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ORIENTATIONAL SELECTIVITY OF THE HUMAN VISUAL SYSTEM

BY F. W. CAMPBELL AND J. J. KULIKOWSKI*
From the Physiological Laboratory, Cambridge

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SUMMARY

1. It is known that an object is less detectable when it is viewed against a background containing structures similar to the object. The effect of changing the orientation between the object and background is investigated.

2. Gratings of variable contrast were generated on two oscilloscopes; these were superimposed optically. The angle of orientation between them could be changed. The threshold of one grating, the test grating, was determined in the presence of the other, the masking grating.

3. When the gratings were presented with the same orientation (and locked in phase) the increment threshold of the test grating was found to be proportional to the suprathreshold contrast of the masking grating.

4. As the angle between the test and masking gratings was increased the masking effect fell exponentially.

5. At 12° on either side of a vertical test grating the masking effect was reduced by a factor of two with respect to its maximum value. This angle was independent of the contrast level of masking, the focus, and also the phase coherence of the masking grating.

6. If the test grating was presented obliquely the effect of masking was slightly less.

7. The narrow orientationally tuned channels found psychophysically by this masking technique are compared with the orientationally sensitive cells discovered electrophysiologically in the visual cortex of the cat.

INTRODUCTION

Hubel & Weisel (1959, 1962) have shown that many of the cells in the visual cortex of the cat respond only to lines with a certain orientation. Each cell has a particular angle to which it is most responsive. The population of this type of cell has representatives from all angles of orientation.

* On leave from the Institute of Automatic Control, Polish Academy of Sciences, Warsaw, Poland.

Is it possible to demonstrate in man psychophysically a similar orientational sensitivity?

The experiment was designed as follows: A test target consisting of a fine grating was presented at a fixed orientation. The subject could adjust the contrast (Fig. 1) of the grating to a threshold value. A second masking grating of the same spatial frequency could be superimposed optically on the test grating; that is, it was added to the test grating without obscuring it. The contrast of the masking grating could be set to any level by the experimenter, and its angle of presentation could be altered relative to the test grating. The mean luminance of the combined test and masking grating was always constant and independent of their contrast settings. This apparatus enables us to evaluate angular interaction between the two gratings in terms of the contrast threshold of the test grating.

The reason for selecting gratings as test and masking stimuli was the expectancy that a large number of orientationally sensitive 'line detectors' from different parts of the visual field would be simultaneously involved, and thus thresholds might be determined with less variability.

METHODS

Gratings were generated on each face of two oscilloscopes using the television technique of Schade (1956) and modified as described by Green & Campbell (1965). The first oscilloscope carried the test gratings which had a sinusoidal modulation of the contrast along one axis. The test grating frequency was always 10 c/deg of arc. Its contrast (Fig. 1) could be varied by the observer. A second similar oscilloscope carried the masking grating, also with a frequency of 10 c/deg.

The observer looked at the test grating through an artificial pupil of 2·8 mm diameter and a spectacle lens to correct for the viewing distance. A beam-splitting cube was placed close to the spectacle lens and positioned so that the masking grating could be superimposed upon the test grating. In other words, the observer could see one grating added to the other. The superimposed gratings were contained in a circle subtending 2° and a screen subtending 10° surrounded this; the screen and the test field were matched in colour and had a luminance of 40 cd/m^2 as seen by the observer. The masking and the test gratings could be rotated through a range of 360° by two Dove prisms in the optic axis of each grating system.

As the screens of the oscilloscopes had an equal luminance, it is clear that the maximum contrast that can be achieved by the masking grating alone is 0·5, for its contrast is diluted by half the additional luminance from the test screen. In some experiments it was important to test the effects of high contrast levels of masking and this was done by decreasing the luminance of the test grating by the required amount. The luminances of the screens were measured with an S.E.I. (Ilford) photometer.

In order to generate a stationary grating of uniform spatial frequency and contrast, the beam intensity (Z-axis) of the oscilloscope was modulated with a pure sinusoidal frequency from an oscillator, and the time base controlling the X-axis was locked to the oscillator wave form. To generate a grating which did not have constant phase coherence, the Z-axis was supplied with a voltage from a noise generator which was passed through a tuneable narrow-band filter with a Q of 25. This produces a pattern like a grating, but in this case the position of each bar of the pattern is constantly moving in relation to the screen. The pattern has a constant mean spatial frequency and is easily recognized as a grating. The mean contrast of the grating is also constant, but each portion of it is continuously varying. In this way a masking pattern without spatial phase coherence was generated.

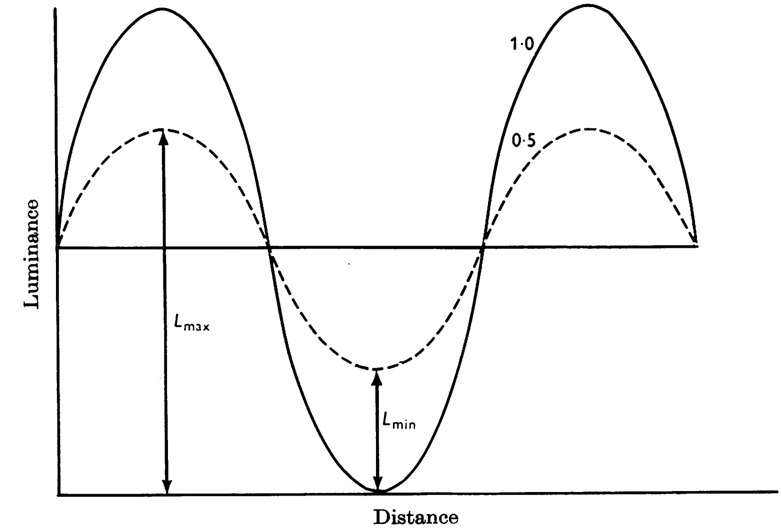

Fig. 1. Contrast is defined as $(L_{max} - L_{min})/(L_{max} + L_{min})$. Two values of contrast are illustrated: 1 and 0·5; the mean luminance level remains constant. Spatial frequency is defined as the reciprocal of the angular distance between successive maxima in the sinusoidal luminance distribution. Contrast sensitivity $= (L_{max} + L_{min})/(L_{max} - L_{min})$.

RESULTS

In the initial experiment the test grating was vertically oriented and the masking grating was presented horizontally. The contrast sensitivity of the test grating (a reciprocal of the contrast threshold) was determined in the presence of different levels of contrast of the masking grating. The findings are shown in Fig. 2, results for 90°. Clearly, the threshold is not affected by the presence of a perpendicular masking grating even when its contrast is as high as 0·3. For higher contrasts there is only a slight effect. All contrast values are quoted relative to the combined luminance masking and test gratings.

In the next experiment, the masking as well as the test grating were vertically oriented and were in phase with each other; that is, the contrast distribution was peak-on-peak and trough-on-trough. Findings are shown in Fig. 2, results for 0°. The arrow marks the contrast threshold for the masking grating, which is constantly present while the test grating appears for 1 sec every alternate 1 sec. When the masking grating has a contrast of less than 0·002 it does not produce a detectable effect on the contrast sensitivity of the test grating. From this contrast level up to

0·008, sensitivity is enhanced (i.e. contrast threshold decreases) in proportion to the contrast of the masking grating. This is expected on physical grounds for the contrast of the two gratings must add optically. After this point it is possible to perceive the masking grating continuously. To determine thresholds at higher levels of masking contrast, the subject adjusted the test grating to a contrast level equal to a 'just noticeable difference' of contrast (j.n.d.). The absolute value of the j.n.d. increases in proportion

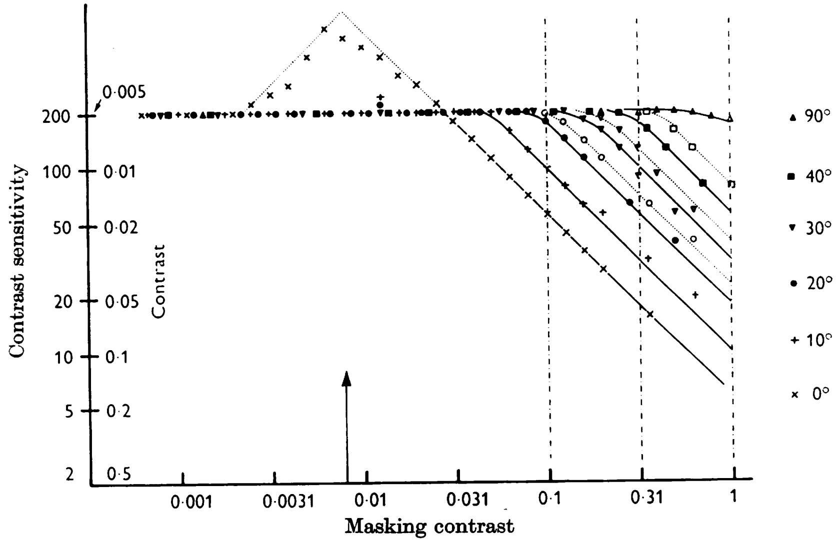

Fig. 2. Contrast sensitivity of the test grating as a functon of masking contrast at different orientation angles: × 0°, + 10°, ● 20°, ▼ 30°, ■ 40°, ▲ 90°. Open symbols (○, ▽, □) and dotted lines denote results of measurements uncorrected for the reduction in contrast sensitivity of the masking grating.

to the masking contrast. *Effective masking* occurs with contrasts greater than 0·028, the point at which the j.n.d. reaches the contrast threshold of the test pattern. Thus, contrast sensitivity, the reciprocal of j.n.d., decreases in direct proportion to the masking contrast.

In the same manner, the contrast sensitivities for different amounts of masking contrast were determined for orientation angles of 20°, 30°, and 40°. The log contrast threshold of effective masking increases almost in proportion to the angle of orientation. It is well established that the contrast sensitivity for a grating in the oblique orientations is lower than that for a grating presented either horizontally or vertically (Campbell, Kulikowski & Levinson, 1966). In Fig. 2, the measured contrast sensitivities for these three orientations (open symbols) have been corrected for this effect (solid symbols). In all cases the corrected absolute value of the j.n.d. increases in proportion to the effective masking contrast.

To illustrate more clearly the effect of the angle of orientation of the masking grating on the contrast sensitivity of the test grating, the results shown in Fig. 2 were replotted for three selected contrast levels of 1, 0·31 and 0·1 (vertical dot-dashed lines in Fig. 2) in terms of a masking ratio R. The masking ratio, R, was obtained from contrast sensitivities of unmasked (S_{unmasked}) and masked (S_{masked}) gratings by subtracting the logarithms of these sensitivities:

$$\log R = \log S_{\text{unmasked}} - \log S_{\text{masked}}.$$

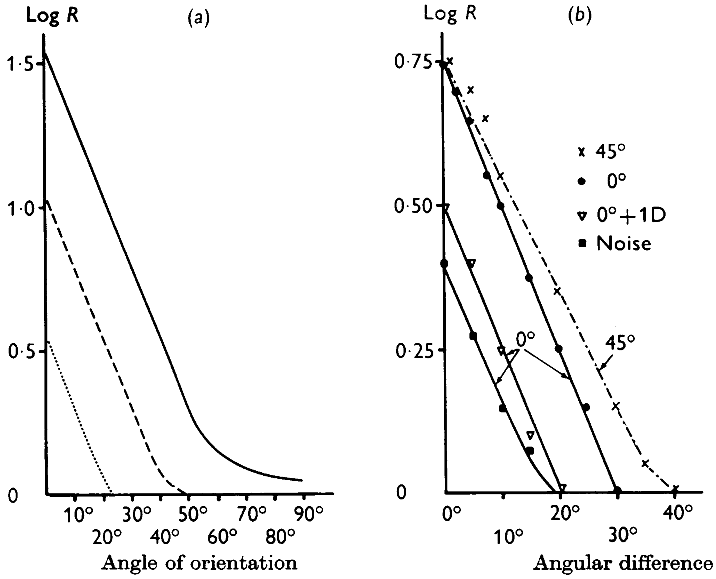

Fig. 3. The masking ratio, R, as a function of the orientation angle. (a) Results replotted from Fig. 2 for three masking-contrast levels of 1 (continuous line) 0·31 (interrupted line) and 0·1 (dotted line); these three levels of masking contrast are marked by three vertical lines in Fig. 2. (b) The masking ratio measured under different conditions—(1) vertical orientation of the test grating (0°): ● phase coherent sinusoidal masking grating, □ phase incoherent masking grating, ▽ test and masking gratings defocused + 1 D; (2) oblique orientation of the test grating (45°): × phase coherent masking grating.

The $\log_{10}$ of these ratios are plotted against the angle of orientation on a linear scale, and illustrated graphically in Fig. 3a. It is evident that an exponential function adequately describes the angular effect of masking. Since the straight portions of the characteristics are parallel the exponent is constant for all levels of the masking contrast.

In the previous experiments, the masking and test gratings were in phase. The next experiment was designed to test the significance of phase location. This was done by generating a grating using a narrow-band noise source. In this way the position of each bar of the grating was arranged to change constantly. The resulting grating had a definite mean spatial frequency. Although it did not appear to vary in its spatial frequency, each bar varied constantly about its mean position and contrast. Thus, there was no constant relation between the phase of the masking grating and the fixed test grating. The effect of the orientation angle on the masking ratio is shown in Fig. 3*b* (squares).

For comparison the effect of a masking grating locked in phase on the masking ratio is also shown in Fig. 3*b* (circles) for a contrast of 0·2. It will be noted that the exponent for the two types of grating is similar. We may conclude that similar masking occurs with both in phase and changing phase gratings.

So far the masking ratio characteristics have had a constant exponent. Two further experiments were designed to find whether this slope could be changed. Since the resolving power for gratings is less in the oblique orientations (Campbell *et al.* 1966), we examined the effect of a masking gratings on a test grating presented obliquely (45°). The experiment was done in the same manner as described previously for the vertical grating. Results are shown in Fig. 3*b* (× and dot-dashed line). There is a well marked change in slope which indicates a reduction of the exponent amounting to 25%. Is this decrease connected simply with the reduction of resolving power associated with the oblique presentation? This may be tested by decreasing the resolving power in another way and again determining the masking ratio.

The resolving power of the eye was reduced by placing +1D lens in front of the artificial pupil. The resulting myopia decreased the contrast sensitivity of the test and masking gratings by 0·6 logarithmic unit, as could be expected from the findings of Campbell & Green (1965). The masking ratio was subsequently measured and results are shown in Fig. 3*b* (triangles). The exponent was found to be identical to a vertical test grating measured with an in focus eye.

DISCUSSION

These experiments were designed to establish whether some channels in the visual system were sensitive to the angle of orientation of contours. Using gratings of variable contrast and a masking technique we have obtained some psychophysical results suggesting such organization. Figure 2 gives threshold values of contrast at which masking begins for various angles of orientation. The reciprocal of the masking-contrast threshold is plotted in Fig. 4*a*. We call this the masking sensitivity, S_M. It will be noticed that the upper part of this characteristic is identical to the masking ratio characteristic (Fig. 3*a*, continuous line). To illustrate this phenomenon more convincingly it is convenient to plot the masking sensitivity as a normalized quantity in a linear scale and in polar co-ordinates. This is shown in Fig. 4*b* for the two investigated orientations of test gratings, 0° and 45° (only one lobe of each is shown). At the half-value of the maximum masking sensitivity (0·5) the half-width of the characteristic is 12° for the vertical presentation and 15° for the oblique presentation. This is a convenient measure of angular selectivity.

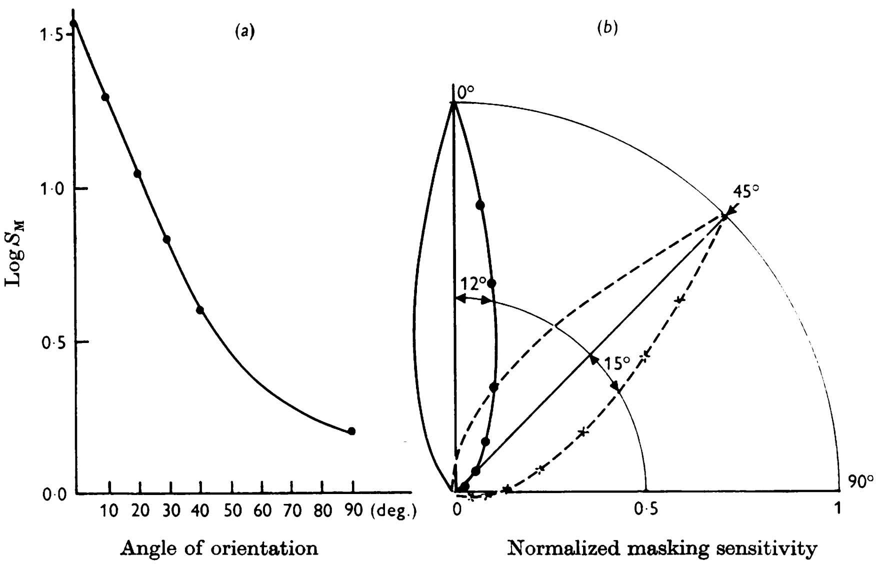

Fig. 4. Masking sensitivity as a function of orientation of the masking grating. (*a*) Logarithm of the masking sensitivity for the test grating vertically oriented. (*b*) Normalized masking sensitivity plotted in polar co-ordinates for two orientations of the test grating: ● vertical (0°) and × oblique (45°). Notice differences of the half width at half height of the characteristics: 12° for vertical and 15° for oblique presentations of the test grating.

It is, of course, not possible to argue convincingly from psychophysical data to neurophysiological description of the visual system. Nevertheless, it is interesting to compare the description of the orientational sensitivity of the cortical cells of the cat (Hubel & Wiesel, 1965) with our results. They found that most cells respond actively to straight-line stimuli, either a white or a dark line. This type of stimulus is effective only when presented in an orientation that is characteristic for the given cell. There is usually no response when the stimulus is presented at right angles to the optimum orientation. The range of orientations over which a response may be evoked is not more than 30° for a given cell. To give but one example taken from a description of a 'lower order hypercomplex cell' we quote: 'The orientation of the edge was critical, since changing it by more than 10°–15° produced a marked decrease in the response, and a 30° change made the stimulus ineffective.'

This semiquantitative description of the orientation sensitivity of cortical cells of the cat agrees surprisingly well with the angular selectivity found psychophysically. It should be possible to investigate electrophysiologically the angular selectivity of these cortical cells with a stimulation technique similar to that we have used. Such an investigation might establish more critically whether there is indeed any connexion between this psychophysical phenomenon and neurophysiological mechanisms.

The finding that the angular selectivity for the 45° presentation is 25% worse than that for the vertical orientation agrees quantitatively with the finding of other workers that the visual resolving power for a variety of test conditions (reviewed by Taylor, 1963) including an alignment task (Andrews, 1965) is also reduced approximately by the same amount. We find that degrading the optical image by defocusing by $+1$ D does not change the angular selectivity. It may therefore be concluded that the poorer angular selectivity for the oblique presentation cannot be due to optical factors. Using a different method Campbell *et al.* (1966) also concluded that the orientational variation of the visual acuity was not due to optical factors. This suggests that these orientational effects are connected with a specific property of the visual nervous system.

The striking similarity of the findings with a wide variety of visual tasks suggest some common basic explanation. In the previous paper (Campbell *et al.* 1966), 90° orientational differences in visual resolving power might have suggested a Cartesian-co-ordinate system. However, we find the angular-selectivity characteristic much narrower than would be expected on a simple Cartesian-co-ordinate system. This implies that there must be numerous orientationally selective channels, closely separated in angle, in order to signal adequately all orientations. Hubel & Wiesel (1965) give a minimum estimate of 10–15 orientations originating from a given small retinal area. This suggests a maximum angular separation of 12°–15° between each channel, a value which would be adequate to represent all orientations.

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