

SPATIAL VISION OF THE ACHROMAT: SPATIAL FREQUENCY AND ORIENTATION-SPECIFIC ADAPTATION

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SUMMARY

1. The psychophysical technique of selective adaptation to stationary sine-wave gratings of varying spatial frequency and orientation was used to investigate the central processing of spatial information in the visual system of the complete achromat.

2. For adapting spatial frequencies of 1 and 2 cycles/deg, the spatial frequency and orientation selectivity of contrast threshold elevation is similar for achromatic and trichromatic vision.

3. For adapting frequencies below 1 cycle/deg, the achromat shows threshold elevations of normal magnitude with symmetrical spatial frequency and orientation tuning for adapting frequencies as low as 0.09 cycles/deg with 'bandwidth' estimates similar to those found at high frequencies in the trichromat. Below 0.66 cycles/deg no after-effect could be obtained in the trichromat, and the frequency tuning at 0.66 cycles/deg was skewed towards higher frequencies.

4. The interocular transfer of low-frequency adaptation in the achromat was 50%, which is the same value obtained at higher frequencies.

5. The time course of the decay of low spatial frequency adaptation in the achromat was similar to that found at higher frequencies.

6. Control experiments show no low-frequency adaptation in peripheral vision or in central vision in the dark-adapted trichromat indicating that low spatial frequency adaptation cannot be elicited through the rod system of the trichromat.

7. It is proposed that the observed range shift of adaptable spatial frequency mechanisms in the achromat's visual cortex is the result of an arrest at an early stage of sensory development. The visual cortex of the achromat is comparable, with respect to spatial processing, to that of the young, visually normal human infant.

INTRODUCTION

Achromatopsia is a rare visual anomaly characterized by a complete absence of colour vision, extremely low visual acuity and moderate-to-strong photophobia

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(Duke-Elder, 1963). The condition was first described by Huddart (1777), whose observations were interpreted a century later by Galezowski (1868) in terms of the then young duplicity theory of Schultze (1866). Galezowski suggested that the achromat's retina totally lacked cone photoreceptors. This hypothesis has been more recently debated, since histological examinations of the achromat retina have demonstrated the presence of some cones (Glickstein & Heath, 1975), and early psychophysical investigations of dark adaptation and the Stiles-Crawford effect gave some evidence of residual cone function (Sloan, 1954, 1957; Walls & Heath, 1954; Alpern, Falls & Lee, 1960). Sakitt (1976) argued, however, that two-branched dark adaptation curves in achromats could easily appear as a result of experimental artifacts, and more recent data on dark adaptation (Sakitt, 1976; Zwas & Alpern, 1976; Skottun, Nordby & Magnussen, 1980; Nordby, Stabell & Stabell, 1984; Stabell, Stabell & Nordby, 1986), spectral sensitivity (Nordby *et al.* 1984) and the Stiles-Crawford effect (Sharpe & Nordby, 1984) convincingly demonstrate that in, at least, some achromats, cones, if present, are not functional.

Most psychophysical investigations of achromats have dealt with aspects of the visual process that are closely associated with photoreceptor function. But recently, Hess and his co-workers (Hess & Nordby, 1986*a, b*; Hess, Nordby & Pointer, 1987) have conducted an extensive series of experiments on the spatial and temporal properties of rod vision in the complete achromat. These experiments show that the spatial contrast sensitivity function – i.e. the inverse of contrast threshold *versus* the spatial frequency of sinusoidal gratings – of the achromat under optimal conditions at mesopic luminance levels reaches a peak sensitivity around 1 cycle/deg and exhibits an acuity limit of 6 cycles/deg. For scotopic luminance levels, contrast sensitivity of the achromat is similar to that of the trichromat, but as luminance is increased to photopic levels, the spatial acuity of the achromat rapidly deteriorates, whereas that of the trichromat increases to a value of 50–60 cycles/deg (Hess & Nordby, 1986*a*). A further study of the achromat's ability to discriminate spatial and temporal frequencies at threshold revealed that five discriminable steps in spatial frequency and one step in temporal frequency could be made by the achromat, and as such is comparable to the rod-based vision of the trichromat (Hess & Nordby, 1986*b*). These results and several other findings obtained in this subject are consistent with the notion that achromat vision reflects normal rod-based vision, and that the achromat's spatial performance can be completely accounted for by the coarse spatial organization of rod input to the retinal ganglion cells.

The present study addresses the question whether the absence of functional cone photoreceptors, and thus high spatial frequency input from the retina, affects the development of the achromat's visual cortex. Neurones in the visual cortex of the cat and monkey are highly selective to the spatial frequency and orientation of visual stimuli (e.g. Orban, 1984; Shapley & Lennie, 1985). In cat, the spatial frequency selectivity of cortical neurones is crude at birth, but rapidly develops to adult values within about 6 weeks (Derrington & Fuchs, 1981). The final organization obtained depends apparently on early visual experience (Movshon & Van Sluyters, 1981; Fregnac & Imbert, 1984). The distance between the 'preferred' spatial frequency and orientation of these neurones, their density at a given retinal location, as well as the operational range of their selectivity must determine the fidelity and extent of

spatial discriminations that can be made on a perceptual level. Due to the absence of functional cones, the achromat's retina transmits an unusually coarse neural image to his brain. This changed neural input creates a natural state of selective pattern deprivation, which in turn must have some consequence for the development of spatial selectivity of cortical neurones.

We explored the organization of the visual system of the complete achromat using the method of selective adaptation: if an observer inspects for a few minutes a high-contrast sinusoidal luminance grating, the contrast threshold for detecting gratings of similar spatial frequencies is subsequently increased (Pantle & Sekuler, 1968; Blakemore & Campbell, 1969). The spatial frequency 'bandwidth' – i.e. the extent to which adaptation at a given spatial frequency affects the contrast threshold at neighbouring frequencies – is fairly constant for various adapting frequencies (Blakemore & Campbell, 1969), the adaptation effect is selective to orientation (Gilinsky, 1968), it transfers interocularly (Blakemore & Campbell, 1969), and the frequency selectivity of the transferred effect is the same as that found for monocular testing (Björklund & Magnussen, 1981). As the responses of retinal ganglion cells and cells in the lateral geniculate nucleus show, at best, only crude orientational biases (Daniels, Norman & Pettigrew, 1977; Levick & Thibos, 1980; Vidyasagar, 1985), and binocular afference is first demonstrated in the visual cortex (Hubel & Wiesel, 1962) these properties of threshold elevation must reflect properties of mechanisms in the human cortex, analogous to those defined by single-unit recordings in cat and monkey cortex. Further evidence for this correlation is provided by the well-established finding that cortical neurones exhibit adaptation effects (Maffei, Fiorentini & Bisti, 1973; Movshon & Lennie, 1979; Dean, 1983; Albrecht, Farrar & Hamilton, 1984; Ohzawa, Sclar & Freeman, 1985), whereas geniculate cells do not (Maffei *et al.* 1973; Ohzawa *et al.* 1985), and in parallel to psychophysical findings, adaptation in binocularly driven neurones does not require stimulation of the same eye during adaptation and testing (Sclar, Ohzawa & Freeman, 1985). Therefore, selective adaptation may be used to explore psychophysically the visual processing of spatial information.

METHODS

In the experiments to be presented, sinusoidal luminance gratings were generated on a high-resolution cathode ray tube (Joyce Electronics, Cambridge). The display has a white (P4) phosphor and a space-average luminance of 150 cd/m². Analog signals under microprocessor control determined the position, spatial frequency and contrast of the grating stimuli, the luminance of which was modulated sinusoidally along one dimension. The grating's contrast is defined by the equation:

$$C = (L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$$

where L_{\max} and L_{\min} give the maximal and minimal luminance levels of the grating. The display was viewed binocularly with natural pupils at a distance of 57 cm, at which distance the screen subtended 22 × 30 deg of visual angle at the eye. During all of the experiments, the observers wore light-tight goggles fitted with neutral density filters which reduced the mean luminance at the eye to 1.5 cd/m². The observer rested his chin and forehead on a support to assure constant viewing distance and head orientation.

Contrast thresholds were measured using a temporal two-alternative forced-choice procedure. Here, a grating of variable contrast but fixed spatial frequency and orientation was presented in

one of two temporal intervals (2.5 s in duration) delineated by auditory signals. The grating was presented randomly in one of these intervals, and the grating contrast was incremented to the desired value during 360 ms as a raised cosine function of time. The total duration of the stimulus was 1 s. The observers indicated by pressing one of two switches in which interval the grating appeared. Contrast was decreased after correct responses and increased following incorrect responses according to a single staircase procedure with a fixed step size of 0.1 log unit. A total of forty trials were conducted for each threshold determination, which were based on an average of eight to ten reversals of the contrast staircase. The average standard deviation for a threshold estimate was usually less than 0.1 log unit.

To produce an after-effect, the observer adapted for 4 min to a stationary, high-contrast ($C = 0.4$) sine-wave grating. During adaptation, subjects slowly moved their eyes along a large fixation circle in the middle of the screen to avoid after-images and to create an after-effect which was random with respect of spatial phase. Following the initial adaptation, the adapting grating was turned off and the testing period was conducted as described above, with the exception that now each trial was preceded by a 15 s readaptation period in which the adapting grating was again presented. This was done to insure a steady level of adaptation throughout the testing period. Threshold elevation is defined as the difference between the logarithm of contrast thresholds before and after adaptation.

To test the spatial frequency and orientational selectivity of the after-effect, a constant adapting frequency and orientation was chosen, while the spatial frequency or the orientation of the test grating was varied in steps of fixed size for each threshold measurement. The orientation of the grating was changed by first blanking the screen and then rotating the deflection coil of the display via a stepping motor to the desired orientation for testing. The coil was returned to the original adapting orientation in the same manner after the test period was completed. The different spatial frequencies and orientations of the test grating were tested in random order to avoid any possible sequential effects. Adequate time was given between experiments to guarantee that no residual adaptation was carried over into the next measurement. No form of feed-back regarding the accuracy of the observer's responses was given during testing.

Adaptation to 0.09 cycles/deg

Due to the limits set by the size of the display used, for the experiments where the spatial frequency of the adapting grating was 0.09 cycles/deg a back-projection technique was employed during adaptation and testing. This was required for a grating of at least four complete cycles at the lowest spatial frequency tested (0.045 cycles/deg). Adapting and test gratings were created by passing the beam of a projection system through a filter, which occluded the light path as a sinusoidal function of space along the horizontal axis. The beam was then passed through a cylindrical lens which produced a one-dimensional sinusoidal distribution of light onto the projection screen. The contrast of the test grating was varied by positioning a polarizing filter in front of the light beam. Contrast changed as a linear function of the density of this circular wedge, the position of which was controlled by a stepping motor. Two projectors were used, one for the adapting stimulus and another for the test stimulus. As in the other experiments, the adapting stimulus had a constant contrast of 0.4, the spatial frequency was constant at 0.09 cycles/deg and its orientation was vertical. Mean luminance of adapting and test stimuli was 1.5 cd/m². The spatial frequency of the test grating was varied by inserting slides into the projection beam with a greater or lesser number of periods on them. The orientation of the test grating was varied by positioning a Dove prism in the light path and rotating it to the desired orientation.

Contrast thresholds were measured in this experiment using the method of adjustment. Before and after adaptation the observers were asked to press a button, which stopped the rotating wedge at the point in time when either the test grating was no longer visible (descending) or just became visible (ascending). Each threshold estimate was based on twenty such trials. The variability of this technique did not substantially differ from that found in the other experiments.

Observers

The observers were the achromat K.N. (one of the authors), who has been the subject of a number of earlier investigations (e.g. Nordby *et al.* 1984, Hess & Nordby, 1986*a,b*; Sharpe, Collewijn & Nordby, 1986) and a normal trichromat (author M.W.G.). Both subjects wore their ophthalmic corrections during the experiments (+6 D and -5 D, respectively). The difference in

the ophthalmic correction (11 D) led to a slightly lower spatial frequency at the achromat's entrance pupil.

RESULTS

Contrast sensitivity

Figure 1 shows the contrast sensitivity function for vertical gratings measured in the achromat and trichromat subjects at their approximate optimal luminance levels in the mesopic (1.5 cd/m^2) and photopic (150 cd/m^2) range, respectively. As is

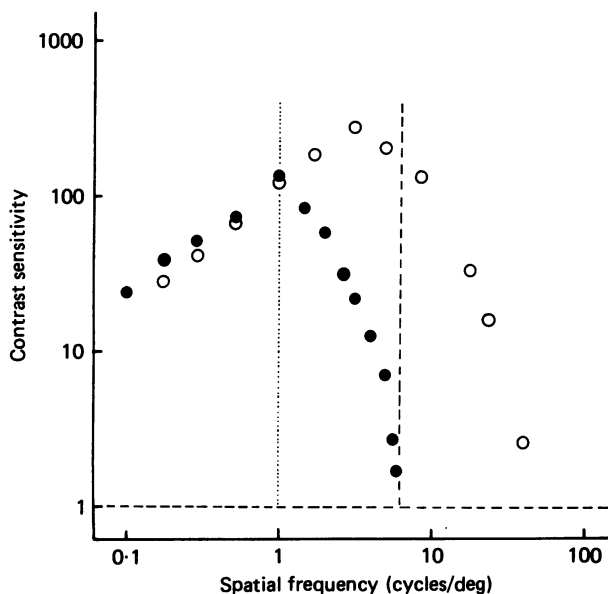


Fig. 1. Contrast sensitivity (1/threshold) is plotted as a function of the spatial frequency of sine-wave gratings. Data for the achromat are shown by filled, those for the trichromat by open circles. Observers viewed the gratings at their respective optimal luminance level: 1.5 cd/m^2 for the achromat and 150 cd/m^2 for the trichromat. The dotted line depicts the point where the sensitivity of the trichromat begins to surpass that of the achromat, and the dashed line shows the acuity limit of the achromat.

conventional, contrast sensitivity – the reciprocal of the contrast needed to detect the presence of the grating – is plotted as a function of spatial frequency of the grating on double-logarithmic axes. In these and the following Figures, data for the achromat are represented by filled symbols, those for the trichromat control subject by open symbols. The curves for the two subjects coincide below 1 cycle/deg, at higher spatial frequencies the achromat's contrast sensitivity declines rapidly with a cut-off point around 6–7 cycles/deg, which represents an approximate 3 octave loss in spatial acuity in the frequency domain compared to cone vision. The findings replicate the results of Hess & Nordby (1986a) who used horizontal gratings.

Adaptation at 1 cycle/deg and above

The dashed lines in Fig. 1 indicate the range in the spatial frequency domain where the achromat and trichromat both show adaptation effects, assuming that the lowest

spatial frequency showing a normally 'tuned' after-effect is around 1 cycle/deg in the trichromat (Tolhurst, 1973). We explored this region of common sensitivity using adapting frequencies of 1 and 2 cycles/deg.

Figure 2 (upper panel) shows the results for the achromat after adaptation to 1 (circles) and 2 (squares) cycles/deg. The elevation in log contrast threshold is plotted

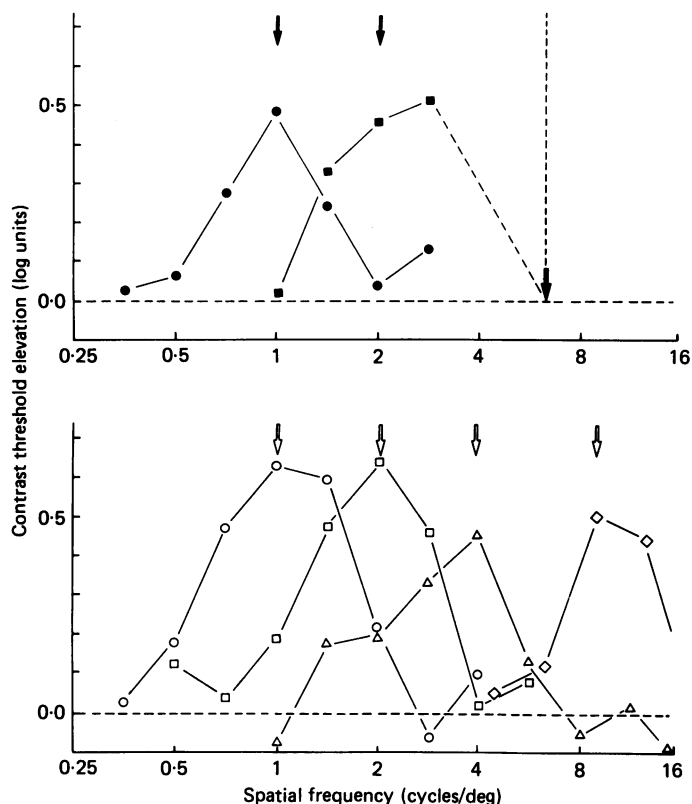


Fig. 2. Contrast threshold elevation (log adapted threshold - log unadapted threshold) is plotted as a function of the spatial frequency of the test grating. The parameter represents the spatial frequency of the adapting grating, which is denoted by the horizontal arrows (\bullet, \circ , 1 cycle/deg; \blacksquare, \square , 2 cycle/deg; \triangle , 4 cycles/deg; \diamond , 9 cycles/deg). The acuity limit of the achromat is given by the dashed vertical line (upper panel). Upper panel, achromat; lower panel, trichromat.

for test frequencies varying between -1.5 and $+1.5$ octaves. At both adapting frequencies, the maximum elevation in threshold is about 0.5 log unit. For the 2 cycles/deg adapting grating, threshold elevation peaks at 3 cycles/deg rather than at the adapting frequency itself, which may be due to the difficulty the achromat had in detecting test gratings near his acuity limit after adaptation. Beyond 3 cycles/deg, we could obtain no reliable post-adaptation threshold measurements, because pre-adaptation threshold values were too near the maximal contrast level produced by the display. The elevation in threshold shows a normal tuning function towards lower spatial frequencies. This spread of adaptation is thought to reflect the

'bandwidth' of the underlying adapted mechanism (Blakemore & Campbell, 1969), and may be expressed in terms of the octave difference between adapting and test frequencies where the adaptation effect is reduced to half of its maximal value. The tuning functions for 1.0 and 2.0 cycles/deg adaptation were fitted by polynomial regressions indicating full bandwidths of 1.1 and 1.6 octaves, respectively. The bandwidth of adaptation is thus similar to that found in trichromat subjects, as is confirmed by the results shown for the trichromat in the lower panel of Fig. 2. The overall effect of adaptation in the trichromat is slightly larger, which, for spatial frequencies above 1 cycles/deg, could be due to the greater difference between threshold contrast and the adapting contrast of 0.4 as compared to the achromat.

For comparison, Fig. 2 also presents tuning functions for 4.0 and 9.0 cycles/deg adapting frequencies for the trichromat, which lie close to or beyond the acuity limit of the achromat. At these frequencies, the bandwidth of adaptation is similar to that found at lower spatial frequencies.

Adaptation below 1 cycle/deg

Blakemore & Campbell (1969), working with a very small stimulus field (1.5 deg in diameter), found the lowest adapting frequency at which threshold elevation exhibited a symmetric tuning function to be around 3 cycles/deg. Tolhurst (1973) found with a larger display (4.1 deg) a symmetric tuning function with a peak at 1.5 cycles/deg. At lower frequencies, the tuning functions tended to be skewed towards higher frequencies with a peak near 1.5 cycles/deg. Figure 3 presents our results for adapting frequencies ranging from 0.09 to 0.66 cycles/deg.

The results for the trichromat subject (lower panel) confirm and extend the earlier findings of Tolhurst (1973). For 0.33 and 0.66 cycles/deg adapting frequencies, some elevation in contrast threshold is observed, but in both cases the tuning functions were markedly skewed peaking around 1.0 cycles/deg rather than at the adapting frequency itself. Thus, the elevation in threshold at these frequencies appears to reflect a change in the sensitivity of mechanisms with a 'preferred' spatial frequency near 1.0 cycle/deg. Very similar results were obtained for a second trichromat control subject (author S.M.). At the even lower adapting frequencies of 0.09 and 0.17 cycles/deg, no statistically significant threshold elevation could be observed at any test frequency in the trichromat.

In contrast, the results for the achromat (Fig. 3, upper panel) show after-effects of normal magnitude, and a symmetric spatial-frequency tuning for the complete range of adapting frequencies tested. The estimated bandwidths of adaptation are similar to those found at higher frequencies. These were 1.2, 1.6, 1.1 and 0.95 octaves for the 0.66, 0.33, 0.17 and 0.09 cycles/deg adapting frequencies, respectively.

Interestingly, changing to a larger adapting field and from two-alternative forced-choice to adjustment techniques for the 0.09 cycles/deg adapting frequency experiment (see Methods) produced results which were very similar to those obtained with the standard procedure, suggesting that the frequency tuning of threshold elevation is robust and not dependent on methodological details.

These results show that, unlike earlier results based on tests of retinally controlled aspects of vision, the functional organization of the achromat's visual cortex is not simply that of a trichromat's cortex minus high spatial frequency processing. The

loss of high-frequency processing is apparently compensated for by additional low-frequency mechanisms covering at least 3 octaves in the spatial-frequency domain below the lowest adaptable spatial frequency in the trichromat. To further compare selective adaptation in the achromat and the trichromat, we have investigated the orientational selectivity, the interocular transfer of adaptation and temporal characteristics of low-frequency adaptation effects found in the achromat.

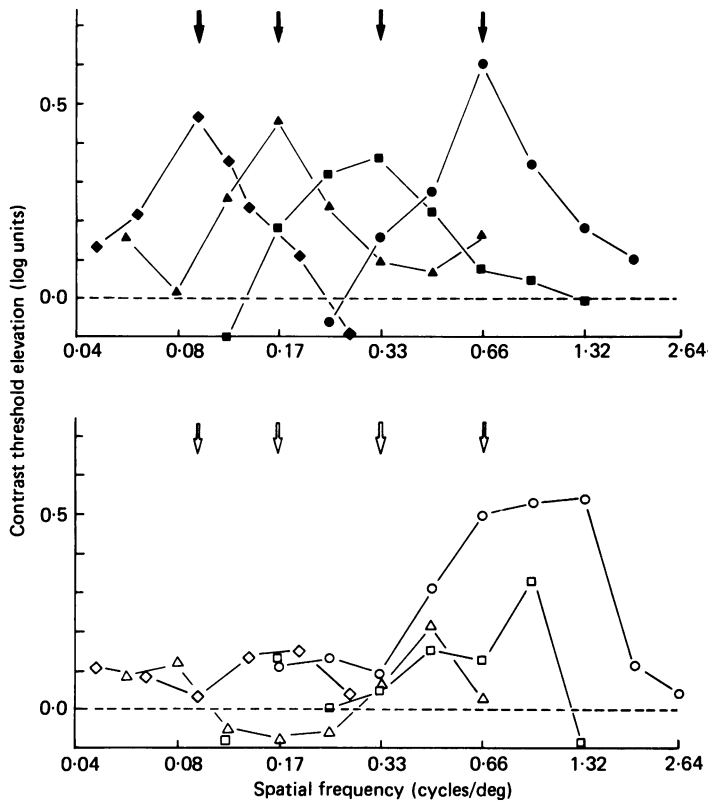


Fig. 3. Contrast threshold elevation is plotted as a function of the spatial frequency of the test gratings. The parameter is the spatial frequency of the adapting grating: ●, ○, 0.66 cycles/deg; ■, □, 0.33 cycles/deg; ▲, △, 0.17 cycles/deg; ◆, ◇, 0.09 cycles/deg. The position of the adapting frequency on the spatial frequency axis is denoted by arrows. Upper panel, achromat; lower panel, trichromat.

Orientalional selectivity of adaptation

Movshon & Blakemore (1973) found that the orientational selectivity of the elevation in contrast threshold was similar for high (20 cycles/deg) and low (2.5 cycles/deg) spatial frequencies. The results shown in Figs 4 and 5 suggest that this invariance extends to very low spatial frequencies found here in the achromat. Figure 4 shows the elevation in contrast threshold as a function of the angular difference between orientation of the adapting and test gratings for 0.09 and 2.0 cycles/deg spatial frequencies. For the achromat, the spread of adaptation in the

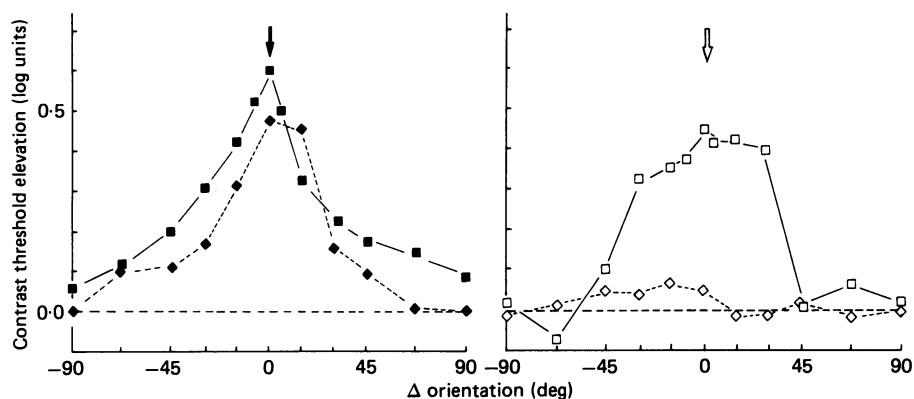


Fig. 4. Contrast threshold elevation following adaptation to a vertically oriented grating is plotted as a function of the difference between the orientation of the adapting and test grating (in angular degrees). Data for the achromat are shown in the left panel, those for the trichromat in the right panel. The parameter is the spatial frequency of the adapting grating (■, □, 2 cycles/deg; ◆, ◇, 0.09 cycles/deg). The condition where the orientation of the adapting and test gratings was the same (vertical) is denoted by the arrow.

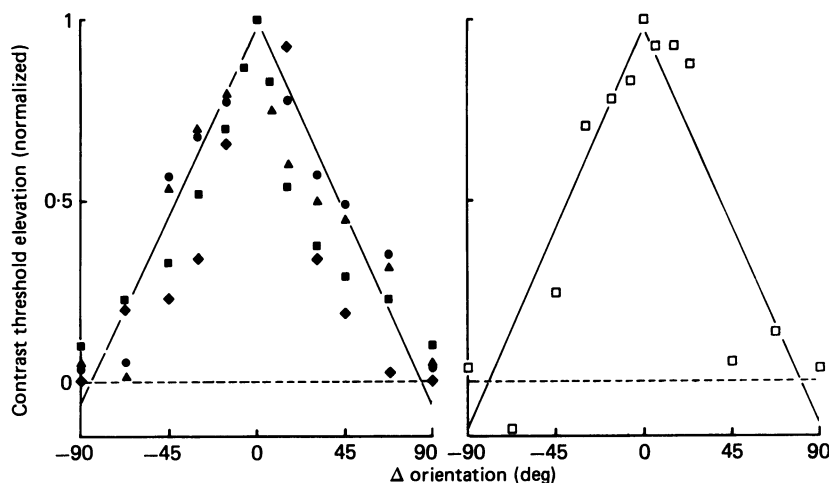


Fig. 5. The data in Fig. 4 are replotted on a normalized scale, where the maximum threshold elevation is assigned the value of one, along with data from 0.33 (●) and 0.17 cycles/deg (▲) adaptation for the achromat (left panel). Normalized threshold elevations are shown for comparison for the trichromat following 2.0 cycles/deg adaptation (right panel). Regression lines fitted by least-squares methods.

orientation domain is similar to that found for the 0.09 and 2.0 cycles/deg adapting frequencies, which in turn is similar to the orientational selectivity exhibited by the trichromat after adaptation to 2.0 cycles/deg. The trichromat showed no elevation in threshold following adaptation to 0.09 cycles/deg for any test orientation. In Fig. 5 (left panel) a set of orientation tuning curves are shown for the achromat for different adapting frequencies. The values are normalized to allow comparison over these

spatial frequencies. Here, the data from Fig. 4 are replotted together with data for 0.17 and 0.33 cycles/deg adaptation, the latter having been gained with slightly different conditions and the method of adjustment (see Greenlee, 1986). The width of the tuning functions vary between 50 and 90 angular degrees (full bandwidth at half-height), and are thus similar to the full bandwidth of 72 deg found for the trichromat at the 2.0 cycles/deg adapting frequency (Fig. 5, right panel).

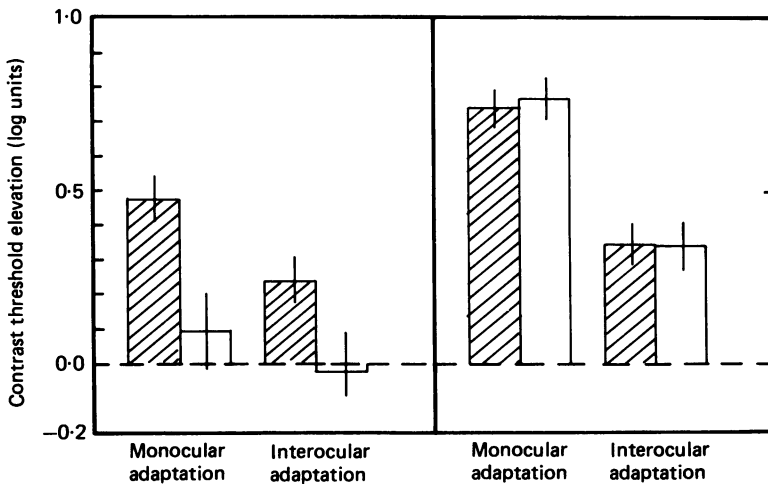


Fig. 6. Contrast threshold elevations following adaptation to a grating of 0.17 cycles/deg (left) and 2 cycles/deg (right) are shown for monocular and interocular conditions. Mean values of two measurements are shown for the achromat by hatched, those for the trichromat by open columns. Error bars show ± 2 standard errors of the mean values.

Interocular transfer of adaptation

To test the interocular transfer of adaptation we devised an occluder that could be positioned in front of the goggles worn by the observers. In this way, either eye could be occluded during adaptation or testing. The subjects adapted to the grating with their left eye and were either tested with their left eye (monocular adaptation) or with their right eye (interocular adaptation).

The results of these experiments are shown in Fig. 6. Findings for the achromat are given by hatched, those for the trichromat by open, columns. Two adapting and test frequencies were used: 0.17 (left half) and 2 (right half) cycles/deg. Error bars give ± 2 s.e. of the mean of two runs. Both subjects exhibited adaptation effects following monocular adaptation to 2 cycles/deg, which transferred by 50% to the unadapted eye. In contrast, only the achromat showed significant elevations in threshold following adaptation to 0.17 cycles/deg, which also transferred by 50% to his unadapted eye. The amount of transferred adaptation is similar to that reported earlier (Bjorklund & Magnussen, 1981).

The time-course of adaptation

Spatial adaptation represents fairly long-term changes in the sensitivity of neurones in the visual cortex. Recent experiments on the elevation of contrast

threshold show that it builds up during approximately 1 h of continuous adaptation and decays also in about 1 h, both build-up and decay functions being linear on log time-log contrast threshold elevation axes and having similar slopes (Magnussen & Greenlee, 1985).

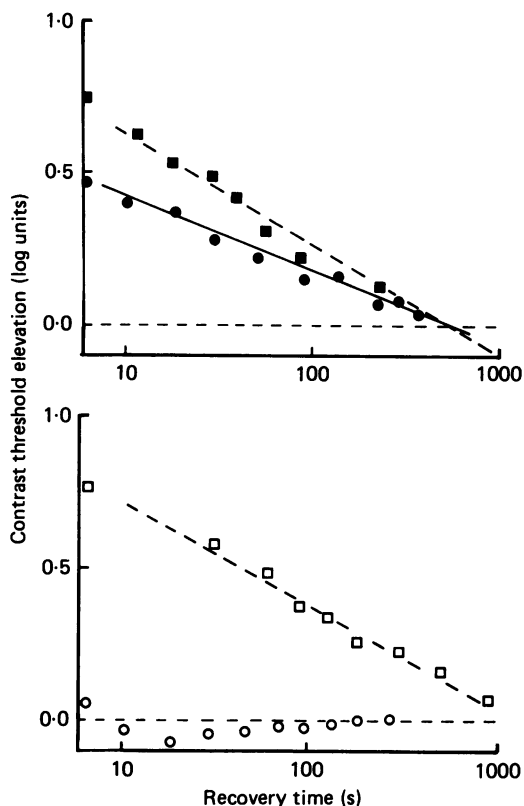


Fig. 7. The decay of contrast threshold elevation is presented for the achromat (upper panel) and trichromat (lower panel) for different adapting frequencies (for the achromat, ■, 0.33 cycles/deg; ●, 0.17 cycles/deg; for the trichromat, □, 1.0 cycle/deg, ○, 0.17 cycles/deg). The data are fitted by a straight line using least-squares methods on log-log co-ordinates.

In this experiment the subject adapted for 4 min to a 0.4 contrast adapting grating. Afterwards the adapting grating was switched off and contrast thresholds were tracked over time using the method of constant stimuli. Here, a pre-defined test contrast was given and the test grating was presented until the subject could just detect the grating. After the subject signalled that the grating was visible, a lower contrast value was given and the subject again pressed the response switch at the point in time when the grating was visible. Figure 7 shows the decay functions for a 0.33 cycles/deg adapting grating (squares) and a 0.17 cycles/deg grating (circles) for the achromat, and a 1.0 cycle/deg adapting grating (squares) and a 0.17 cycles/deg grating (circles) for the trichromat. Clearly, the time constant of the decay of adaptation is similar between the two subjects, if an elevation in threshold occurs.

Control experiments

The foregoing experiments strongly indicate the existence of adaptable mechanisms in the visual cortex of the achromat selectively sensitive to low spatial frequencies. However, before accepting these results as indicating a unique property of the achromat's visual system as opposed to the normal visual system, three control experiments need to be considered.

First, we used large (22×30 deg) field gratings with free viewing, so that it is possible that the achromat and trichromat subjects may have been using different retinal regions to detect the gratings. Thus the observed differences could reflect differences in the central and peripheral visual fields. In two different experiments we therefore adapted the trichromat subject to a 0.33 cycles/deg adapting grating presented 10 or 20 deg in the temporal visual field. A fixation circle was drawn on the surround mask to assist the subject to fixate during adaptation and testing. Otherwise the conditions were as in the main experiments. At both eccentricities no elevation in contrast threshold could be obtained in the trichromat.

Second, the experiments were performed at mesopic luminance levels, where the trichromat data mainly reflect the organization of cone input and are thus not strictly comparable to those of the achromat. While there is both psychophysical (Graham, 1972) and neurophysiological (Bisti, Clement, Maffei & Mecacci, 1977) evidence that the spatial tuning of cortical neurones remain unchanged at low luminance levels, it is possible that low-frequency mechanisms in the trichromat may be inhibited at higher luminance levels. Such mechanisms would thus only be disclosed at scotopic light levels. We therefore repeated the experiment with low-frequency adaptation in the dark-adapted trichromat at scotopic luminance levels: the subject first dark adapted for 30 min. The mean luminance of the grating was reduced at the eye to 0.01 cd/m^2 by placing appropriate neutral density filters on the goggles worn by the subject. He then adapted for 4 min to a sine-wave grating whose spatial frequency was either 0.66 or 0.33 cycles/deg and a contrast of 0.4. The results revealed a slight (0.2 log unit) elevation in contrast threshold following adaptation to 0.66 cycles/deg, but this is less than that found at mesopic luminance levels (Fig. 4). No reliable elevation in threshold could be obtained for the 0.33 cycles/deg adapting grating.

Third, nystagmoid eye movements orthogonal to the grating's orientation may increase contrast sensitivity at low spatial frequencies (Dickinson & Abadi, 1985). It might be argued that the enhanced adaptability of the achromat's visual system at low frequencies is simply the result of some kind of interaction between eye movements and the grating's spatial frequency. This explanation is unlikely for the following reasons: the experiments were performed at luminance levels where the pendular nystagmus of the achromat is less severe (Sharpe *et al.* 1986). Furthermore, the contrast sensitivity function measured for vertical and horizontal gratings was similar in the achromat. In addition, both subjects were instructed to move their eyes continuously along a fixation circle during adaptation, which would tend to cancel any systematic effect of nystagmus. We checked this point carefully, however, by repeating the 0.33 cycle/deg adapting condition in the achromat with horizontal adapting and test gratings. The same elevation in threshold was found in this control experiment as in the main experiment with vertical gratings.

DISCUSSION

The results of the present investigation suggest the existence of mechanisms in the visual system of the complete achromat selective to the spatial frequency and orientation of coarse, stationary spatial information. Using the method of spatial adaptation to stationary gratings we have shown that the achromat exhibits after-effects having normal spatial selectivity, time course and interocular transfer for adapting frequencies as low as 0.09 cycles/deg. This is more than 3 octaves below the best frequency of the lowest adaptable mechanism in normal vision under the same conditions.

Spatial frequency selectivity of low-frequency adaptation

The extent to which adaptation to a certain spatial frequency affects the sensitivity at other neighbouring spatial frequencies is of considerable interest, since this type of analysis reveals the degree of selectivity of the adapted mechanisms. Several procedures are available to estimate this spread of adaptation, which is thought to be an indirect reflection of the bandwidth of the adapted mechanisms (Blakemore & Campbell, 1969; Blakemore & Nachmias, 1971; Swift & Smith, 1982; Georgeson & Harris, 1984). We used the straightforward *adapt-to-one-test-at-many procedure*, and fitted polynomials to the data. While this may not reveal the true nature of the underlying neural selectivity (Blakemore & Campbell, 1969; Georgeson & Harris, 1984), it provides an adequate basis for comparing the relative effect of such selectivity in normal and anomalous visual systems.

Figure 8 gives a summary of the achromat-trichromat comparisons showing a plot of the 'symmetric' tuning functions for the different adapting frequencies. For each subject the data have been normalized by assigning the maximal elevation the value of one. An analysis of the individual tuning functions for the trichromat indicates that there is a slight tendency for larger adaptation bandwidths to occur at lower spatial frequencies. An adaptation bandwidth of 0.95 octaves was found for the 9 cycles/deg adapting frequency, whereas a bandwidth of 1.6 octaves was evident after 1.0 cycle/deg adaptation. This tendency was not, however, evident in the achromat. The average bandwidth of adaptation was slightly narrower in the achromat than in the trichromat (1.1 ± 0.2 versus 1.3 ± 0.3 octaves, respectively). Thus, in the achromat, the bandwidth of adaptation does not become larger with lower spatial frequencies.

Figure 8 also provides additional evidence against any eye movement hypothesis to explain our results. If the horizontal nystagmus of the achromat would have introduced a transient component into the visual stimulus, thereby stimulating low-spatial-frequency transient mechanisms (Tolhurst, 1973), we would expect the bandwidth of adaptation to be either larger than that for 'sustained' adaptation in the trichromat at higher spatial frequencies or should demonstrate a low-pass characteristic (Legge, 1978).

Our results confirm those of Tolhurst (1973), who found that the lowest spatial frequency showing a symmetric tuning curve was near 1.0 cycle/deg in the normal trichromat. It should, however, be noted that there are two reports in the literature on adaptation in trichromats at low spatial frequencies. An abstract by Kranda & Kulikowski (1976) suggests that frequency-selective adaptation can be found as low as 0.2 cycles/deg in photopic and scotopic luminance levels, but the results are

difficult to evaluate before the complete findings of the experiments have been published. Stromeyer, Klein, Dawson & Spillman (1982) likewise reported some evidence for adaptation at 0.12 cycles/deg, but their technique of scaling apparent contrast before and after adaptation appears vulnerable to subject and experimenter effects. There may also be differences between threshold and suprathreshold effects of adaptation. Our results, based on two-alternative forced-choice methods of threshold measurement, do not completely exclude the possibility that adaptation below 0.8–1.0 cycles/deg can occur in the trichromat, but they do show that the neural mechanisms sensitive to these low frequencies are much more difficult to adapt, in comparison to those in the achromat.

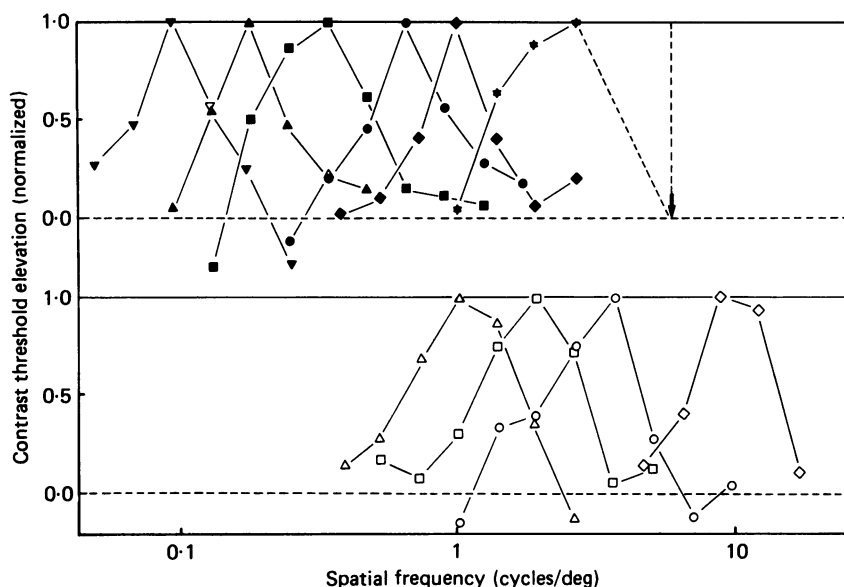


Fig. 8. Data presented in Figs 2 and 3 have been normalized and replotted as a function of spatial frequency for the achromat (upper panel) and the trichromat (lower panel). The parameter is the adapting frequency. The achromat's acuity limit is denoted by the vertical dashed line and arrow (upper panel). The spatial frequency selectivity of the adaptation effects was estimated based on polynomial least-squares regression for these data (see text). Adapting frequency (cycles/deg): \blacktriangledown , 0.09; \blacktriangle , 0.17; \blacksquare , 0.33; \bullet , 0.66; \blacklozenge , 1.0; \star , 2.0; \triangle , 1.0; \square , 2.0; \circ , 4.0; and \diamond , 9.0.

Our results further indicate that low-frequency adaptation is orientationally selective in the achromat, and that the extent of this selectivity is again similar to that found in the trichromat at higher spatial frequencies (cf. Fig. 4). This suggests that the underlying mechanisms have similar characteristics as those encoding the orientation of higher spatial frequencies. Furthermore, normal recovery times and a 50% transfer of adaptation interocularly suggest that these low-frequency mechanisms in the achromat share the same characteristics as high-spatial-frequency mechanisms in the trichromat. Thus, the only parameter we can find that differs in the achromat's adaptation functions is their range of preferred spatial frequency, which is shifted downwards by one decade in spatial frequency. This shift matches

the one decade loss in spatial acuity suffered by the achromat. In the following section we present a developmental hypothesis to explain these findings.

Influence of the cone pathway in shaping spatial frequency selectivity

Anatomical (Garey, 1984), neurophysiological (Movshon & Van Sluyters, 1981; Fregnac & Imbert, 1984) and behavioural (Atkinson, 1984; Boothe, Dobson & Teller, 1985) data all point to large changes taking place in the visual system during the first weeks and months of life. In man, anatomical studies show that the macular region of newborn retina is immature with few and underdeveloped foveal cones, and does not reach maturity until about 2 years of age (Yuodelis & Hendrickson, 1986). Thus, in the first few months of life vision may be dominated by the extrafoveal retina. Spatial acuity measured behaviourally develops over a period of at least 12 months, and may not reach adult values until 2–3 years. Interestingly, the acuity of 4–6 month old visually normal child corresponds to that of the adult achromat (van Hof-van Duin & Mohn, 1986). The resolving power of the achromat retina is thus comparable, in this respect, to that of the immature retina of the young trichromatic infant – or to the adult cat (Blake, 1978). The development of the retina of the complete achromat is obviously limited by the lack of cone photoreceptors. The fine spatial resolution performed by the cone mosaic (Williams, 1986) is irreversibly lost, so that the retinal ganglion cells are severely limited as to their own resolving power.

Derrington & Fuchs (1981) and Braastad & Heggelund (1985) have shown that for cells in the cat's visual cortex the preferred spatial frequency increases with age. A four- to fivefold increase in the 'best' spatial frequency, and a corresponding decrease in the width of the discharge zones of these cell's receptive fields were found in the kitten from 10 days of age to 8 weeks, where near adult values were obtained. Interestingly, Braastad and Heggelund compared findings from Rusoff & Dubin (1977) on the age-dependent change in the width of the receptive fields of retinal ganglion cells in the young cat. This comparison showed that the decrease in cortical receptive fields occurs in parallel to a corresponding decrease in retinal receptive field size. It appears, therefore, as if the development of the retina determines the development of the visual cortex, because high-spatial-frequency information must first be encoded by the retina before it can reach the visual cortex. This conclusion is not unreasonable, since stimulus-dependent aspects of development in the visual cortex are, by definition, reliant on the fidelity of the afferent retinal information. Thus, the immature retina acts like a low-pass filter, the cut-off frequency of which increases with age. The cortical units would accordingly lag slightly behind the development of retinal ganglion cells, and such a lag can be seen in the comparisons made by Braastad & Heggelund (1985).

The normal development of spatial frequency selectivity thus consists of a range shift in the preferred or best spatial frequencies of the underlying neural mechanisms, and we propose that in the achromat this development is arrested and that the visual cortex is consolidated at an early stage of functional organization. This hypothesis is parsimonious, since there is no need to consider a more complex, instructive role of experience (Movshon & Van Sluyters, 1981), nor is there a need to assume the degeneration of cortical cells normally devoted to high-spatial-frequency encoding.

In fact, our results suggest that except for the range shift in spatial frequency, the organization of the achromat's visual cortex with regard to the processing of spatial information is completely normal. Studies of the visual-evoked potential in the achromat point to the same conclusion (Van der Tweel & Spekreijse, 1973). Also consistent with our hypothesis are the findings of Sclar *et al.* (1985), who show that the neurones in the kitten cortex respond best and adapt well to low-spatial-frequency gratings, more so than those in the adult cat. If these considerations are correct, neurones in the newborn cortex sensitive to low spatial frequencies should be just as adaptable as neurones in the adult cortex sensitive to high frequencies, and the 'lowest adaptable channel' – using Tolhurst's (1973) expression – in the human infant would shift towards higher spatial frequencies in pace with the improvement in spatial resolution. This is a testable assumption, but to our knowledge no data on spatial adaptation in human infants have so far been reported.

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REFERENCES

- ALBRECHT, D. G., FARRAR, S. B. & HAMILTON, D. B. (1984). Spatial contrast adaptation characteristics of neurones recorded in the cat's visual cortex. *Journal of Physiology* **347**, 713–739.
- ALPERN, M., FALLS, H. & LEE, G. (1960). The enigma of typical total monochromasy. *American Journal of Ophthalmology* **50**, 996–1011.
- ATKINSON, J. (1984). Human visual development over the first 6 months of life: a review and a hypothesis. *Human Neurobiology* **3**, 61–74.
- BISTI, S., CLEMENT, L., MAFFEI, L. & MECACCI, L. (1977). Spatial frequency and orientation tuning curves of visual neurones in the cat: effects of mean luminance. *Experimental Brain Research* **27**, 335–345.
- BJÖRKLUND, R. A. & MAGNUSSEN, S. (1981). A study of the interocular transfer of spatial adaptation. *Perception* **10**, 511–518.
- BLAKE, R. (1978). Spatial vision in the cat. In *Frontiers in Visual Science*, ed. COOL, S. J. & SMITH III, E. L., pp. 209–219. Berlin: Springer.
- BLAKEMORE, C. & CAMPBELL, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology* **203**, 237–260.
- BLAKEMORE, C. & NACHMIAS, J. (1971). The orientational specificity of two visual after-effects. *Journal of Physiology* **213**, 157–174.
- BOOTHE, R. G., DOBSON, V. & TELLER, D. (1985). Postnatal development of vision in human and nonhuman primates. *Annual Review of Neuroscience* **8**, 495–545.
- BRAASTAD, B. O. & HEGGELUND, P. (1985). Development of spatial receptive-field organization and orientation selectivity in kitten striate cortex. *Journal of Neurophysiology* **53**, 1158–1178.
- DANIELS, J. D., NORMAN, J. L. & PETTIGREW, J. D. (1977). Biases for orientational moving bars in lateral geniculate nucleus neurons in normal and stripe-reared cats. *Experimental Brain Research* **29**, 155–172.
- DEAN, D. F. (1983). Adaptation-induced alteration of the relation between response amplitude and contrast in cat striate cortical neurones. *Vision Research* **23**, 249–256.
- DERRINGTON, A. M. & FUCHS, A. F. (1981). The development of spatial-frequency selectivity in kitten striate cortex. *Journal of Physiology* **316**, 1–10.

- DICKINSON, C. M. & ABADI, R. V. (1985). The influence of nystagmoid oscillation on contrast sensitivity in normal observers. *Vision Research* **25**, 1089–1096.
- DUKE-ELDER, S. (1963). *System of Ophthalmology*, vol. 3, *Normal and Abnormal Development*. London: Kimpton.
- FREGNAC, Y. & IMBERT, M. (1984). Development of neuronal selectivity in the primary visual cortex of the cat. *Physiological Reviews* **64**, 325–434.
- GALEZOWSKI, X. (1868). *Du Diagnostic des Maladies des Yeux par la Chromatoscopie Retinienne*. Paris: J.-B. Baillière.
- GAREY, L. J. (1984). Structural development of the visual system of man. *Human Neurobiology* **3**, 75–80.
- GEORGESON, M. A. & HARRIS, M. G. (1984). Spatial selectivity of contrast adaptation: models and data. *Vision Research* **24**, 729–741.
- GILINSKY, A. S. (1968). Orientation-specific effects of patterns of adapting lights on visual acuity. *Journal of the Optical Society of America* **58**, 13–18.
- GLICKSTEIN, M. & HEATH, G. G. (1975). Receptors in the monochromat eye. *Vision Research* **15**, 633–636.
- GRAHAM, N. (1972). Spatial frequency channels in the human visual system: effects of mean luminance and pattern drift rate. *Vision Research* **12**, 53–68.
- GREENLEE, M. W. (1986). *Spatial Adaptation in the Achromat*. Doctoral Thesis, Faculty of Biology, University of Freiburg, F.R.G.
- HESS, R. F. & NORDBY, K. (1986*a*). Spatial and temporal limits of vision in the achromat. *Journal of Physiology* **371**, 365–385.
- HESS, R. F. & NORDBY, K. (1986*b*). Spatial and temporal properties of rod vision in the achromat. *Journal of Physiology* **371**, 387–406.
- HESS, R., NORDBY, P. & POINTER, J. S. (1987). Regional variation of contrast sensitivity across the retina of the achromat: sensitivity of human rod vision. *Journal of Physiology* **388**, 101–119.
- HUBEL, D. H. & WIESEL, T. N. (1962). Receptive fields, binocular interactions and functional architecture in the cat's visual cortex. *Journal of Physiology* **165**, 559–568.
- HUDDART, J. (1777). An account of persons who could not distinguish colours. *Philosophical Transactions of the Royal Society* **67**, 260–265.
- KRANDA, K. & KULIKOWSKI, J. J. (1976). Adaptation to coarse gratings under scotopic and photopic conditions. *Journal of Physiology* **257**, 35–36*P*.
- LEGGE, G. (1978). Sustained and transient mechanisms in human vision: temporal and spatial properties. *Vision Research* **18**, 69–81.
- LEVICK, W. R. & THIBOS, L. N. (1980). Orientation bias of cat retinal ganglion cells. *Nature* **268**, 389–390.
- MAFFEI, L., FIORENTINI, A. & BISTI, S. (1973). Neural correlate of perceptual adaptation to gratings. *Science* **182**, 1036–1038.
- MAGNUSSEN, S. & GREENLEE, M. W. (1985). Marathon adaptation to spatial contrast: saturation in sight. *Vision Research* **25**, 1409–1411.
- MOVSHON, J. A. & BLAKEMORE, C. (1973). Orientation specificity and spatial selectivity in human vision. *Perception* **2**, 53–60.
- MOVSHON, J. A. & LENNIE, P. (1979). Pattern-selective adaptation in visual cortical neurones. *Nature* **278**, 850–852.
- MOVSHON, J. A. & VAN SLUYTERS, R. C. (1981). Visual neural development. *Annual Review of Psychology* **32**, 477–522.
- NORDBY, K., STABELL, B. & STABELL, U. (1984). Dark-adaptation in the human rod system. *Vision Research* **24**, 841–849.
- OHZAWA, I., SCLAR, G. & FREEMAN, R. (1985). Contrast gain control in the cat's visual system. *Journal of Neurophysiology* **54**, 651–667.
- ORBAN, G. A. (1984). *Neuronal Operations in the Visual Cortex*. Berlin: Springer.
- PANTLE, A. & SEKULER, R. (1968). Size-detecting mechanisms in human vision. *Science* **162**, 1146–1148.
- RUSOFF, A. C. & DUBIN, M. W. (1977). Development of receptive-field properties of retinal ganglion cells in kittens. *Journal of Neurophysiology* **40**, 1188–1198.
- SAKITT, B. (1976). Psychophysical correlates of photoreceptor activity. *Vision Research* **16**, 129–140.

- SCHULTZE, M. (1866). Zur Anatomie und Physiologie der Retina. *Archiv der Mikroskopischen Anatomie* **2**, 175–286.
- SCLAR, G., OHZAWA, I. & FREEMAN, R. D. (1985). Contrast gain control in the kitten's visual system. *Journal of Neurophysiology* **54**, 668–675.
- SHAPLEY, R. & LENNIE, P. (1985). Spatial frequency analysis in the visual system. *Annual Review of Neuroscience* **8**, 547–583.
- SHARPE, L. T., COLLEWIJN, H. & NORDBY, K. (1986). Fixation, pursuit and nystagmus in the complete achromat. *Clinical Vision Sciences* **1**, 39–49.
- SHARPE, L. T. & NORDBY, K. (1984). Receptor function and interaction in a rod monochromat. *Perception* **13**, A7–8.
- SKOTTUN, B. C., NORDBY, K. & MAGNUSSEN, S. (1980). Rod monochromat sensitivity to sine-wave flicker at luminances saturating the rods. *Investigative Ophthalmology and Visual Science* **19**, 108–111.
- SLOAN, L. L. (1954). Congenital achromatopsia. A report of 19 cases. *Journal of the Optical Society of America* **44**, 117–128.
- SLOAN, L. L. (1957). The photopic retinal receptors of the typical achromat. *American Journal of Ophthalmology* **48**, 81–86.
- STABELL, B., STABELL, U. & NORDBY, K. (1986). Dark adaptation in a rod monochromat: effect of stimulus size, exposure time and retinal eccentricity. *Clinical Vision Sciences* **1**, 75–80.
- STROMEYER III, C. F., KLEIN, S., DAWSON, B. M. & SPILLMANN, L. (1982). Low spatial frequency channels in human vision: adaptation and masking. *Vision Research* **22**, 225–233.
- SWIFT, D. J. & SMITH, R. A. (1982). An action spectrum for spatial-frequency adaptation. *Vision Research* **22**, 235–246.
- TOLHURST, D. (1973). Separate channels for the analysis of the shape and movement of a moving visual stimulus. *Journal of Physiology* **231**, 385–402.
- VAN DER TWEEL, L. H. & SPEKREIJSE, H. (1973). Psychophysics and electrophysiology of a rod-achromat. *Documenta ophthalmologica*, Proceedings Series 2, 163–173.
- VAN HOF-VAN DUIN, J. & MOHN, G. (1986). The development of visual acuity in normal fullterm and preterm infants. *Vision Research* **26**, 909–916.
- VIDYASAGAR, T. R. (1985). Geniculate orientation biases as Cartesian coordinates for cortical orientation detectors. In *Models of the Visual Cortex*, ed. ROSE, D. & DOBSON, V. G., pp. 390–395. New York: Wiley.
- WALLS, G. L. & HEATH, G. G. (1954). Typical total color blindness reinterpreted. *Acta ophthalmologica* **32**, 253–297.
- WILLIAMS, D. R. (1986). Seeing through the photoreceptor mosaic. *Trends in Neurosciences* **9**, 193–198.
- YUODELIS, C. & HENDRICKSON, A. (1986). A qualitative and quantitative analysis of the human fovea during development. *Vision Research* **26**, 847–855.
- ZWAS, F. & ALPERN, M. (1976). The density of human rhodopsin in the rods. *Vision Research* **16**, 121–127.