ORIENTATION DIFFERENCES FOR PERCEPTION OF SINUSOIDAL LINE STIMULI

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Abstract—The effect of orientation on the sensitivity of sinusoidal lines of different spatial frequencies, was measured on four observers. As with conventional vernier stimuli, the sensitivity for obliquely oriented stimuli was poorer than that for stimuli that were either vertical or horizontal. This reduction in sensitivity was approximately constant at about 30% for stimuli of spatial frequencies between 0.15 and 10 c/deg. This pattern of change of sensitivity with spatial frequency could not be mimicked by either spherical or cylindrical optical defocus, by reduction in the mean luminance, or by peripheral viewing. The reduction in periodic vernier acuity for oblique sinusoidal lines is therefore a unique neural loss.

Oriental variations in the resolving power of the eye were first investigated half a century ago by French (1920) in a study of vernier acuity. Subsequently the superiority of resolution for vertical and horizontal over oblique stimuli, which is sometimes referred to as the “oblique effect”, has been well documented for a wide variety of visual tasks (see Taylor, 1963; Howard and Templeton, 1966; Appelle, 1972). Simple optical explanations for this effect have been convincingly eliminated by the demonstration that the meridional variations in resolution persist even when the measurements are made using interference fringes generated directly on the retina (Campbell, Kulikowski and Levinson, 1966; Mitchell, Freeman and Westheimer, 1967). Since the effect cannot be attributed to simple optical factors, the explanation must be sought in terms of some asymmetry in the neural organization of the visual system.

Recent measurements of the meridional differences that exist in the contrast sensitivity for gratings as a function of spatial frequency have provided an important insight into the nature of the neural involvement in this effect. These studies, which represent a logical extension of the classical measurements of grating acuity, have shown that meridional variations in contrast sensitivity are confined to spatial frequencies above about 5 c/deg (Campbell et al., 1966; Mitchell and Wilkinson, 1974; Berkley, Kitterle and Watkins, 1975; Freeman and Thibos, 1975). When contrast sensitivity is plotted against spatial frequency on semilogarithmic coordinates, data for spatial frequencies in excess of about 5 c/deg can be approximated by straight lines. The slope of the line that fits the data for these higher spatial frequencies changes with orientation and is generally steeper for gratings that are oblique than those that are either vertical or horizontal (Campbell et al., 1966; Berkley et al., 1975; Freeman and Thibos, 1975). (It should be noted in passing that this change of slope with grating orientation is not apparent in all observers; for example, subject JJK of Campbell et al., 1966; Fig. 7 of Mitchell and Wilkinson, 1974.) These results are somewhat different from those produced by simple errors of focus, which tend to result in a uniform decrease of contrast sensitivity for gratings of spatial frequencies higher than about 5 c/deg (Campbell et al., 1966; Mitchell, 1976). Therefore, the neural deficit that is observed in the oblique meridian does not appear to mimic the effect of a simple error of focus in that meridian.

By analogy with these studies, we thought that measurements made with sinusoidal lines, similar to those developed by Tyler (1973), might provide even further insight into the mechanism of the oblique effect. The typical vernier alignment task is a measure of the sensitivity with which two line segments can be aligned. A periodic version of this task (Tyler, 1973) employs as a stimulus a sinusoidal wavy line similar to those shown in Fig. 1. The method measures the sensitivity with which the sinusoidal line modulation can be discriminated as a function of the spatial frequency of the modulation. The periodic vernier task involves comparison in two dimensions of visual space, in contrast with other measures of acuity which are limited to a single dimension of stimulus variation. Since typical cortical receptive fields are elongated, i.e. non-homogeneous in two-dimensional space, periodic vernier acuity might be expected to show greater sensitivity to neural deficits than other acuity measures. We therefore used it to distinguish between two hypotheses of neural loss, namely:

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Fig. 1. Periodic vernier stimuli (T) of four different spatial frequencies of curvature and orientations. A straight line, C situated about 2° to one side of the vernier stimuli, was added as a comparison stimulus.

(i) a "neural blurring" hypothesis, which proposed that the defect of meridional anisotropy (the oblique effect) mimics the effect of some kind of optical blur, and

(ii) the hypothesis that some other kind of neural decrement which does not mimic optical blurring underlies the oblique effect.

METHOD

The sinusoidal line stimuli were generated on the face of a dual beam Telequipment D83 oscilloscope by applying a sinusoidal signal to one of the vertical amplifiers. An unattenuated version of the same signal was used to trigger the oscilloscope time base in order to provide stationary lines with sinusoidal curvature whose amplitude and spatial frequency could be varied by alteration of the amplitude and frequency of the signal applied to the Y4 axis. The second oscilloscope amplifier was grounded to provide a straight line to compare with the periodic stimuli. The lines subtended 6.7° in height and about 3° in width at the observation distance of 85 cm. The oscilloscope face was illuminated by a tungsten lamp through a green filter to provide a background luminance of 17 cd/m². The diameter of the observer's pupil was about 6 mm under these conditions. The lines themselves had a luminance of 430 cd/m². The oscilloscope sat on its end on a large circular turntable and was viewed by the observer through a mirror placed directly above the oscilloscope face; the orientation of the stimuli could then be altered very simply by rotating the turntable underneath the oscilloscope.

The observers were positioned by means of a head and chinrest and viewed the stimuli monocularly. (The two ammetropic observers wore their normal refractive corrections for all measurements.) The amplitude of the periodic line modulation could be set to threshold by the observer rotating the knob of a 10-turn potentiometer. In order to make the threshold settings easier, and thereby reduce variability, we departed from the procedure employed by Tyler (1973) in two important ways. First, a straight line located approx 2° to one side of the sinusoidal line target was added as a comparison stimulus (line C of Fig. 1). Secondly, both stimuli were presented intermittently for 350 msec every 1.6 sec instead of being continually exposed. Observers adjusted the amplitude of the periodic stimulus to threshold by slowly altering the amplitude down or up starting from a suprathreshold value until the stimulus line just appeared straight.

In most sessions threshold settings were made for vertical, horizontal and oblique (45° and 135°) stimuli of eight different spatial frequencies from 0.15 to 10.0 cycles per degree. The order in which the measurements were made was randomized; the spatial frequency was chosen first and one threshold setting was made for each of the different stimulus orientations which were presented in a haphazard order. This procedure was repeated at least once and sometimes two or three times so that there was a minimum of two threshold settings for each condition. In two of the observers (CM and MLS) measurements were restricted to stimuli of only two orientations, vertical and left oblique (135°).

Observers

Two of the four observers, FG and CM, were emmetropic, while the remainder, MLS and CWT, were well corrected myopes who wore their refractive corrections for all the measurements.

RESULTS

Oblique effect for periodic vernier activity

Periodic vernier acuity for the sinusoidal line stimuli was measured in all four majors meridians on two of the observers but the measurements were made with only vertical and left oblique (135°) stimuli on the other two observers. The individual results for all four observers are plotted in Fig. 2A on log-log coordinates as a function of the spatial frequency of the stimulus. The ordinate depicts the threshold line modulation amplitude in arc min. The scale is marked with displacement amplitude units increasing downwards so that the line modulation sensitivity increases reading upwards. For FG and CWT the filled circles depict the mean of the results obtained with vertical and horizontal stimuli while the open circles plot the corresponding means of the data obtained with oblique lines. In the case of the other two observers the filled and open symbols depict the results obtained with vertical and left oblique (135°) stimuli, respectively. The mean of the data for the four observers is plotted in Fig. 2B. The bars drawn through the data points at 2 c/deg depict ±1 S.E.M.

The general form of the functions is similar to that described earlier by Tyler (1973). Line modulation sensitivity progressively improved with increasing spatial frequency reaching a peak sensitivity at between 2 and 6 c/deg. The peak sensitivity, which ranged between 6° and 9° for the four observers, was comparable to commonly accepted values for classic vernier acuity (Westheimer, 1972). The slope of the increase is rather less than the slope of 1 (Fig. 2B) that had been found previously (Tyler, 1973), presumably because of the spatial reference for straightness provided in the present study by the reference line and the brief presentation of the stimuli. Indeed, the surprising aspect of the results is the degree of loss in sensitivity at low frequencies in the presence of such clear comparisons for straightness. Earlier Tyler (1973) pointed out that in this range acuity may be limited by the ability of the visual system to detect
the greatest difference in orientation of any two parts of the sinusoidal waveform; where the sensitivities conform to a slope of unity detection is limited by an absolute orientation discrimination limit. This orientation limit was calculated to be 20' and 30' for Tyler's (1973) two observers. The lesser slope exhibited in Fig. 2B reflects an increased sensitivity beyond this orientation limit to a limit of about 15' at the lowest frequencies, presumably due to the addition of the references for straightness.

The individual data of Fig. 2A show that each observer exhibits a reliable reduction in sensitivity for oblique stimuli but that there are small individual differences between the four observers, some showing a maximum difference at low frequencies and some at high. These small differences were not systematically related to the refractive state of the eyes.

The mean data (Fig. 2B) show that overall the reduction in periodic vernier sensitivity for oblique stimuli is approximately constant, about 30%, at all spatial frequencies. This contrasts with equivalent results from studies of grating resolution where the oblique effect is essentially confined to spatial frequencies above 5 c/deg (Campbell et al., 1966; Mitchell and Wilkinson, 1974; Berkley et al., 1974; Freeman and Thibos, 1975).

Effects of optical errors

Previous investigators of the oblique effect have attributed the diminished sensitivity for oblique stimuli as arising from two principle sources, namely optical and neural factors. The phenomenon cannot be wholly attributed to optical factors as suggested by Weymouth (1959) since the reduced sensitivity for oblique gratings persists even when the optics of the eye are bypassed (Campbell et al., 1966; Mitchell et al., 1967). The oblique effect must therefore be mainly a result of neural factors. It is possible to distinguish between two classes of neural loss; neural blurring, in which the neural loss mimics the effects of optical blurring, and other neural factors, in which it does not. The reduction in sensitivity in the oblique meridian is often very similar to that produced by a simple error of focus. Campbell et al. (1966) have shown that the contrast sensitivities for obliquely oriented sinusoidal gratings are depressed in a manner reminiscent of the reduction in sensitivity that results when the stimulus is optically defocussed. While close examination of the data indicates that the form of the contrast sensitivity function is slightly different from that which is produced by a simple error of focus, nevertheless the question remains whether the neural deficit in the oblique meridian always closely mimics the effects of optical blurring or whether the two can be distinguished for stimuli other than sinusoidal gratings. In order to examine this question in greater detail in the periodic vernier acuity task with sinusoidal lines, we compared the effects of changing the orientation of a clear stimulus with those produced by blurring a stimulus of constant orientation with either spherical or cylindrical lenses.
Figure 3 shows the effects on the periodic vernier acuity for a vertical sinusoidal line stimulus of placing positive spherical lenses of 1.5 and 3D in front of the eye of two observers. The results demonstrate that spherical blur mainly affects the sensitivity for high spatial frequency stimuli. Indeed, the sensitivity for a stimulus of low spatial frequency is little affected by the smallest (1.5D) error of focus although this is enough to produce at least a 30% reduction at high frequencies. These findings are quite different from the results shown in Fig. 2 for oblique stimuli. Clearly, the neural loss of sensitivity in the oblique meridian does not correspond to spherical blurring since periodic vernier acuity for oblique stimuli fails to exhibit any systematic frequency specificity (Fig. 2B).

However, it could be argued that as periodic vernier acuity involves the simultaneous processing of visual information in more than one meridian (since detection involves elements of the wavy-line stimulus that are at more than one orientation), selective blurring of the image in one meridian, as in astigmatism, might affect periodic vernier sensitivity in a more complex manner than can be achieved with a spherical lens and could conceivably mimic the observed loss in sensitivity for oblique stimuli. We therefore measured periodic vernier acuity in the same manner as before but with the sinusoidal line stimuli viewed through positive cylindrical lenses of various powers. Measurements were made with the stimulus line either parallel or orthogonal to the axis of the cylindrical lens.

The results of the measurements made with cylindrical lenses of 1.5, 3 and 6D on two observers are shown in Fig. 4. For clarity of display the data for
the various lens powers have been displaced downward by arbitrary amounts.

The results show that there is indeed an interaction between the periodic vernier sensitivity and the axis of the astigmatism induced by the cylindrical lens. Not only was there the expected loss of sensitivity when the stimulus line was defocussed, i.e. parallel to the axis of the cylindrical lens (open circles), but also there was a marked reduction in sensitivity when it was in the orthogonal unblurred orientation (filled circles). The peak sensitivities were always very different for these conditions. The peak sensitivity occurred with stimuli of higher spatial frequency when the stimuli were blurred (open circles) than when they were in the unblurred orientation. Under neither condition did the cylindrical lens produce a uniform reduction in sensitivity at all spatial frequencies. Instead the reduction in sensitivity was selective so that the curves for the two conditions cross each other with sensitivity best at low spatial frequencies when the stimuli were orthogonal to the axis of the cylindrical lens while at higher spatial frequencies sensitivity was greater when the stimuli were parallel to the axis of cylindrical blur. A detailed analysis of this result is presented elsewhere (Mitchell and Tyler, in preparation).

Effects of luminance

At low luminance levels the contrast thresholds for gratings are increased at all spatial frequencies (Campbell and Green, 1965; Patel, 1966; Van Nes and Bouman, 1967), presumably as a result of a functional reorganization in the retina leading to an increased convergence of receptors onto ganglion cells. Reducing the luminance of the stimuli thus provides another way of producing a neural loss of sensitivity. In the next experiment periodic vernier acuity was measured on observer FG at 5 luminance levels each separated from the next by one log unit, in order to see if sensitivity was lost equally at all spatial frequencies. The observer wore goggles containing neutral density filters for these measurements and adapted to each new luminance level (beginning at the highest) for at least 10 min prior to each set of measurements. The results shown in Fig. 5 indicate that the sensitivity was reduced most for stimuli of high spatial frequency at low luminance levels. Thus the effects produced by reduction of the mean luminance, which were similar to the effects of simple spherical blurring (Fig. 3) in showing a progressive loss at high spatial frequencies, again did not mimic the effects of oblique viewing (Fig. 2).

Fig. 5. The effect of luminance level on periodic vernier acuity for observer FG. Filled circles, 430 cd/m²; open circles, dashed line, 43 cd/m²; open circles, full line, 4.3 cd/m²; open squares, 0.43 cd/m²; open triangles, 0.043 cd/m².

**REFERENCES**


