The dependence of monocular rivalry on orientation

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Abstract. If two gratings with a sinusoidal luminance profile are crossed and if each has a different colour then they are seen to alternate; first one dominates and then the other. Part of the time both are seen. The rate of this monocular rivalry varies with the angle between the two gratings. If the two are lined up in parallel the percept is quite stable and remains so until their orientation is about 15° to 20° apart. The rate of alternation then increases rapidly reaching a maximum rate of 30 per minute.

The orientational selectivity of the rivalry suggests that the orientational properties of the neurones in the visual cortex discovered by Hubel and Wiesel are involved.

1 Introduction

In 1899 Breese reported the phenomenon of 'monocular rivalry'. He found that if a red square crossed by thin diagonal lines and a green square crossed by lines at right angles to those on the red fell on the same retinal area then "... a rivalry of the colors was perceptable. Neither disappeared entirely: but at times the red would appear very distinctly while the green would fade; then the red would fade and the green appear distinctly. The two sets of lines showed the same fluctuation, keeping pace with the changing intensities of the colors. Sometimes one of them would disappear altogether" (p.42). A related effect has been noted for alternation of after-images of bars in differing orientations (Atkinson, 1972).

Campbell and Howell (1972) noticed monocular rivalry using sinusoidal gratings, and found a much more marked effect for sine waves than for square waves. They also found that the effect is not confined to gratings crossed at right angles. In the present investigation we study the relation between the rate of alternation and the relative orientation of the two gratings.

Although in this paper we use a red and green coloured grating, it is not necesary to do so as the alternation occurs with a black and white crossed grating. However, they do alternate at a higher rate when different colours are used (Rauschecker, Campbell and Atkinson, 1973).

2. Method

The various targets were photographed on black—white lantern slides (2 in \times 2 in) and projected by two conventional lanterns onto a white screen. Monochromatic dye-impregnated filters were inserted in the light paths to change the colour. Green was Ilford filter 625 and red, filter 205. The voltage to the lanterns could be adjusted to control the luminance of the projected targets. A circular mask placed close to the target slides provided a circular display on the screen. Most of the observations were made with the circular display subtending 8 degrees, and a luminance of 1 cd m⁻². The contrast of the sinusoidal grating was about 0.5 and there were 6 bars of the grating within the field.

The rate of alternation was found by the use of an ink pen-recorder that responded to the turning of a potentiometer. Periods of observation were 30, 75, and 150 s in duration. The subjects turned the potentiometer to the extreme left or

extreme right, depending on which phase was dominant, or kept the switch in midposition when the pattern appeared unified and stable.

3 Results

3.1 Red and green

For 0° to 20° relative orientation of the crossed gratings there is no alternation at all. The percept is absolutely stable. Figure 1 shows the result on two observers. For greater angles there is some alternation and the rate of alternation increases fairly smoothly up to about 60° to reach a peak of about 30 changes per minute. Thereafter the rate of alternation decreases slightly up to 90° (figure 1).

Several control conditions were used to make sure that the rivalry noted was not due to eye movements. Of course, there are two special situations where eye movements must affect the observations. If the pattern is stabilised on the retina, it will cease to be seen after some time, so that both gratings will fade out along with everything else in the field. If a fixation point is provided so that accurate voluntary fixation can be exercised, both gratings may momentarily wash out due to partial stabilisation. At the other extreme, if the subject makes a large voluntary eye movement in a direction parallel to one of the gratings, the grating at right angles to the direction of movement may be encouraged to fade, presumably due to temporal smearing, as would happen because of the drop in contrast for the grating in this meridian. This would be analogous to the smearing that occurs on a photographic negative due to handshake. This raises the issue of whether the normal eye movement patterns which occur when we "just look at the pattern" could account for the alternation. The following observations refute this view.

We mounted a picture of the coloured crossed gratings on a disk that can be rotated about its centre. The speed of rotation is not critical providing that it is not so fast that the pattern is blurred out. All observers agreed that the pattern alternated in the identical manner to that which occurs when it is stationary. As the pattern is sweeping through all orientations, no one orientation can be adapted more than any other. The same pattern predominates through several rotations of the disk.

A possible explanation for some or all of the alternation could be that the longitudinal chromatic aberration of the eye causes fluctuations of accommodation, so that some of the time one colour is in focus, and at other times the other colour is in focus. This explanation is not correct, for presbyopic subjects still see the phenomenon normally. To make doubly sure, we paralysed the ciliary and

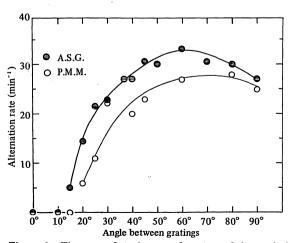


Figure 1. The rate of rivalry as a function of the angle between the two gratings for two subjects.

sphincter muscles of one eye with 1% atrophine sulphate and then examined the crossed gratings with the normal eye and the paralysed eye. No difference was noted. Furthermore, any explanation of this type has to account for the absence of alternation when the two gratings are parallel or displaced by up to $15-20^{\circ}$.

4 Discussion

It is possible that the monocular rivalry noted depends upon particular properties of orientation-selective units in the visual cortex. Hubel and Wiesel (1959, 1965, 1968) first discovered such units in the cat cortex. Their degrees of selectivity were quantified by Campbell et al. (1968). It is likely that the human visual system contains similar orientation-selective units. A variety of techniques, both psychophysical and electrophysiological, have shown that the human orientation units have effective half-widths of 8-12° (Gilinsky, 1968; Gilinsky and Mayo, 1971; Campbell and Kulikowski, 1966; Campbell and Maffei, 1970).

We would like to put forward the hypothesis that if the two gratings activate mainly one set of orientation neurones then no alternation occurs. But if two separate, and not significantly overlapping, populations of neurones are activated by the gratings, then alternation can occur.

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References

- Atkinson, J., 1972, "Visibility of an afterimage in the presence of a second afterimage", Perception and Psychophysics, 12 (3), 257-262.
- Breese, B. B., 1899, "On inhibition", Psychol. Monog., 3 (1), 1-65.
- Campbell, F. W., Cleland, B. G., Cooper, G. F., Enroth-Cugell, C., 1968, "The angular selectivity of visual cortical cells to moving gratings", J. Physiol., 198, 237-250.
- Campbell, F. W., Howell, E. R., 1972, "Monocular alternation: A method for the investigation of pattern vision", J. Physiol., 225, 19-21P.
- Campbell, F. W., Kulikowski, J. J., 1966, "Orientational selectivity of the human visual system", J. Physiol., 187, 437-445.
- Campbell, F. W., Maffei, L., 1970, "Electrophysiological evidence for the existence of orientation and size detectors in the human visual system", J. Physiol., 207, 635-652.
- Gilinsky, A. S., 1968, "Orientation-specific effects of patterns of adapting light on visual acuity", J. Opt. Soc. Amer., 58, 13-18.
- Gilinsky, A. S., Mayo, T., 1971, "Excitatory and inhibitory effects of orientational adaptation", J. Opt. Soc. Amer., 61, 689-690.
- Hubel, D. H., Wiesel, T. N., 1959, "Receptive fields of single neurones in the cat's striate cortex", J. Physiol., 148, 574-591.
- Hubel, D. H., Wiesel, T. N., 1965, "Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat", J. Neurophysiol., 28, 229-289.
- Hubel, D. H., Wiesel, T. N., 1968, "Receptive fields and functional architecture of monkey striate cortex", J. Physiol., 195, 215-243.
- Rauschecker, J. P., Campbell, F. W., Atkinson, J., 1973, "Colour opponent neurones in the human visual system", *Nature* (in the press).