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Meridional anisotropy of spatial displacement detection

PAUL C. QUINN, CYNTHIA F. MOSS, and STEPHEN LEHMKUHLE
Brown University, Providence, Rhode Island

The influence of spatial and temporal frequency on possible meridional variations in spatial displacement detection were examined. The results indicate that a spatial displacement detection oblique effect occurs at high spatial frequencies and low temporal frequencies. This anisotropy is not due to differences in perceived contrast along the vertical and oblique axes, since the orientations were equated for perceived contrast in each of the stimulus conditions. The spatial-displacement oblique effect is similar to both the contrast sensitivity and perceived contrast oblique effects in its dependence on the spatial and temporal properties of a stimulus. These different oblique effects are discussed in terms of a possible common neural basis.

The term "oblique effect" refers to the wide variety of instances in which both human and animal performance is superior for horizontal and vertical stimulus orientations than it is for oblique stimulus orientations (Appelle, 1972). Oblique effects have been divided into two general classes: Class 1 effects, which involve basic aspects of visual functioning at an immediate sensory level, and Class 2 effects, which appear in some cognitive aspects of stimulus processing, such as storage in memory (Essock, 1980). The Class 1 oblique effects have been observed in two different types of visual psychophysical tasks. First, they have been reported in tasks that examine the perception of contrast, including contrast sensitivity (Berkley, Kitterle, & Watkins, 1975; Camisa, Blake, & Lema, 1977; Essock & Lehmkuhle, 1982; Quinn & Lehmkuhle, 1983) and magnitude estimation of apparent contrast (Essock, 1982). Second, they have been demonstrated in tasks that measure an observer's ability to detect spatial displacement, including vernier and periodic vernier acuity (Corwin, Moskowitz-Cook, & Green, 1977; Tyler & Mitchell, 1977).

The magnitude of the oblique effects observed in the contrast domain increases at higher spatial frequencies and lower temporal frequencies (Berkley et al., 1975; Camisa et al., 1977). The tasks in which the vernier and periodic vernier acuity oblique effects have been observed do not, however, easily lend themselves to manipulations of spatial and temporal frequency. As a result, it is not currently known to what extent these spatial displacement detection anisotropies are related to those observed in contrast perception.

To determine whether the contrast and spatial-displacement oblique effects are similar in nature, we examined the influences of spatial and temporal frequency on possible meridional variations in spatial displacement sensitivity in a task similar to one employed by Westheimer (1978). Westheimer measured an observer's ability to detect a change in the position of a vertical sinusoidal grating target. He observed that lateral displacement thresholds were constant across different spatial frequencies and comparable to those observed for a single line. Our task involved the detection of square-wave displacements of vertical and oblique sinusoidal gratings at suprathreshold levels of contrast. At these levels of contrast and at high spatial frequencies, an oblique effect of perceived contrast is observed (Essock, 1982) and can confound an interpretation of meridional variations in performance on a displacement task. To avoid this problem, we matched the perceived contrast of the vertical and oblique gratings by obtaining magnitude estimates of the perceived contrast of these gratings under the same stimulus conditions for which the displacement thresholds were later measured. The pattern of results obtained in these experiments suggests that the oblique effects of contrast perception and spatial displacement detection are influenced in similar ways by the spatial and temporal properties of the stimulus.

EXPERIMENT 1

Experiment 1 was a magnitude estimation task. Observers were asked to judge the apparent contrast of vertical and oblique stimuli relative to a standard stimulus of a fixed physical contrast, presented at an orientation halfway between vertical and oblique. These estimates of apparent contrast were obtained for three stimulus conditions: (1) a high spatial frequency and a low temporal

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frequency, (2) a low spatial frequency and a low temporal frequency, and (3) a high spatial frequency and a high temporal frequency.

Method

Subjects

Three males, aged 22, 23 and 26 years, served as observers in these experiments. They were one of the authors (P.C.Q.—moderate myope) and two experienced psychophysical observers who were naive to the purposes of the experiment (D.J.U. and S.B.S.—slight myopes). Each participant was screened for possible uncorrected astigmatic errors by determining spatial resolution limits for 0°, 90°, 45°, and 135°. For all three observers, resolution limits for 0° and 90° were equivalent, as were those for 45° and 135°.

Apparatus and Stimuli

The stimuli were sinusoidal grating patterns that were counterphased in a square-wave fashion. They were generated on a Tektronix Model 535 CRT (blue P11 phosphor) by conventional techniques (see, e.g., Campbell & Robson, 1965). The spatial frequency, temporal frequency, and orientation of the stimuli could all be controlled independently. The average luminance of the display was 17 cd/m². Contrast was defined as (L max − L min)/(L max + L min), where L max and L min refer to the maximum and minimum luminances, respectively. Contrast varied from 0 to 0.52 and was independent of the average luminance.

A dove prism made it possible to change the orientation of the grating optically 90° or 45° counterclockwise from horizontal. The face of the CRT was masked to a circular area of 3° of visual angle in diameter by a field stop interposed between the CRT and the dove prism. The field stop was illuminated to match the CRT for color. The observer was positioned in a head- and chinrest and viewed the display monocularly at a distance of 85.5 cm.

The high-spatial-frequency, low-temporal-frequency condition was conducted at 9 cycles/deg (cpd) and 2 Hz, since pilot work had indicated that all three of the observers showed a significant contrast threshold oblique effect for this spatial and temporal frequency combination. The spatial and temporal frequency values for the other two conditions were chosen so as to significantly reduce the size of each observer's contrast threshold oblique effect. For Observers P.C.Q. and S.B.S., in the low-spatial-frequency, low-temporal-frequency condition, the spatial frequency was 3 cpd and the temporal frequency was 2 Hz. For Observer D.J.U., the spatial frequency was 1 cpd and the temporal frequency was 2 Hz. In the high-spatial-frequency, high-temporal-frequency condition, we used a 9-cpd grating with a temporal frequency of 16 Hz for all three subjects.

Procedure

Contrast thresholds. For each of the three stimulus conditions, each observer's vertical and oblique contrast thresholds were obtained in a method of adjustment task. Each observer adjusted the contrast of the grating to threshold by turning the knob of a 10-turn linear potentiometer. The thresholds for each stimulus condition were obtained in separate sessions. Within a session, six threshold settings were obtained for each orientation. The order of presentation of the two orientations was counterbalanced within a session.

Magnitude estimation of perceived contrast. For the two stimulus conditions in which the low temporal frequency was employed, contrast was fixed in steps of .15, .30, .45, .60, .75 and .90 log units above each observer's oblique contrast threshold. For the stimulus condition using the high temporal frequency, contrast was fixed in steps of .10, .20, .30, .40, and .50 log units above each observer's oblique contrast threshold. The smaller range of stimulus contrasts was used here because of the limits of our equipment. The observers were asked to provide magnitude estimates for the apparent contrast of each of these gratings. Separate sessions were conducted for each observer at each of the three stimulus conditions. Within a particular session, four magnitude estimates were obtained at each of the two stimulus orientations and at each of the six contrast levels. The trials were presented in blocks of a single orientation, and the order of these blocks was counterbalanced. The order of presentation of the contrast values was randomized within each orientation block.

A standard stimulus was presented before each of the comparison stimuli. The standard and the comparison stimuli were each presented for 5 sec. There was an interval of approximately 5 sec between the presentation of the standard and the comparison during which the observer viewed a homogeneous field of the same mean luminance as the gratings. The intertrial interval was approximately 10 sec in length, and here also the observers viewed a homogeneous field of the same mean luminance as the gratings. The standard had the same spatial and temporal frequency as the comparison stimuli, but was set to an intermediate orientation (67.5° counterclockwise from horizontal). For the two low-temporal-frequency conditions, the standard was set to a physical contrast .45 log units above the observer's oblique contrast threshold. For the high-temporal-frequency condition, the standard was set to a physical contrast .30 log units above the observer's oblique contrast threshold. The observers were instructed to assign the contrast of the standard stimulus a value of 10 and to judge all comparison stimuli in relation to that value. On each trial, the observers were allowed to respond either during the presentation of the comparison stimulus or after it was turned off.

Results and Discussion

Contrast Thresholds

The vertical and oblique contrast thresholds of the three observers in the three stimulus conditions are plotted in Figure 1. For the high-spatial-frequency, low-temporal-frequency condition (top panel), all three observers showed lower thresholds for the vertical grating. A t test indicated that these orientation threshold differences were significant [correlated groups: S.B.S., $t(5)=6.24$, $p<.01$, two-tailed; P.C.Q., $t(5)=9.79$, $p<.001$, two-tailed; D.J.U., $t(5)=8.39$, $p<.001$, two-tailed].

The effects of decreasing the spatial frequency and increasing the temporal frequency on the magnitude of the contrast threshold oblique effect are shown in the bottom two panels of Figure 1. At the lower spatial frequency, no differences between the vertical and oblique contrast thresholds were found for any of the observers [correlated groups: S.B.S., $t(5)=0.49$, $p>.20$, two-tailed; P.C.Q., $t(5)=0.82$, $p>.20$, two-tailed; D.J.U., $t(5)=-0.38$, $p>.20$, two-tailed]. At the higher temporal rate, the contrast threshold oblique effect was no longer present for Observer P.C.Q. [correlated groups, $t(5)=1.51$, $p>.10$, two-tailed]. For Observer S.B.S., it was reduced to a smaller (from 0.28 to 0.14 log units), but still statistically significant, effect [correlated groups, $t(5)=3.84$, $p<.02$, two-tailed]. That the contrast sensitivity oblique effect decreases at lower spatial frequencies and a higher temporal frequency is consistent with previous reports (Camisa et al., 1977; Essock & Lehmkuhle, 1982; Quinn & Lehmkuhle, 1983).

Magnitude Estimates

The magnitude estimation data were fit with a power

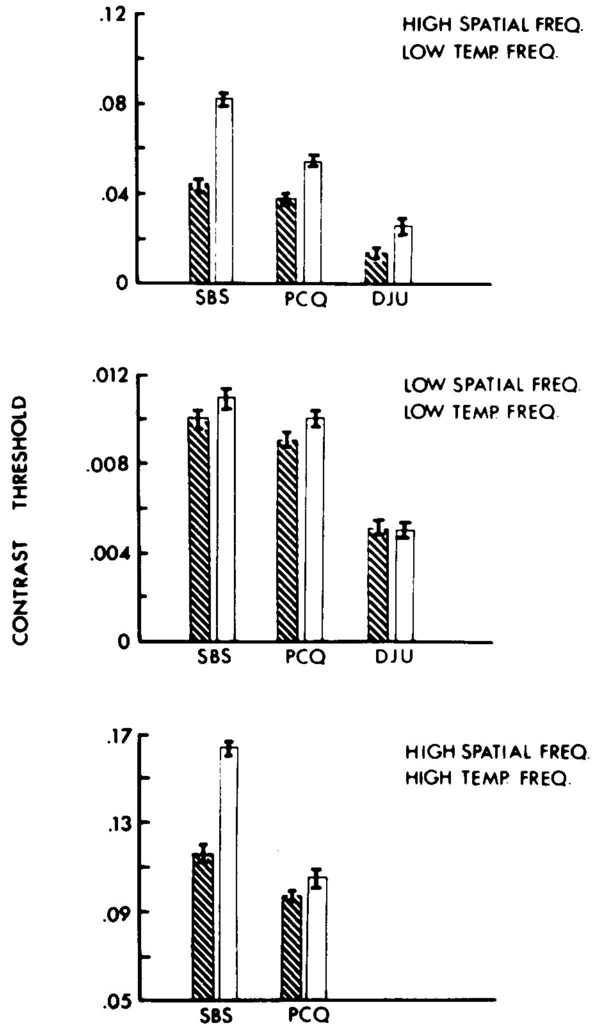

Figure 1. Contrast thresholds for the vertically (shaded bars) and obliquely oriented gratings (open bars) for the three observers (S.B.S., P.C.Q., and D.J.U.) in each stimulus condition. Error bars indicate one standard error of the mean. Note that the range of values on the contrast threshold axis changes with the stimulus condition.

function in the form of LogR = nLogC + LogK, where R is the perceived contrast, C is the physical contrast of the grating, K is a constant describing the unit of measurement used by the observers, and n is the exponent of the power function. The magnitude estimates for the three observers in each of the three stimulus conditions are shown in Figure 2. In the high-spatial-frequency, low-temporal-frequency condition, shown in the top panel, all observers perceived the vertical gratings to be of a higher contrast than oblique gratings of the same physical contrast [S.B.S., $F(1,3)=39.82$, $p<.01$; P.C.Q., $F(1,3)=53.94$, $p<.01$; D.J.U., $F(1,3)=103.55$, $p<.01$]. For two of the observers, the anisotropy was largest at the lower contrasts and decreased with increasing contrast [S.B.S., $F(5,15)=6.60$, $p<.01$; P.C.Q., $F(5,15)=7.28$, $p<.01$]; for the third observer, the anisotropy remained relatively constant across all physical contrasts [D.J.U., $F(5,15)=2.51$, $p>.05$]. A different pattern of results was observed in the low-spatial-frequency, low-temporal-frequency condition. As can be seen in the middle panel, all three observers judged the vertical and oblique gratings to have similar apparent contrasts across all physical contrasts tested [S.B.S., $F(1,3)=0.14$, $p>.25$; P.C.Q., $F(1,3)=5.47$, $p>.10$; D.J.U., $F(1,3)=0.14$, $p>.25$]. Finally, the high-spatial-frequency, high-temporal-frequency condition is depicted in the bottom panel; although orientation did not affect the contrast estimates of one observer [P.C.Q., $F(1,3)=0.57$, $p>.10$], a second observer did display the anisotropy [S.B.S., $F(1,3)=11.76$, $p<.05$]. This second observer's anisotropy was, however, of a smaller magnitude than that observed in the high-spatial-frequency, low-temporal-frequency condition.

The anisotropy of perceived contrast observed here is similar to that reported by Essock (1982), who found this anisotropy for stationary, 16-cpd gratings. The present results extend Essock's findings by showing that the suprathreshold anisotropy parallels the threshold anisotropy in its dependence on spatial and temporal frequency. Both anisotropies of contrast are largest at higher spatial frequencies and slow stimulus speeds. It is interesting to note that both studies leave open the question of what happens perceptually above 50% contrast. Data from Observer E.A.E. in the Essock study and Observers S.B.S. and P.C.Q. in the present study indicate that the suprathreshold contrast anisotropy decreases with increasing contrast. Data from Observer M.D.K. in the Essock study and Observer D.J.U. in the present study, however, suggest that the effect remains relatively constant across all physical contrasts.

EXPERIMENT 2

The purpose of Experiment 2 was to determine spatial displacement detection thresholds for the vertical and oblique gratings studied in Experiment 1. These thresholds were obtained using a temporal, two-alternative forced-choice procedure in which observers were required to judge which of two stimulus presentations contained the grating that was being displaced in a square-wave fashion.

Method

Subjects

The three observers of Experiment 1 participated in Experiment 2.

Apparatus and Stimuli

The grating patterns were generated as in Experiment 1, except that they were laterally displaced by predetermined amounts in a square-wave fashion at temporal frequencies of 2 and 16 Hz. Temporal frequency refers here to the number of lateral displacement cycles that occurred in a 1-sec observation interval. The grating pattern that had a temporal rate of 2 Hz thus shifted back and forth twice during the 1-sec observation interval. A circuit continually triggered the 200-Hz sweep of the oscilloscope. The grating was

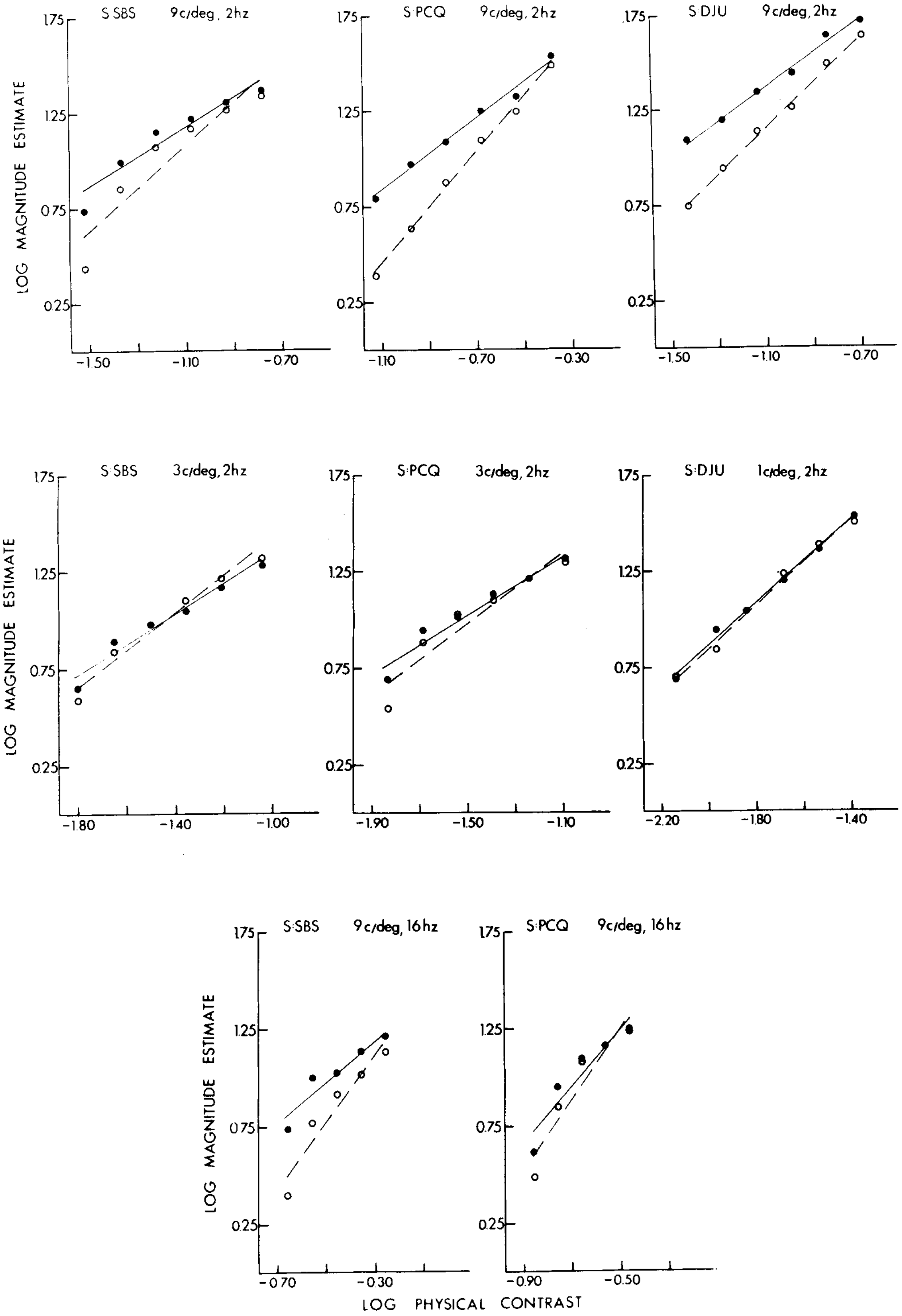

Figure 2. Log magnitude estimates of the three observers plotted against log physical contrast for each of the stimulus conditions (high spatial frequency, low temporal frequency—top row; low spatial frequency, low temporal frequency—middle row; high spatial frequency, high temporal frequency—bottom row). Estimates for the apparent contrast of the 90° grating are represented by the filled circles; those for the 45° grating are represented by the unfilled circles. Regression lines were fit by the least squares criterion (oblique grating: -----; vertical grating: ———). Note that the range of the log physical contrast values differs for different observers and stimulus conditions.

Table 1
Values of Physical Contrast Used in Experiment 2

	S.B.S.	P.C.Q.	D.J.U.
High-Spatial-Frequency, Low-Temporal Frequency Condition			
90°	0.08	0.17	0.05
45°	0.09	0.25	0.07
Low-Spatial-Frequency, Low-Temporal-Frequency Condition			
90°	0.07	0.05	0.02
45°	0.06	0.05	0.02
High-Spatial-Frequency, High-Temporal-Frequency Condition			
90°	0.38	0.28	
45°	0.47	0.28	

then displaced by delaying the trigger pulse. The extent of the lateral displacement of the grating was directly proportional to the delay of the trigger pulse. This delay or amount of displacement could be preset by the sweep trigger circuit. The onset of the observation period and the square-wave signal that displaced the grating were not temporally synchronized. To the observer, the grating appeared to repeatedly shift laterally between two fixed positions.

Procedure

Since this second experiment was conducted at suprathreshold levels of physical contrast, data from Experiment 1 were used to control for perceived contrast differences between the vertical and oblique axes. This was accomplished by first fitting the data with a threshold-corrected power function. The threshold-corrected power function was used instead of the more traditional form of the power function because the threshold-corrected power function provided a slightly better fit for most of the individual observer's functions relating perceived contrast to physical contrast. This finding was consistent with that of Gottesman, Rubin, and Legge (1981). We chose one perceived contrast estimate and found the corresponding vertical and oblique physical contrasts from the regression lines. The log of the perceived contrast estimate chosen was 1.2. This value was used for all observers and in each stimulus condition, with the one exception of S.B.S., whose log magnitude estimate of 1.1 was used in the high-spatial-frequency, high-temporal-frequency condition. This exception was necessary because the log of S.B.S.'s largest magnitude estimate along the oblique axis in this condition was smaller than 1.2. The resulting physical contrasts used for each of the observers in the three stimulus conditions are shown in Table 1.

Thresholds were measured using a temporal, two-alternative forced-choice procedure. Each trial consisted of two 1.2-sec observation intervals, separated by a blank interval of 1.5 sec. One of the observation intervals always contained a grating that was being displaced in a square-wave manner; the other interval always contained a stationary grating. From trial to trial, the square-wave displacement varied in magnitude. During the blank interval, the observers viewed a homogeneous field of the same mean luminance as the gratings presented in the observation intervals. The task was to choose which of the two observation intervals contained the grating that was being displaced in a square-wave fashion. They responded after each trial by verbally reporting "one" or "two" to indicate a choice.

For each stimulus condition, five ½-h sessions were conducted. Over the course of these five sessions, 30 trials were presented at each magnitude of displacement. The order of the displaced and stationary grating presentations was randomized from trial to trial. The trials were presented in blocks of a single orientation, and the order of these orientation blocks was counterbalanced within a session. One practice session was conducted for each of the stimulus conditions in order to locate an approximate range of displacements that would span the observer's threshold.

Results

In order to determine minimum detectable spatial displacements, separate psychometric functions were plotted for each observer in each of the three stimulus conditions. These functions were plots of the z-score of the percent correct responses versus the magnitude of displacement expressed in seconds of arc. Each of the resulting psychometric functions was fitted with a straight line by the method of least squares. Using these lines of best fit, the displacement magnitude that could be distinguished from a stationary grating 75% of the time was interpolated and this value was designated as the minimum detectable displacement for each observer. The psychometric functions obtained for a representative observer under the three stimulus conditions are depicted in Figure 3. This figure shows that only in the high-spatial-frequency, low-temporal-frequency condition do the vertical and oblique psychometric functions appear to differ. The function for the vertical grating starts at a lower displacement value and is steeper than the function for the oblique grating.

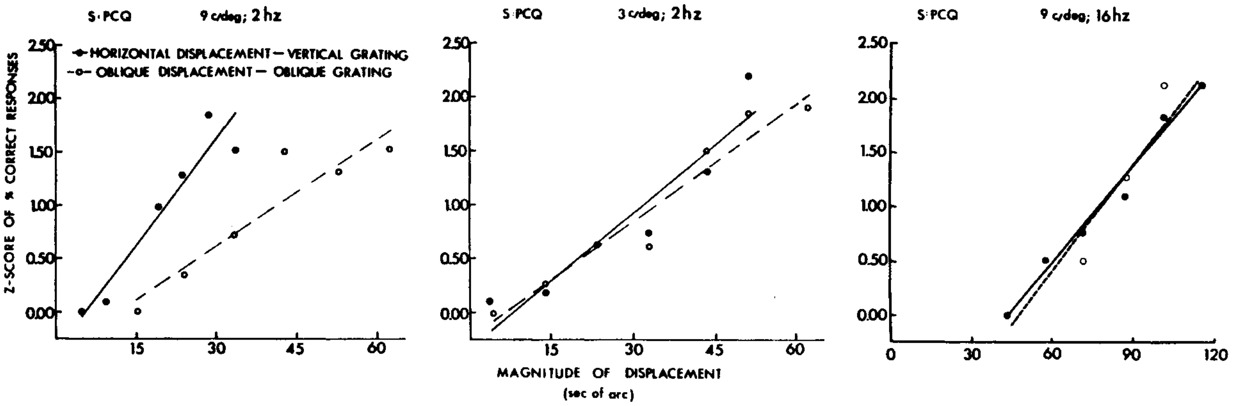

Figure 3. Z score of percent correct responses plotted against magnitude of displacement for Observer P.C.Q. in the three stimulus conditions. Regression lines were fit by the least squares criterion. Note the different range of displacement values for the high-spatial-frequency, high-temporal-frequency condition.

The spatial displacement detection thresholds derived from the psychometric functions for each observer and stimulus condition are shown in Figure 4. Consider first the thresholds obtained in the high-spatial-frequency, low-tempoal-frequency condition (top panel). For all three observers, the minimum detectable displacements obtained along the oblique axis were higher than those found along the vertical axis. In order to test the statistical reliability of these orientation differences, a minimum detectable displacement was calculated for each experimental session. This procedure yielded five spatial displacement detection thresholds at each orientation. When correlated t tests were performed on these thresholds, it was found that all of the observers showed a significantly lower spatial displacement detection threshold for the vertical orientation than for the oblique orientation [S.B.S., $t(4)=3.41$, $p<.05$, two-tailed; P.C.Q., $t(4)=2.51$, $p<.05$, one-tailed; D.J.U., $t(4)=8.90$, $p<.001$, two-tailed]. By contrast, in the low-spatial-frequency, low-temporal-frequency condition shown in the middle panel, no significant differences in the spatial displacement detection thresholds for the two orientations were observed for any of the observers [S.B.S., $t(4)=0.12$, $p>.20$, two-tailed; P.C.Q., $t(4)=-0.06$, $p>.20$, two-tailed; D.J.U., $t(4)=0.83$, $p>.20$, two-tailed]. Finally, in the high-spatial-frequency, high-temporal-frequency condition, shown in the bottom panel, one observer displayed similar vertical and oblique thresholds [P.C.Q., $t(4)=0.08$, $p>.20$, two-tailed], whereas a second observer's threshold was higher along the oblique axis than along the vertical axis, although this difference was not statistically significant [S.B.S., $t(4)=0.90$, $p>.10$, two-tailed].

The data of Figures 1 and 4 are replotted in Figure 5. This figure shows the log threshold difference between the vertical and oblique meridians for both the contrast threshold (shaded bars) and spatial displacement threshold (open bars) tasks at each stimulus condition. The dashed line represents equal thresholds for the two orientations. As can be observed, under the stimulus condition in which the contrast threshold oblique effect is largest (high spatial frequency and low temporal frequency), the spatial displacement threshold anisotropy is largest. For the other two conditions, the threshold differences between the two orientations in the two tasks decrease in a parallel manner.

GENERAL DISCUSSION

The results of Experiment 2 demonstrate an oblique effect of spatial displacement detection that depends upon the spatial and temporal properties of the stimulus. The magnitude of this spatial displacement detection anisotropy is largest at high spatial frequencies and low temporal frequencies—stimulus conditions that also result in contrast threshold and perceived contrast oblique effects. It is important to emphasize, however, that the spatial displacement detection anisotropy cannot be attributed to differences in perceived contrast between the vertical and oblique grating patterns. The primary goal of obtaining the magnitude estimates in Experiment 1 was to insure that the vertical and oblique grating patterns used in the second experiment would be matched in terms of perceived contrast. Previous investigations of meridional variations in vernier acuity have not controlled for perceived contrast differences between the vertical and oblique axes

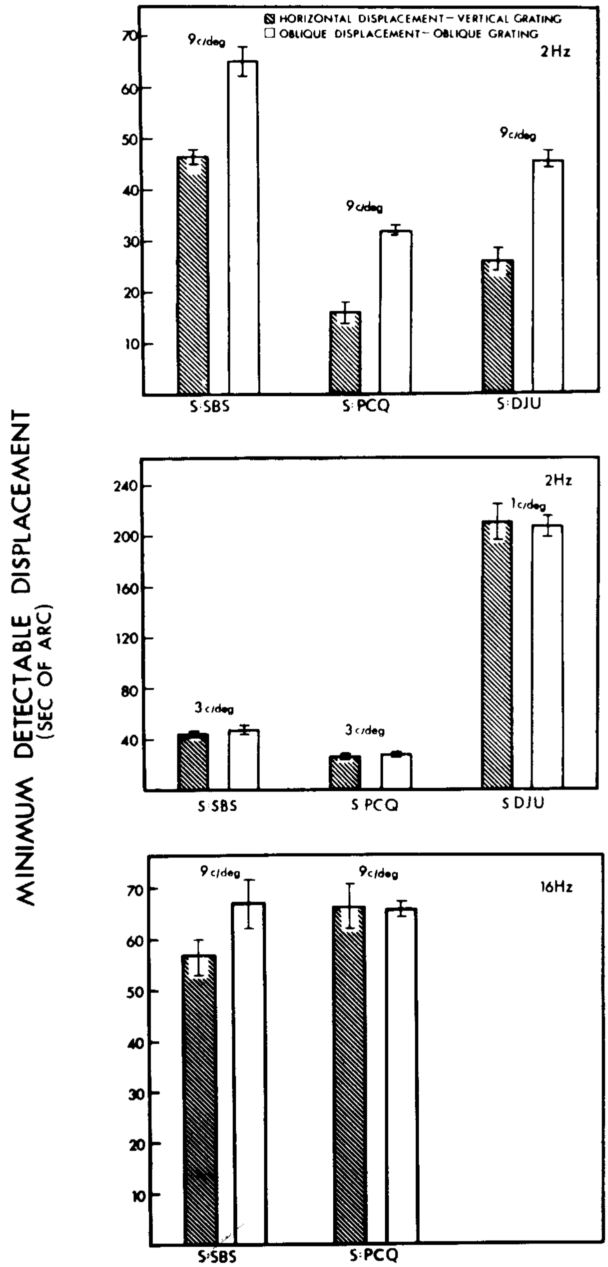

Figure 4. Minimum detectable displacement thresholds for the three observers in each of the three stimulus conditions (high spatial frequency, low temporal frequency–top panel; low spatial frequency, low temporal frequency–middle panel; high spatial frequency, high temporal frequency–bottom panel). Error bars indicate one standard error of the mean. Note the change in the range of minimum detectable displacement values for the low-spatial-frequency, low-temporal-frequency condition.

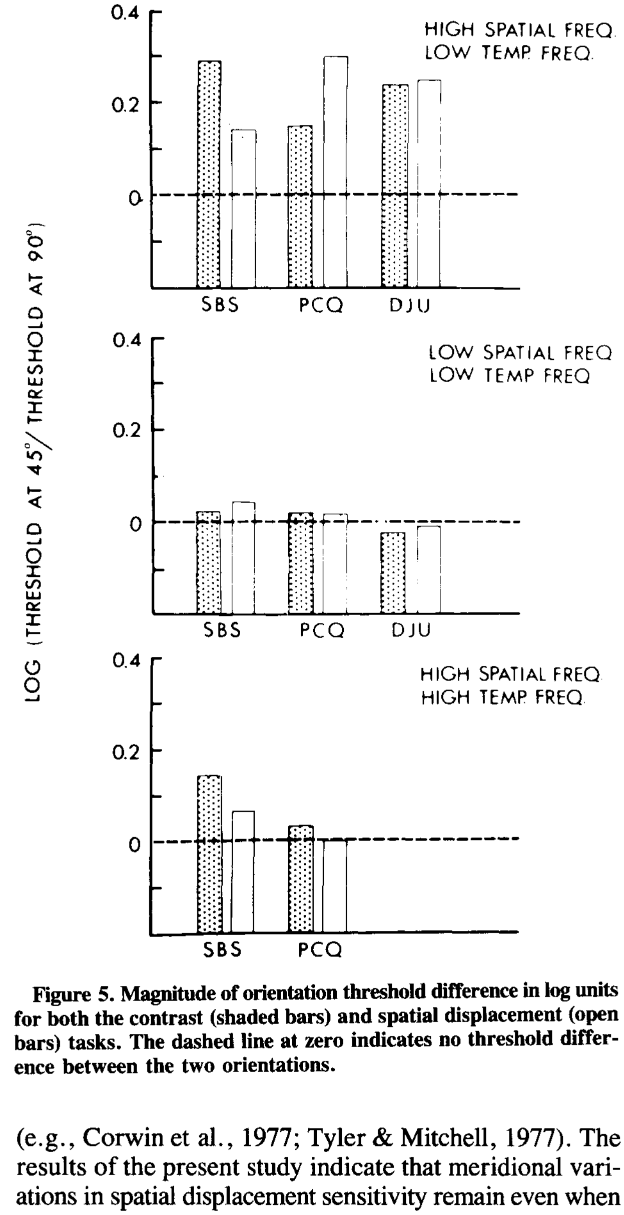

Figure 5. Magnitude of orientation threshold difference in log units for both the contrast (shaded bars) and spatial displacement (open bars) tasks. The dashed line at zero indicates no threshold difference between the two orientations.

(e.g., Corwin et al., 1977; Tyler & Mitchell, 1977). The results of the present study indicate that meridional variations in spatial displacement sensitivity remain even when these perceived contrast differences are controlled.

Inasmuch as the contrast and spatial displacement threshold anisotropies are influenced similarly by spatial and temporal frequency manipulations, one might speculate that these two oblique effects have a common neural basis. The spatial and temporal stimulus conditions that give rise to the contrast-perception oblique effects have led several investigators to speculate that cortical cells with spatial and temporal response properties similar to geniculate X cells may mediate the anisotropy (Essock, 1982; Essock & Lehmkuhle, 1982; Quinn & Lehmkuhle, 1983; Stone, Dreher, & Leventhal, 1979). In addition, a predominant number of cat cortical cells that respond maximally to thin, slowly moving stimuli have also been found to respond maximally to main-axis-oriented stimuli as opposed to obliquely oriented stimuli, thus providing a physiological basis for such speculation (Leventhal & Hirsch, 1975, 1977, 1980). Since the spatial-displacement-detection oblique effect is observed under the same stimulus conditions for which the contrast-perception oblique effects are observed, it is tempting to speculate that both anisotropies result from an orientation bias in the same population of cortical cells.

REFERENCES

Appelle, S. (1972). Perception and discrimination as a function of stimulus orientation: The oblique effect in man and animals. *Perception & Psychophysics*, **78**, 266-278.

Berkley, M. A., Kitterle, F., & Watkins, D. W. (1975). Grating visibility as a function of orientation and retinal eccentricity. *Vision Research*, **15**, 239-244.

Camisa, J. M., Blake, R., & Lema, S. (1977). The effects of temporal modulation on the oblique effect in humans. *Perception*, **6**, 165-171.

Campbell, F. W., & Robson, J. G. (1965). Application of Fourier analysis to the visibility of gratings. *Journal of Physiology* (London), **197**, 551-556.

Corwin, T. R., Moskowitz-Cook, A., & Green, M. A. (1977). The oblique effect in a vernier acuity situation. *Perception & Psychophysics*, **21**, 445-449.

Essock, E. A. (1980). The oblique effect of stimulus identification considered with respect to two classes of oblique effects. *Perception*, **9**, 37-46.

Essock, E. A. (1982). Anisotropies of perceived contrast and detection speed. *Vision Research*, **22**, 1185-1191.

Essock, E. A., & Lehmkuhle, S. W. (1982). The oblique effects of pattern and flicker sensitivities: Implications for mixed physiological input. *Perception*, **11**, 441-455.

Gottesman, J., Rubin, G. S., & Legge, G. E. (1981). A power law for perceived contrast in human vision. *Vision Research*, **21**, 791-799.

Leventhal, A. G., & Hirsch, H. V. B. (1975). Cortical effect of early selective exposure to diagonal lines. *Science*, **190**, 902-904.

Leventhal, A. G., & Hirsch, H. V. B. (1977). Effects of early experience upon orientation sensitivity and binocularity of neurons in visual cortex of cats. *Proceedings of the National Academy of Science*, **74**, 1272-1276.

Leventhal, A. G., & Hirsch, H. V. B. (1980). Receptive-field properties of different classes of neurons in visual cortex of normal and dark reared cats. *Journal of Neurophysiology*, **43**, 1111-1132.

Quinn, P. C., & Lehmkuhle, S. W. (1983). An oblique effect of spatial summation. *Vision Research*, **23**, 655-658.

Stone, J., Dreher, B., & Leventhal, A. (1979). Hierarchical and parallel mechanisms in the organization of visual cortex. *Brain Research Reviews*, **1**, 345-394.

Tyler, C. W., & Mitchell, D. E. (1977). Orientation differences for perception of sinusoidal line stimuli. *Vision Research*, **17**, 83-88.

Westheimer, G. (1978). Spatial phase sensitivity for sinusoidal grating targets. *Vision Research*, **18**, 1073-1074.

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