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Orientation specificity and spatial selectivity in human vision

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Abstract. An adaptation method is used to determine the orientation specificity of channels sensitive to different spatial frequencies in the human visual system. Comparison between different frequencies is made possible by a data transformation in which orientational effects are expressed in terms of equivalent contrast (the contrast of a vertical grating producing the same adaptational effect as a high-contrast grating of a given orientation). It is shown that, despite great variances in the range of orientations affected by adaptation at different spatial frequencies ($\pm 10^\circ$ to $\pm 50^\circ$), the half-width at half-amplitude of the orientation channels does not vary systematically as a function of spatial frequency over the range tested ($2 \cdot 5$ to 20 cycles deg^{-1}). Two subjects were used and they showed significantly different orientation tuning across the range of spatial frequencies. The results are discussed with reference to previous determinations of orientation specificity, and to related psychophysical and neurophysiological phenomena.

1 Introduction

Neurophysiological studies, starting with the work of Hubel and Wiesel (1962, 1968), have demonstrated that cells in the visual cortex of cats and monkeys are selectively sensitive to the orientation and spatial dimensions of visual stimuli. These findings have stimulated psychophysical experiments on the spatial and orientational selectivity of the human visual system. The bulk of these investigations have used gratings of sinusoidal luminance profile as test stimuli. Campbell and Kulikowski (1966) measured the contrast threshold for one grating in the presence of a high-contrast masking grating, and found that the threshold rises as the masking and test patterns are made increasingly similar in orientation. An orientation-specific increase in threshold can also be demonstrated with an aftereffect paradigm in which the test grating is presented after a high-contrast adapting grating (Gilinsky, 1968). This aftereffect is also dependent on the relative spatial frequency of test and adapting gratings (Pantle and Sekuler, 1968; Blakemore and Campbell, 1969). The fact that changes in psychophysical sensitivity after adaptation are accompanied by changes in the occipital potential evoked by the test pattern (Blakemore and Campbell, 1969; Campbell and Maffei, 1970) has strengthened the argument that these aftereffects are localised in the visual cortex.

If, as the evidence suggests, the orientation-specific and spatial-frequency-specific aftereffects are due to adaptation of the same neural mechanism, it might be possible to account for both specificities with a single model of the receptive fields of human cortical neurones. As one step towards the design of such a model it is essential to know the exact orientation specificity of channels with different optimal spatial frequencies. Blakemore and Nachmias (1971) have measured orientation specificity for threshold elevation using a single spatial frequency ($8 \cdot 4$ cycles/degree) in the middle of the detectable range. In this paper we used their experimental and analytical techniques to measure the orientational tuning of threshold elevation for several different spatial frequencies of the adapting and test gratings.

1.1 *Definitions*

A grating is a pattern of alternate dark and light bars. In the present experiments the gratings always had sinusoidal luminance profile across the bars.

Contrast is the ratio $(I_{\max}-I_{\min})/(I_{\max}+I_{\min})$ where $I_{\max}$ and $I_{\min}$ are the maximum and minimum luminances in the grating.

Mean luminance is $\frac{1}{2}(\mathrm{I}_{\max}+\mathrm{I}_{\min})$.

Spatial frequency is the number of cycles of the grating per degree of visual angle.

2 Method

2.1 *Stimulus*

From a distance of 114 cm the subjects (J.A.M., a well corrected myope, and R.D.L., an emmetrope) looked at an oscilloscope tube with a yellow-green (P-31) phosphor. The screen was masked to a rectangular area subtending 4 deg in width by 3 deg in height. Sinusoidal gratings were produced on the screen by the method of Schade (1956) as modified by Green and Campbell (1965). The grating could be turned on and off and its contrast varied up to about 0·7 without appreciable change in mean luminance, which was 4·8 cd m^{-2}. The luminance of the dim background was 0·05 cd m^{-2} throughout.

For threshold determinations the subject controlled the contrast of the grating, which was flashed on and off at 1·5 Hz, by means of a high-precision logarithmic potentiometer. He pressed a button to display the voltage across a ganged linear potentiometer on a digital voltmeter and printer. This gave a direct measure of the contrast in logarithmic units.

Above the oscilloscope was an apparatus to display similar gratings of any orientation. A sheet of opal Perspex was illuminated from behind by a projector and masked, except for a rectangular area of the same size as the masked oscilloscope screen below. A negative of a photograph of a high-contrast sinusoidal grating was mounted in a rotatable frame over the aperture. By means of suitable filtering of the projector the mean luminance and colour of all the transilluminated gratings were made the same as those of the oscilloscope tube below. These transilluminated, rotatable gratings were used as adapting stimuli. They had spatial frequencies of 2·5, 3·5, 5·0, 7·1, 10·0, 14·2, and 20·0 cycles $\deg^{-1}$. Their contrast was estimated approximately by matching it with a grating generated on an oscilloscope; it was 0·7 or slightly more in all cases.

2.2 *Procedure*

The subject adapted either to the high-contrast rotatable gratings, or to vertical gratings (not flashing) of variable contrast, on the oscilloscope screen itself. To avoid the formation of a conventional negative afterimage during adaptation, the subject moved his gaze back and forth along a small horizontal fixation bar in the middle of the grating. The flashing test grating generated on the oscilloscope was always vertical and always of the same spatial frequency as the adapting pattern. The subject made his settings of contrast threshold as quickly as possible, in about 2-3 s.

As in previous studies, we used 3 min initial adaptation with 15 s re-adaptation between successive readings. Four settings were always taken for each adaptation condition. In addition eight baseline settings were taken before each experimental session with adaptation to the completely blank screen, in order to check that there was no residual threshold elevation from the previous session and to provide a measurement of normal contrast threshold against which to measure the increase in threshold during the following adapted settings.

2.3 *The equivalent contrast transformation*

Blakemore and Nachmias (1971) developed a technique that allows comparison of orientation specificity under different conditions, and even for different kinds of aftereffect, without any reference to the units in which the aftereffect is measured. The method is analogous to the so-called Crawford transformation (Crawford, 1947) in which the absolute threshold after a period of time in the dark is compared with the increment threshold for a particular background luminance. Blakemore and Nachmias measured the elevation of threshold for vertical test gratings under two different adapting conditions: (i) with high-contrast gratings of various orientations, (ii) with vertical gratings of various contrasts. Thus they were able to relate the orientation of the adapting grating to the contrast of a vertical adapting grating producing the same degree of threshold elevation (figure 1). In this way the orientation of the adapting grating can be expressed as the equivalent contrast of a vertical adapting pattern.

In figure 1 the transformation is demonstrated for hypothetical functions in which threshold elevation is linearly related to both adapting orientation and adapting contrast. If x is adapting orientation, y adapting contrast, and z threshold elevation, then

$$z = mx + b \quad \text{(for the upper left hand function)}$$
$$z = ny + c \quad \text{(for the right hand function),}$$

whence

$$mx + b = ny + c$$

and

$$y = \frac{m}{n}x + \frac{b-c}{n} ,$$

which is the equation of the transformed line in the lower graph.

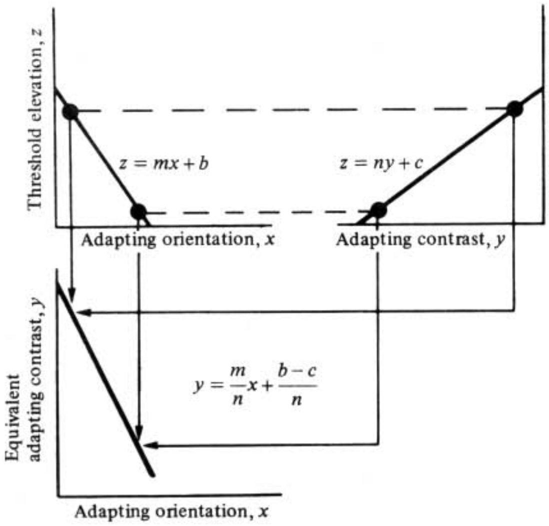

Figure 1. A graphical demonstration of the equivalent contrast transformation. The transformed line below is generated from two points with identical ordinates on each of the linear data lines above. The abscissa of the upper right-hand plot is rotated 90° to generate the ordinate of the transformed function, the abscissa of which is identical to the upper left hand plot. The equations of the lines shown next to them are described in the text.

The transformation is equally straightforward for any two nonlinear parametric equations. In fact in this study the two functions were reduced to straight lines by expressing threshold elevation and adapting contrast in logarithmic units.

3 Results

For each spatial frequency the subject first adapted to vertical gratings of various contrasts generated on the oscilloscope screen, and tested his threshold with vertical gratings of the same frequency turning on and off at 1·5 Hz. (The use of a flickering test pattern, rather than a static one, made it easier for the subject to set his threshold quickly and reproducibly without substantially altering the magnitude of threshold contrast over the spatial frequency range used.) The results of these experiments are shown for one of the subjects on the right in figure 2, where the increase in threshold (compared with the mean of the previous, unadapted baseline

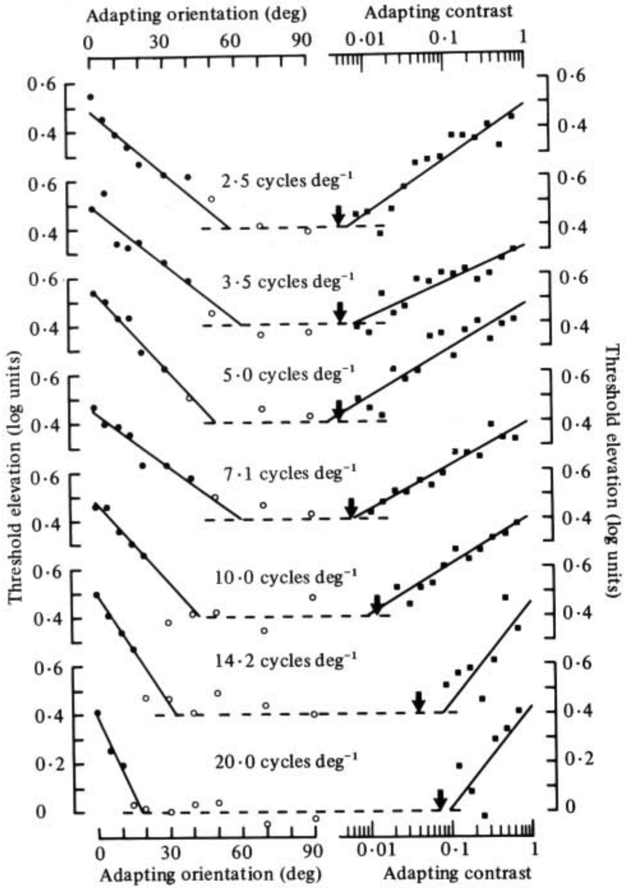

Figure 2. Results for subject R.D.L., as described in the text. The data for the seven different spatial frequencies are staggered vertically, the ordinates being exactly aligned on the two sides. On the right (solid squares, $N = 4$ for each point) are functions describing the elevation of contrast threshold for vertical test gratings as the contrast of a vertical adapting grating is changed. On the left the points show the decline in threshold elevation as the adapting grating (contrast 0·7) is rotated in either direction from vertical ($N = 8$ for each point). The points indicated by solid circles were used to fit the regression lines, while the open circles (which do not differ from the interrupted horizontal baseline by more than 0·125 log units) were not.

settings) is plotted against the contrast of the adapting grating on the logarithmic abscissa. Results for the seven different spatial frequencies are staggered along the ordinate. The points are fitted by regression lines (average coefficient of correlation, 0·88). For each spatial frequency the interrupted horizontal line indicates the unadapted, baseline threshold, and the arrows on these interrupted lines show the position on the abscissa of the unadapted, baseline contrast threshold for the spatial frequency in question. In every case the extrapolated intersect of the regression line with the interrupted line (i.e. the adapting contrast for zero threshold elevation) lies close to the arrow.

On the left in figure 2 are similar data for exactly the same test conditions in which the orientation of the adapting grating (contrast, ~0·7) was varied. There were no consistent differences between the data for anticlockwise and clockwise rotation of the adapting grating, so they have been pooled, the abscissa being orientation in either direction relative to vertical which is at zero. Hence each point is the mean of eight readings. In order to fit regression lines to these points we adopted the arbitrary criterion of excluding from the analysis all points that differed from the baseline by less than 0·125 log units. Empirically, the remaining points were well fitted by straight lines (average coefficient of correlation, 0·94). The points actually used to fit the lines are plotted as solid symbols, the remainder as open symbols.

Figure 3 shows the equivalent contrast functions derived from the data of figure 2, and the functions for similar experiments on the second subject, J.A.M. For this subject there was so little elevation of threshold at 20·0 cycles deg^{-1} with any adapting orientation other than vertical that regression lines could not be fitted to the data, and hence this spatial frequency is not included.

Clearly, the intercept of each regression line on the right in figure 2 (threshold elevation for a vertical adapting grating) should line up on the corresponding left-hand regression line with the amount of elevation caused by a grating of 0·7, since that was the approximate contrast of the rotatable grating. Thus each equivalent contrast function in figure 3 should intersect the ordinate at an equivalent contrast of 0·7. The small deviations of some of the intercepts from this expected value may reflect slight errors in our estimates of the contrast of the adapting patterns, day-to-day variations in the subjects' performance, or small departures from linearity in the original data to which regression lines were fitted.

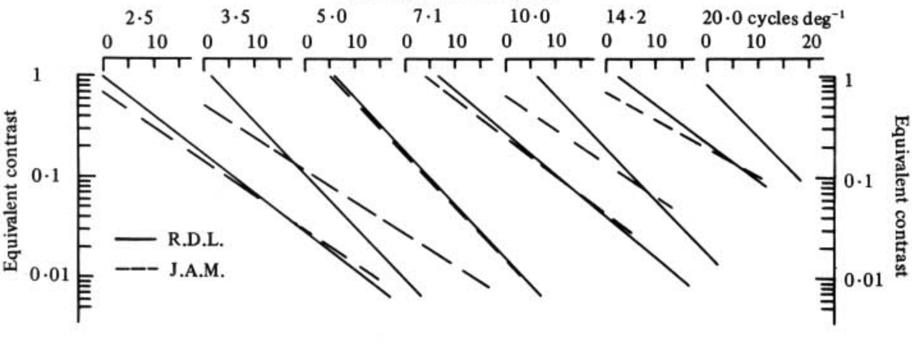

Figure 3. Functions which equate a change in orientation of a fixed-contrast adapting grating to a change in contrast of a vertical adapting grating obtained by transforming the results for R.D.L. (figure 2) and for J.A.M., as described in figure 1. The length of each line indicates the range of contrast available at each spatial frequency.

The half-widths of the functions in figure 3 (i.e. the change in orientation for equivalent contrast to decline by a factor of two) are shown for two subjects in figure 4. For each subject, despite large variations in the original functions relating threshold elevation to adapting orientation at different spatial frequencies, there is rather little change in half-width across the whole frequency range (mean 8·53°, population standard deviation 1·60° for J.A.M.; mean 6·54°, population standard deviation 1·31° for R.D.L.). The half-widths for the two subjects differ significantly from each other (Wilcoxon test, $p < 0{\cdot}05$).

4 Discussion

This study was designed to establish if there is any systematic relationship between orientational selectivity and optimal spatial frequency for spatially selective channels in the human visual system. There are indeed large changes in the range of orientation over which threshold is raised: at high spatial frequencies it is elevated only over a range of about ±10° around vertical, whereas at low frequencies the range is ±50° (figure 2, left side). However, when these data are analysed by the equivalent contrast transformation (figure 3) these apparent variations in orientation selectivity are virtually abolished (figure 4). In other words, the change in orientation of an adapting grating which reduces its equivalent contrast by a factor of two is fairly constant whatever the spatial frequency. This is one more example of the analytical power of the equivalent contrast transformation, which has already been used to compare the orientation selectivity of two different aftereffects (Blakemore and Nachmias, 1971) and to measure both orientation and spatial specificity for a third (Blakemore *et al.*, 1973).

One unexpected finding is the consistent difference in orientation selectivity between the two observers in this study. The mean half-width for J.A.M. (8·53°) was significantly broader than that for R.D.L. (6·54°). This observation of considerable individual variation in orientational tuning makes comparison with other experiments less informative. Nevertheless, the results of some previous studies are reproduced in figure 4. First, Blakemore and Nachmias (1971) used exactly the same methods to measure the orientation sensitivity of the threshold elevation effect for a different subject, and their result agrees very closely with those for R.D.L. Blakemore *et al.* (1973) used the equivalent contrast transformation to measure orientation specificity for a closely related aftereffect, the reduction in apparent contrast of suprathreshold test gratings after adaptation. The results for their two subjects again fall within the range of ours.

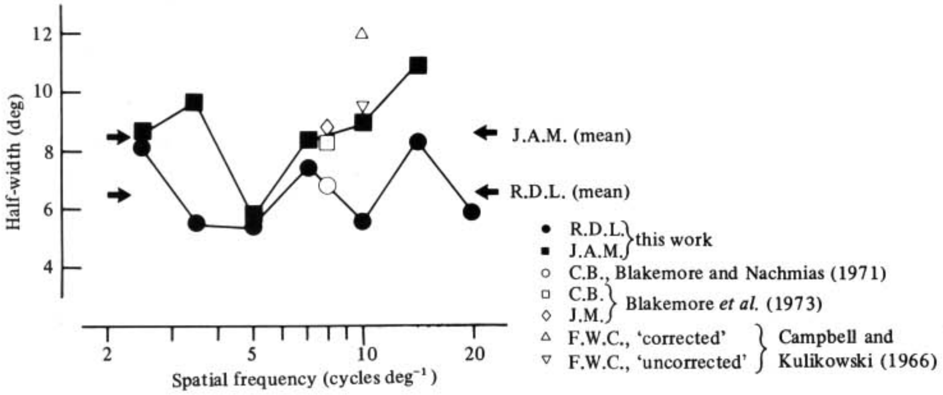

Figure 4. The half-widths at half-amplitude for R.D.L. and J.A.M. taken from figure 3. The mean half-widths are indicated by solid arrows. Some previous measurements are included for comparison.

Comparison with the results of Campbell and Kulikowski (1966) is more complicated. They used a simultaneous masking technique, determining contrast threshold for a vertical grating in the presence of a masking grating of high contrast and variable orientation. Campbell and Kulikowski did not themselves employ the equivalent contrast transformation; however they did report that Weber's law applies when both masking and test gratings are vertical. This means that the function relating threshold elevation to masking contrast has a slope of 1. Thus the transformed equivalent contrast function would be identical in slope to the original graph relating threshold elevation to masking orientation. This function declined exponentially (as does the equivalent contrast function in our adaptation experiments) but the half-width was 12°. This value is well outside the range of the other results.

However, Campbell and Kulikowski (1966) applied an unusual 'correction' to the contrast of the masking grating to compensate for the reduced sensitivity of the visual system at oblique orientations (Campbell *et al.*,1966). This correction assumes that the relative effectiveness of suprathreshold gratings of differing orientation is related to their relative contrast thresholds. We have made no such correction in our experiments, so in order to contrast Campbell and Kulikowski's results with ours we have used their 'uncorrected' data to arrive at a comparable value of the half-width. The result is then 9·5°, which is entirely consonant with all the other data. Hence, although there may indeed be some genuine differences between orientation selectivity measured by masking and adaptation paradigms (Kulikowski, 1972) our finding of considerable variation between subjects suggests that caution must be exercised in the comparison of the results of different experiments and procedures.

It would be interesting to take advantage of the observed differences in orientational tuning in our two subjects to test the hypothesis that orientation-selective channels are involved in such perceptual tasks as the discrimination of different orientations (Andrews, 1965; Campbell and Maffei, 1971) and vernier acuity (Findlay, 1973). One should expect consistent differences in the performance of the two subjects in all situations that require the use of orientation-selective channels.

Ultimately it may be possible to incorporate our results into a general neurophysiological model to account for orientation selectivity and sensitivity to spatial frequency. The optimal bar-width for a simple cortical cell (Hubel and Wiesel, 1962) might be dependent on the width of the central, spatially-summating area of the receptive field. The reduction in response as a bar or grating is rotated away from the axis orientation of the receptive field is presumably related to a reduction in the amount of stimulation of the receptive field centre and increasing intrusion into the inhibitory flanks. Our finding that orientational half-width is quite constant at all optimal spatial frequencies might imply that the ratio of the width of the receptive field centre to its length is fairly constant whatever their absolute dimensions.

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