4a the contrast threshold functions for both horizontal and vertical stimuli presented to each eye are displayed. The thresholds for both the in- and out-of-focus meridians of the ametropic eye were reduced, although thresholds for stimuli probing the myopic meridian were more severely reduced. Each meridian was affected over a similar spatial range. The extent to which the in-focus meridian of the ametropic eye was abnormal may represent the extent of binocular influences whereas the disparity in the results for stimuli probing each meridian of the ametropic eye may represent the consequences of meridional defocus per sé. Contrast-matching experiments were done at two spatial frequencies for three separate conditions. Two of these were dichoptic, the emmetropic and ametropic eye being compared for either vertical or horizontal stimuli. The other was a purely monocular condition. In this condition contrast perception was compared for horizontal and vertical gratings presented to only the amblyopic eye. In this experiment two display screens that were matched for luminance, chromaticity and contrast were used. A careful refraction was performed before testing.

Figure 3d shows results for dichoptic matching of two vertical gratings for amblyope N.N. These results are very similar to those displayed in figure 3a, b for spherical anisometropes. The threshold abnormality, which varies with spatial frequency, gradually decreases as contrast is increased for both 2 and 5 c/deg stimuli. A similar result is also seen for the 10 c/deg stimulus although in this case a small residual deficit remained at high contrast. Spatial frequencies higher than 10 c/deg could not be tested for this subject as their spatial structure was not evident at any contrast level (Hess et al. 1978). Grating acuity was between 20 and 25 c/deg. The anomalous matching results are well approximated by lines of slope 2.

In figure 4a the contrast sensitivity results for anisometrope N.N. are displayed
for gratings of either horizontal or vertical orientation. Inset in this figure is an illustration of the optical condition present in early life. He has plano astigmatism in only one eye which would result in only horizontal stimuli being out of focus. The threshold sensitivity after optical correction reflects an abnormality for both horizontal and vertically oriented stimuli in the ametropic eye. Although both stimulus orientations are affected, vertical stimuli show less of a defect. Figure 4b represents contrast matches for N.N. for different orientations presented either dichoptically or monoptically. Perceived contrast of vertical stimuli is similar to that previously described (figure 3d). However, the perceived contrast of horizontal stimuli is different. The thresholds and supratreshold perception are more severely depressed for horizontal gratings (figure 4a, b). The contrast-matching results for horizontal stimuli are displaced by a constant ratio (factor of 2) from those obtained with vertical stimuli. The monoptic matches between vertical and horizontal stimuli are similarly displaced by a factor of two from the matching line. Similar results were obtained for a 2 c/deg stimulus (not displayed). The contrast loss between eyes may include a binocular factor that is not present when meridia are compared within the one eye. To this extent the contrast loss between the in-focus and previously out-of-focus meridian of the amblyopic eye of N.N. may allow an estimate of the neural effects of blur without any contamination from binocular influences due to later suppression. The neural contrast loss due to defocus per se can be approximated by a constant ratio change. A similar
contrast loss would be expected from a purely optical consideration (Hess & Bradley 1980).

In all of the contrast-matching experiments discussed so far, matches were made between objectively equal spatial frequencies shown to the normal and fellow amblyopic eye. To gauge whether these were also subjectively equal for the normal and amblyopic eye, spatial frequency matches were made for various subjects for fixed contrast (< 60%) stimuli. These results are displayed in figure 5. This figure shows that for some amblyopes, namely anisometropes (spherical or meridional), these frequencies may not have appeared subjectively equal. This discrepancy rarely exceeded 50%, but was more usually between 10 and 30%. In most cases (myopic anisometrope) the amblyopic eye perceived the stimulus as of lower spatial frequency. This spatial frequency shift in the anisometropic eye or anisometropic meridian did not itself influence the matching results. This was experimentally verified for a number of anisometropic amblyopes by assessing contrast matches between spatial frequencies that were seen to be subjectively equal to the normal and amblyopic eyes. Consequently the matching results cannot be attributed to this small perceived change in spatial frequency by the amblyopic eye. Such shifts in apparent size are discussed in detail elsewhere (Bradley & Freeman 1981, Bradley et al. in preparation).

**Effects of luminance**

Contrast-matching suggests that reducing the background luminance affects the apparent contrast of objects differently for strabismic and anisometropic amblyopes. Figure 6 shows the results for two such amblyopes over a 6 logarithmic unit reduction in mean luminance. For the strabismic amblyope (figure 6a) the
threshold deficit evident at 200 cd/m² gradually reduces as the luminance is reduced until at 0.02 cd/m² very little deficit remains. For lower luminances (e.g. at 0.002 cd/m²) the results are seen to follow the same rules that describe the higher contrast results at higher luminances. In contrast to the normal eye, where contrast sensitivity declines rapidly with decreased luminance, the thresholds in the amblyopic eye are seen to actually improve slightly with reducing luminance rather than be maintained at a constant level. The results for the anisometrope are quite different in that the threshold deficit apparent at 200 cd/m² increases as the mean luminance is reduced. This is illustrated in the figure by the non-parallel displacement of the line describing the threshold displacement with luminance (dashed line) from the normal matching line (full line). The contrast-matching results, however, above threshold are similarly displaced relative to the new threshold. Because of the different threshold behaviour as luminance is reduced the anisometrope exhibits similar contrast anomalies at similar subjective contrasts (equal suprathreshold units), whereas the strabismic exhibits similar anomalies at similar objective contrasts. This difference is not dependent on spatial frequency as similar results were obtained when these amblyopes were tested with targets of lower spatial frequency. The accuracy of contrast-matching did not vary for either amblyope as a function of luminance.

**Figure 6.** Contrast matches at and above threshold are displayed for (a) a representative strabismic amblyope, S.C., and (b) a representative anisometropic amblyope, S.C.A., for one spatial frequency (in (a) 1 c/deg; in (b) 10 c/deg) and a range of mean luminances. The starting luminance (0 ND) corresponded to 200 cd/m² and it was reduced in steps of 1 logarithmic unit (i.e. by a factor of 10 each time) to 6 ND. (ND refers to units of optical density for spectrally uniform filters such that $1 \text{ nd} = \log_{10} T^{-1}$ where $T$ is the filter transmission.) Strabismics and anisometropes differ in the form of their suprathreshold contrast response at any one luminance as well as how this function alters with decreasing luminance (see text).
Effect of field size

For the experiments described so far the stimulus field seen by the normal and amblyopic eyes have subtended $10^\circ \times 10^\circ$ of visual angle. The influence of this parameter on thresholds has already been documented to some degree (Hess et al. 1980). In figure 7a-b, contrast matches were assessed for identical spatial frequency stimuli of different extents. For the strabismic, the threshold discrepancy between the normal and amblyopic eye is greatly reduced when the stimulus field size is extended from a $5^\circ \times 5^\circ$ area to a $20^\circ \times 20^\circ$ area. Since, for each stimulus field,

Figure 7. Contrast thresholds (half-filled symbols) and matches (filled symbols) above threshold are displayed for (a) a representative strabismic amblyope, S.C., and (b) a representative anisometropic amblyope, S.C.A., at one spatial frequency (in (a) 1 c/deg; in (b) 6 c/deg) but of different field extents. The results describing the suprathreshold contrast response of the strabismic and anisometropic eye differ at any one field size and as a function of changing field size. Changes in field size reduce the threshold contrast abnormality in strabismic amblyopia but not, to any significant extent, in anisometropic amblyopia.
contrasts are seen close to normal above threshold, the effect of increasing field size for strabismics is to increase the range over which contrast perception can operate. In the example shown in figure 7a, the lower limit of contrast perception was extended from 15 to 3% (marked by arrows).

The effects of a similar change in field size for anisometropes is very small. Results for one anisometrope are displayed in figure 7b. The threshold deficit is not substantially changed and similar suprathreshold matches are obtained for these different-sized fields. These suprathreshold results are consistent with the conclusion suggested by Hess et al. (1980) from the threshold assessment; that is, the anisometropic anomaly is evenly distributed across the visual field (at least out to 10°), whereas the strabismic’s anomaly is predominantly located in the central visual field.

The results so far have concerned the ability of amblyopes to equate the contrast of a standard stimulus shown to the amblyopic eye with that of a stimulus of variable contrast seen by the normal fellow eye. This estimation of sensory magnitude gives no consideration to the coding of incremental contrast changes. One method of evaluating this is to compare the standard deviations of the matching settings (N = 5) at different contrast values and for different degrees of amblyopia. If the incremental sensitivity is grossly anomalous in the amblyopic eye it should be reflected in the accuracy (standard deviation) of contrast matches. It can be seen from all of the previous results that the standard deviation does not vary dramatically with contrast or the degrees of amblyopia, indicating that the accuracy of contrast judgements does not vary dramatically with either of these factors. However, this type of assessment lacks the necessary sensitivity to satisfactorily answer this question which could have importance for evaluating the type of mechanism underlying the sensory magnitude results already discussed. It is for this reason that we have assessed the accuracy of contrast judgements in amblyopic eyes by a more direct incremental contrast discrimination paradigm.

Incremental sensitivity

In figure 8a–c the thresholds for incremental contrast change are displayed as a function of the base contrast level for two strabismics. Strabismic D.M., unlike B.T., exhibited only minimally raised thresholds. Each point represents the threshold derived from 120 trials by using a two alternative, forced choice paradigm and Quest-driven staircase procedure. In both cases the results are similar for the normal and fellow amblyopic eyes. As the contrast level is reduced a proportionally smaller increment can be detected. In each case this increment decreased to a value below that needed for simple detection (arrows). Detection thresholds were determined at the same time (randomly interlaced) and by the same psychophysical procedure. For both subjects, contrast incremental discrimination was normal in the amblyopic eye for stimuli of low to medium spatial frequency. Strabismic B.T. exhibited a grating acuity of 15 c/deg and normal incremental discrimination at 4 c/deg. Strabismic D.M. exhibited a grating acuity of 30 c/deg and normal contrast discrimination at 5 c/deg. For a 10 c/deg stimulus, D.M. displayed a similar, though displaced, relation between discrimination and base contrast (Weber line). For this higher frequency stimulus the
Figure 8. (a) Discrimination thresholds for incremental changes in contrast are displayed for the normal (○) and amblyopic eye (●) of strabismic B.T. The inset shows the contrast-matching abnormality at and above threshold as well as the contrast threshold (arrows in main graph). The results are similar for the normal and amblyopic eye and are well fitted by a line of unit slope. The normal eye's response extends to a range of lower incremental values. Each plotting point represents the estimate from 120 trials. Spatial frequency, 4 c/deg. (b, c) Discrimination thresholds are displayed for the normal and amblyopic eye of strabismic D.M. for two spatial frequencies in (b) 5 c/deg and in (c) 10 c/deg. Thresholds for these stimuli were only minimally raised yet contrast discrimination was normal for the lower frequency and anomalous for the higher frequency. In each case a Weber response was obtained (unit slope). Incremental sensitivity can be anomalous in the suprathreshold contrast range for which matches are equivalent in the normal and amblyopic eye (inset).

The amblyopic eye needed approximately twice the normal increment for reliable discrimination at each base contrast.

Similar results are seen in figure 9a–d which display incremental sensitivity for the normal and amblyopic eye of a meridional amblyope (N.N.) and an anisometropic amblyope (S.C.A.). The results in each of these diagrams show that incremental sensitivity for mid to low spatial frequencies is not impaired in the amblyopic eye. A slight, but measurable impairment in incremental sensitivity is seen however in each of these subjects for higher spatial frequencies (within an
Figure 9. (a, b) Discrimination thresholds are displayed for the normal (□) and amblyopic (■) eye of a representative anisometropic amblyope (N.N.). Thresholds for (a) 5 and (b) 10 c/deg are displayed at a number of base contrasts. At the lower spatial frequency, detection thresholds are anomalous but incremental sensitivity is normal. At the higher spatial frequency, thresholds are raised as are incremental sensitivities. This incremental anomaly does not vary with base contrast and so does not parallel the changes that are observed by using a contrast-matching paradigm (inset). (c, d) Discrimination thresholds are displayed for two spatial frequency stimuli ((c) 10 and (d) 20 c/deg) for a representative anisometropic amblyope (S.C.A.). For the 10 c/deg stimuli, incremental sensitivity was normal, yet at 20 c/deg it was anomalous. This anomaly did not vary with base contrast. This reinforces the general finding of the lack of correspondence between contrast-matching (similar at each of these frequencies: see inset) and incremental sensitivity.

The results obtained from contrast-matching and discrimination paradigms in amblyopia show characteristic differences. This difference is, however, not contradictory as these two procedures are likely to assess different neural attributes. From matching experiments we see that anisometropic and strabismic
amblyopia are similar in that the threshold deficit far outweighs the suprathreshold deficit but that they differ in the way that this transition occurs. From contrast discrimination experiments we see more of a similarity between these two forms of amblyopia; for each, contrast discrimination is normal in the low frequency range and slightly abnormal in the high frequency range. The abnormality at higher frequencies, unlike that for contrast-matching, does not depend upon the base contrast level. Both types of amblyopia, however, displayed the normal Weber relation (unit slope of discrimination function) even for stimuli of higher spatial frequency, but incremental discrimination is anomalous.

**Discussion**

These findings highlight the difference between the two main forms of human amblyopia that have been traditionally viewed as two etiological forms of the same condition and for which common neurophysiological theories have been proposed (Ikeda & Wright 1976). A previous study (Hess et al. 1980) of threshold function at different luminance levels and field size has suggested that the neural anomaly in these two forms of amblyopia may be different and that this difference can be explained by the regional extent of the abnormality in the visual field. In strabismic amblyopia the anomalous region is restricted to the central area of the visual field, whereas in anisometropic amblyopia central and peripheral regions are similarly affected (out to at least 20°). This seems as true of contrast thresholds as it is of Landolt C letter acuity (Hess & Jacobs 1979) and grating acuity (Sireteanu & Fronius 1981). The present investigation extends and supports these previous arguments, which have been based upon threshold data into the suprathreshold domain. They also extend the preliminary report of Hess & Bradley (1980), by showing that these differences occur between strabismic and other varieties of anisometropic amblyopia such as meridional amblyopia (Mitchell et al. 1973). They show that there are differences in the strabismic and anisometropic suprathreshold responses as a function of either reducing luminance or reducing field size and that these differences are consistent with the visual field locus hypothesis already described.

*The strabismic response*

For strabismics with normal thresholds, contrast perception above threshold was normal. There is evidence in some cases for a *slight* but reliable overcompensation in contrast-matching by the amblyopic eye. This is evident in the region above 20% contrast where some strabismics also report perceptual distortion for grating patterns (Hess et al. 1978). Thus their anomalous letter acuity and vision for everyday scenes cannot be solely accounted for by an anomaly in contrast-coding at or above threshold.

For most strabismic amblyopes who exhibit raised contrast thresholds, contrast at and above the raised threshold is perceived normally (or only slightly different) by the amblyopic eye. As Hess & Bradley (1980) pointed out, the shape of the strabismic's contrast-matching function is similar to that of a normal observer matching between centrally (variable) and peripherally (standard) located targets. To this extent, they argued that the abnormality in strabismic ambylopia affected
only the detectors subserving central vision. It is as if the strabismic has only peripheral vision remaining, such that at the raised threshold stimuli are seen at their correct (high) contrast. Thus we see from the present investigation that as the stimulus field is reduced in size or superimposed upon a bright background (each of which favours a more central visual field analysis by the normal eye), the anomalous threshold and truncated suprathreshold range in strabismics are highlighted. When the reverse occurs there is very little difference in the response of the normal and amblyopic eyes. Thus the contrast anomaly in strabismic amblyopia occurs mainly at threshold and is characterized more by a truncation of the range over which contrasts are seen than by a reduction in the sensation per se at any given level. These results are consistent with only the central region of the amblyopic visual field being affected.

In the low–medium frequency range sensitivity to incremental changes of contrast does not seem to be disturbed in the strabismic in the suprathreshold range. In the higher frequency range incremental sensitivity is anomalous at all contrast levels. This is independent of whether a substantial threshold deficit is present or not. The slope of the psychometric function for discrimination and the relation of the discrimination threshold with base contrast are identical to those of normal eyes.

The anisometropic response

The way in which contrast is perceived above the already raised threshold differs for the anisometrope and the strabismic. In the contrast region just above threshold, contrast is perceived anomalously (reduced) by the anisometrope (optically corrected). This contrast anomaly gradually decreases as the objective contrast is increased. The function relating perceived and actual contrast for the anisometrope remains invariant with spatial frequency (in the spatial region where thresholds are raised), background luminance and field size. In all cases there is a simple rule: equal contrast reduction occurs at subjectively similar suprathreshold levels. In other words, the function relating perceived and actual contrast need only be shifted along the diagonal axis to describe all the results for the anisometrope. In all of the results the solid curves that are seen to describe the data well have been fitted according to this rule.

Like the strabismic, sensitivity to incremental contrast change appeared to be normal within the low–medium frequency range. However, in the upper frequency range, close to the acuity limit, sensitivity for contrast discrimination is also anomalous. For these higher frequency stimuli, the amblyopic eye required twice the increment in contrast needed by the normal eye for reliable discrimination at all contrast levels. These incremental sensitivity results bear upon the possible mechanism underlying the disparate threshold and suprathreshold behaviour of amblyopic eyes for contrast judgements. For example, if there were some underlying neural compensation in the form of a steeper contrast–response relation of single neurons in the amblyopic visual system, then incremental discriminations within this contrast range should be better than normal. These results argue against the model proposed by Georgeson & Sullivan (1975) in which the gain of the contrast system is increased to compensate for raised thresholds in normal and
amblyopic eyes. A more likely explanation is that there is more than one contrast
'channel' subserving normal vision and that the more sensitive (lowest threshold)
channel (or channels) is selectively affected in amblyopia. This line of argument
is outlined in more detail in the following paper.

Perceptual significance

Over the past decade many investigations into the neural basis of amblyopia
have relied upon measurement of contrast thresholds for one or another stimulus
of these results various models have been proposed to account for the perceptual
difficulties experienced by amblyopes in everyday life. All of these results have relied
upon the assumption that similar contrast anomalies occur in the suprathreshold
contrast range. The results of this investigation suggest the opposite. Admittedly,
contrast thresholds are raised in amblyopia but this is unlikely to have any severe
consequences for everyday vision, which relies mainly on suprathreshold conditions.
Rarely are we (or amblyopes) asked to detect signals of threshold contrasts. These
results suggest to us that, for the suprathreshold contrasts typical of everyday
images, amblyopes are not greatly impaired in either their steady-state contrast
perception (matches) or their dynamic contrast perception (incremental sensitivity).
More specifically their perceptual inabilities (which certainly do occur above
threshold) may not be adequately explained solely by an anomaly in the coding
or analysis of contrast information.

This is not to say that the slight anomalies that do occur in their contrast-coding
are uninteresting as they have helped highlight differences between the two main
forms of amblyopia and test their possible neural substrate. The ‘litmus test’ of
whether these contrast anomalies are adequate or inadequate explanations of
amblyopia is to ask what would the world look like when seen through the eyes
of normal observers having these ‘amblyopic’ contrast characteristics. This can
be done for the steady-state condition by digitally filtering everyday scenes
through spatial filters having similar contrast responses (see appendix) to those
documented in this study.

The most usual method of digitally filtering pictures involves manipulations
upon a global transform in which only the averaged contrast information for any
specific spatial frequency can be derived (Ginsburg 1978, Lundh et al. 1981, Brettel
et al. 1982). Since there are many experimental indications that the visual system
engages in a series of parallel, more localized spatial analyses across the visual field,
such a contrast-averaging procedure is inappropriate in the present context. On
the other hand, we do not yet know how many ‘analysing patches’ the visual
system utilizes across its visual field. In an effort to coarsely estimate the
perceptual importance of these measured contrast losses in amblyopia we have
digitally filtered a spatially complex scene with three sizes of analysing window:
one involving the whole scene (global), one involving one-quarter of the scene size,
and one involving one-sixteenth of the scene size. As the visual analysis will
undoubtedly involve more than 16 individual ‘patch analyses’ these results will
tend to overestimate the importance of the contrast attenuation explanation of
amblyopia.
These pictures should be viewed at a distance such that they subtend 6.5° square. At this distance the highest horizontal and vertical spatial frequency represented in the original is 19.6 c/deg. The lowest digital frequency is 0.1 c/deg (see Appendix). Figure 10 represents the threshold and suprathreshold transfer characteristics of the amblyopic eyes that are used to filter the scenes. Note that the contrast threshold loss (figure 10a) is the same for both amblyopes and the cut-off frequency (16 c/deg) was adjusted to be only slightly different from the highest spatial frequency represented in the original scene (19.6 c/deg). This allows a more critical examination of the contrast loss within the resolution limit uncontaminated by the acuity restriction. The suprathreshold transfer characteristics typical of the strabismic and anisometrope as previously discussed in this paper are displayed in the lower two frames of figure 10. In the strabismic case, the contrast filter acted as a simple 'threshold filter' whereas in the anisometropic case the transformed contrast was a function of both spatial frequency and the original contrast level. In applying these experimental contrast-matching results obtained for single spatial frequencies to the filtering of spatial frequencies in a complex scene we make the assumption of linear additively.

The processed pictures are displayed in figure 11, plate 1, and illustrate two important points. First, the perceptual difference for the strabismic and anisometrope is not great for any size of analysing window. Secondly, as the
number of 'analysing windows' increases the quality of the resultant 'amblyopic' picture improves.

Since the visual system is very likely to have many more than 16 'analysing windows' across its visual field, these 'digital' simulations will tend to overestimate the importance of this contrast deficit in explaining amblyopic vision. Thus, it seems likely from the filtered scenes in figure 11c that the measured loss of contrast information cannot solely explain the visual difficulties experienced by amblyopes for everyday scenes.

While this conclusion that amblyopia is not solely explained by a defect in contrast-coding is contrary to the present tide of experimental approaches in this area it is not at all surprising in view of the remnants of reliable physiological data available on 'amblyopic' animals. Contrast-coding is likely to occur early on in the visual process (retinal and early cortical processing) and amblyopia in general and suppression in particular affects mainly, if not exclusively, later (cortical) stages. A more likely site for the main disturbance in human amblyopia would be after the contrast signal from different spatial channels has been derived. It is the processing of these outputs that separates neural coding from its later analysis. It is likely in amblyopia that the afferent transmission of information is only minimally defective but its subsequent analysis is grossly anomalous. This suggestion gains further momentum from the finding that amblyopes can detect simple stimuli when presented in isolation, but cannot discriminate between more complex patterns (having more than one spatial component) made up of these component stimuli (Hess et al. 1981, Lawden et al. 1982). Thus amblyopia may be more an anomaly of later frequency analysis than initial contrast coding.

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References


original strabismic anisometropic

Figure 11. An original and two digitally filtered photographs (see Appendix) are displayed, one an anisometropic and the other a strabismic simulation (see figure 10). The photograph is filtered either globally or for two different-sized analysing patches, one-quarter of image size and one-sixteenth of image size (see text). As the size of analysis patch is reduced and the visual analysis more adequately modelled, the perceptual impairment produced by these two different matching anomalies decreases for suprathreshold imagery. Similarly, the perceptual importance of the difference in the strabismic and anisometropic contrast-matching responses also decreases. Thus an adequate explanation for the anomalous suprathreshold perception of amblyopes must extend to more than just the contrast deficit.

(Facing p. 328)
Neural differences in amblyopia


Appendix

All digital images were processed on an I.B.M. 370/165 with input being scanned from a 35 mm black-and-white negative by a Joyce-Loebl Scandig microdensitometer. This instrument, of the high-speed, rotating-drum type, measured the optical density of the film on a two-dimensional grid. The recorded data were stored on a magnetic tape to be read by the computer.

The output device was an Optronics rotating-drum Photowriter filmwriter and performed the converse process to the microdensitometer. Digital grey levels,
prepared on a magnetic tape by the computer, were used by the device to control the film exposure. The film type was Kodak, high speed infrared 4143 thick (Estar base).

Each digital image consists of 256 by 256 pixels with the original scenes being displayed in 256 grey levels. The grey levels are linear in optical density. The number of levels available is more than sufficient to avoid visible edge effects due to quantization. In addition, the pixel resolution posed no problem of sampling artefacts at the chosen viewing distances.

All images presented as simulations of amblyopic vision were filtered in the Fourier domain by the appropriate filter. Spatial frequency contrast was calculated from the two-dimensional discrete Fourier transform by using the relation

\[ \text{contrast} = 2 \times \frac{\text{amplitude}}{\text{d.c.}} \]

where d.c. represents the zero frequency component. The factor of 2 takes into account the distributed encoding of spectral energy between the positive and negative transform frequencies. Amplitude components of all image frequencies were then attenuated by a psychophysical weighting function derived from the appropriate amblyopic data (figure 10). The only exception was the image d.c. value which remained unaltered.

Since no information was available regarding how the spectral phase was to be processed it remained unmodified. Owing to the absence of orientational information the weighting functions were applied isotropically.

Upon inverse Fourier transformation of the filtered transforms the image pixels were rounded to the nearest grey level and displayed. The processed values were not scaled, so that a direct comparison could be made between the original and processed pictures. For correct viewing the digital images should subtend 6.5° square visual angle. At this distance the highest horizontal/vertical digital frequency is 19.6 c/deg.

**Strabismic filter**

The mathematical filter which incorporates the strabismic response acts as a simple 'threshold filter' in the frequency domain. Each image spatial frequency can undergo one of two possible actions. If the computed contrast of a digital frequency is less than its, psychophysically determined, threshold level then the frequency is set to zero; otherwise it is passed unaltered. This criterion for deciding how to weigh the image transform relies on the assumption that frequencies below the strabismic's threshold cannot be detected. Their elimination is therefore justified and a reasonable simulation of the amblyopic eye's sensitivity (figure 10).

One additional constraint on the strabismic filter is that all digital frequencies less than or equal to 0.3 c/deg are subject to the same criterion.

Logarithmic interpolation was used by the filter to derive intermediate data values.

**Anisometropic filter**

Unlike the strabismic filter the anisometropic weighting function is a function of both spatial frequency and contrast. Two-dimensional logarithmic interpolation was therefore used to obtain intermediate attenuations. In addition, digital frequencies less than 1.5 c/deg were passed unaltered (figure 10).