Orientation discrimination as a function of orientation and spatial frequency

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Orientation discrimination was measured with a yes-no signal detection procedure at two reference orientations, 90° and 45°. For the first of two experiments, the stimuli were disk-shaped gratings, 2.5° in diameter. Their spatial frequencies ranged from 1.8 cpd to 17.6 cpd. For the second experiment, the stimuli were either gratings or bars consisting of the center cycle of the corresponding grating. As expected, the results showed a highly significant reference orientation factor, with smaller just noticeable differences at 90° than at 45° (the *oblique effect*). However, orientation discrimination was independent of spatial frequency and bar width. Implications of the findings are discussed in relation to a holographic model that relates the oblique effect to meridional differences in the number of orientation-tuned cortical cells.

In a variety of sensory, perceptual, and cognitive visual tasks, performance is superior when stimuli are oriented along the horizontal or vertical meridian rather than along the oblique meridians. One manifestation of this *oblique effect* was studied in the present experiments, in which we measured just noticeable differences (JNDs) for slant. Our research was guided by a model that assumes a proportionality between orientation sensitivity for a given stimulus and the number of orientation-tuned cortical cells that respond to it. According to this theory, first considered by Bouma and Andriessen (1968), meridional differences in orientation sensitivity result from meridional anisotropies in the numbers of such cells, with fewer neurons tuned to the oblique meridians than to the main meridians. (See Figure 9b and the related discussion in Bouma & Andriessen, 1968, for a description of their model.¹)

Since the number-of-neurons theory was proposed, a substantial body of physiological evidence has accumulated that supports the existence of the postulated neural anisotropy (De Valois, Yund, & Hepler, 1982; Mansfield, 1974; Mansfield & Ronner, 1978; Orban & Kennedy, 1981; Pettigrew, Nikara, & Bishop, 1968; but see Finlay, Schiller, & Volman, 1976, and Poggio, Doty, & Talbot, 1977). Moreover, the theory itself was recently expanded and modified to incorporate the results of a study of orientation sensitivity in short-term memory (Thoms, 1981). In that study, memory for orientation decayed more rapidly at 90°, where sensitivity was greater, than at 45°. Thoms related this memorial manifestation of the oblique effect to the theory about the neural basis of the corresponding sensory effect by making the following as-

sumptions: (1) Orientation sensitivity in memory, as in sensation, is a function of the number of responding orientation-tuned cells in an appropriately chosen subset of such cells. (2) More cells fire to stimuli presented at the main meridians than to stimuli presented at the obliques. (3) The rate of decay in the number of responding neurons depends at any moment on the number of active cells.

Matin and Thomas (1984) further elaborated the preceding suggestions about sensitivity and amount of stored information in terms of the number of responding neurons by relating them to ideas about holographic methods of information storage. The linkage was established through the following property of a holographic image: storage of the object as a whole is retained while the total amount of information (detail and resolving power) is decreased if pieces of the hologram are replaced by opacities. In the physiological context we are considering, the neurons that cease to respond during memorial decay are the analogues of the lost (opaque) pieces of the hologram. More generally, in both sensation and memory, the number of neurons corresponds to the effective size of the hologram and thus to the amount of resolving power. In the specific case we are considering, the larger number of orientation-sensitive neurons at the main meridians relative to the obliques provides the physiological substrate for the anisotropy in ability to discriminate among slants. (See Matin & Thoms, 1984, for further details.)

In this description we have focused on aspects of the number-of-neurons question that are particularly relevant to orientation discrimination; however, neural meridional anisotropies have also been proposed as the possible physiological correlate of other psychophysical oblique effects, particularly meridional differences in contrast sensitivity (e.g., Mansfield, 1974). Moreover, the concept was recently generalized beyond the oblique effect entirely when De Valois, Albrecht, and Thorell (1982) proposed numerical differences among the sets of neurons tuned to various spatial frequencies as the physiological correlate of the contrast sensitivity function (CSF). Their sug-

This report was supported by Grant R01 EY02951 from the National Eye Institute and by an award from the Research Committee of the C. W. Post Campus, Long Island University. We thank Vincent Valle, who wrote our computer programs, Alan Lewis, who performed the visual examinations of our subjects, and George Endler, Jr., who drafted our figures. Requests for reprints should be sent to Ethel Matin, Department of Psychology, C. W. Post Campus, Long Island University, Greenvale, NY 11548.

gestion was based on the discovery that the distribution of the number of cortical cells as a function of spatial frequency in the macaque roughly resembles that animal's psychophysical CSF, which is similar to the human CSF (see De Valois, Albrecht, & Thorell, 1982, Figure 6, and related discussion).² In support of this interesting idea, we call attention to an earlier study of the distribution of cells as a function of spatial frequency in the visual cortex of the cat (see Movshon, Thompson, & Tolhurst, 1978, Figure 3). The latter distribution, which peaks at a very low spatial frequency (near .9 cpd), is very different from the macaque distribution in De Valois et al.'s Figure 6. However, it bears a marked resemblance to the cat's behavioral CSF, which also peaks at a very low frequency (Campbell, Maffei, & Piccolino, 1973).

De Valois, Albrecht, and Thorell's (1982) discoveries provide an interesting way to test the holographic orientation discrimination model independently of the oblique effect that originally gave rise to it. Specifically, the model predicts optimal performance at the medium spatial frequencies, where De Valois et al. found many neurons, and poorer orientation discrimination at the low and high frequencies, where cells are sparse; that is, it predicts an orientation sensitivity function (OSF) similar to the CSF. Accordingly, in Experiment 1, we attempted to test the theory by measuring orientation JNDs with small disk-shaped sinusoidal gratings that ranged in frequency from 1.80 to 17.64 cpd. As will become apparent in the subsequent discussion, this test proved to be inconclusive.

EXPERIMENT 1

Method

Apparatus. Stimuli were presented through a monocular optical system that consisted of two channels combined with a beam splitter. Light for each channel was generated by a tungsten halogen source and was diffused by opal glass. In one channel, the stop was a round hole with sharp, clean edges, visible at all times except when a sinusoidal grating in the other channel was flashed. The purpose of the blank field formed by this stop was to maintain light adaptation and to control fixation. In the second channel, the stop was one of the six sinusoidal gratings ranging in spatial frequency from 1.8 to 17.6 cpd. The gratings were fastened to a metal holder with a round hole identical to the one provided in the adaptation channel. The holder was mounted on a power turntable with a stepper-driven motor (Klinger Scientific, Type UR-100, P/8) interfaced to an Apple II microcomputer. The stop could be positioned with an accuracy of .05° of rotation.

The stops in both channels were mounted 465 mm from the observer's eye, at which distance the field of view subtended a visual angle of 2.5°. By appropriate choice of neutral density filters, luminance of the adaptation field was equated to the space-average luminance of the grating (19 cd/m²). Contrast of the grating was 60%.³ By careful positioning of baffles to eliminate stray light and by accurate superimposition of the adaptation and test fields, all extraneous cues about orientation were eliminated. The subject saw the grating or the adaptation field on an otherwise completely contourless surround.

Subjects. Three women served as observers, each viewing the stimulus monocularly with her right eye. The subjects were refracted for the 465-mm viewing distance and fitted with corrective lenses. Observer A was corrected for a myopia of -.5D and an astigmatism

of -.5D, axis 180° in her viewing eye. Observer B was corrected for a myopia of -.25D and an astigmatism of -.5D, axis 20°. Observer C was corrected for a myopia of -.5D and an astigmatism of -.75D, axis 90°. When the study began, the psychophysical experience of the subjects varied from highly practiced (Observer A) to no practice at all (Observer B).

Procedure. Using procedures that require the presentation of only one stimulus per trial (see Matin & Drivas, 1979, for details), we measured the subjects' orientation discrimination thresholds at six spatial frequencies (from 1.8 to 17.6 cpd) and in two orientation neighborhoods, 90° and 45°, subsequently referred to as reference orientations (ROs). Only one frequency was used throughout an entire block of 20 trials. The grating was presented for a duration of 200 msec per trial at a position either clockwise (C) or counter-clockwise (CC) of a fixed RO. Three values of angular separation between the C and CC orientations (henceforth called separation values) were selected, on the basis of pilot studies, to yield expected proportions of 60%, 75%, and 85% correct responding at each RO and each spatial frequency. Because the pilot studies showed that the RO had a strong influence on orientation discrimination, whereas spatial frequency had little, if any, effect, each subject was assigned a set of three separation values at the 90° condition and another set of three values at the 45° condition, regardless of the spatial frequency of the grating stimulus. As was expected from the literature on the oblique effect, all subjects required larger angular separations at 45° than at 90°.

An experimental day consisted of six sessions. Each session was preceded by a 2-min adaptation period followed by six blocks of trials, one block for each of the three separation values at each of the two reference orientations. The computer began each block by presenting four identification trials to permit a preview of the two slants presented in that block. On the first and third identification trials, the grating appeared in the C orientation relative to a fixed RO; on the second and fourth trials, it appeared in the CC orientation. Twenty data-gathering trials followed. On each of these, the subject received a warning tone followed by the 200-msec flashed grating, which was randomly presented at one of the two possible orientations straddling the RO. After an 800-msec period in which the subject was required to respond either clockwise (c) or counter-clockwise (cc), an auditory feedback signal was sounded identifying the physical orientation of the stimulus as C or CC. If the subject failed to press one of the two response switches in the allotted time, or if both switches were pressed simultaneously, the trial was aborted and replaced by an extra trial.

Experimental design. Data were collected for a total of 24 experimental days, during which the basic experimental design was replicated four times. One replication consisted of 6 experimental days and yielded a measure of discriminability for each of the 36 experimental treatments (3 angular separations at each of the 2 ROs and 6 spatial frequencies). Each day contained six sessions, throughout which only one randomly assigned spatial frequency was presented. A session consisted of six blocks of trials arranged in two sets. For the first set of three successively presented blocks, stimuli were presented at one of the two ROs, 90° or 45°; the other orientation was used in the second set of three blocks. Each of the three blocks in a set corresponded to one of the three separation values assigned to the specified RO. In order to counterbalance possible sequencing effects, a Latin square was used to control the occurrence of separation values within and across sessions. ROs were alternated across sessions and days.

Results

Stimulus-response matrices. For each replication and each subject, the raw data consisted of 36 2×2 stimulus-response matrices, one for each of the possible combinations of spatial frequency × reference orientation × separation.

ration value. The entries in the cells were the four estimated conditional probabilities: $P(cc/CC)$, defined arbitrarily as a hit; $P(c/CC)$, a miss; $P(cc/C)$, a false alarm; and $P(c/C)$, a correct rejection. Assuming Gaussian distributions of equal variance, the signal detection discriminability index (d') was calculated for each stimulus-response matrix (Green & Swets, 1974).

Psychometric functions. We expressed d' as a function of separation at each orientation $\times$ spatial frequency combination to yield a total of 12 psychometric functions per replication. These were fitted with linear functions by the method of least squares. Slopes of the functions were used as the measure of sensitivity to orientation (for rationale, see Matin & Drivas, 1979). The slopes were calculated for each combination of orientation and spatial frequency for each subject and each of four replications. Mean slopes and standard errors over the four replications are plotted in Figure 1, which has the slope on the left vertical axis. For ease of comparison with the more traditional JND, reciprocal of the slope is shown on the right axis.

As is apparent in Figure 1, the oblique effect appeared in each subject; that is, orientation sensitivity was greater at 90° than at 45° . However, there was no systematic ef-

fect due to spatial frequency. An analysis of variance confirmed the visual impressions: The orientation factor was highly significant (Observer A, $F(1) = 36.56$, $p < .001$; Observer B, $F(1) = 148.96$, $p < .001$; Observer C, $F(1) = 97.92$, $p < .001$) and the spatial frequency factor was clearly insignificant (Observer A, $F(5) = .42$, $p = .83$; Observer B, $F(5) = .98$, $p = .44$; Observer C, $F(5) = 1.57$, $p = .19$).

Discussion

As outlined in the introduction, the holographic model implies optimal orientation discrimination at the medium spatial frequencies, where there are many orientation-tuned cells, and poorer performance at the low and high frequencies, where cells are sparse. In effect, the model predicts an OSF similar to the well-known CSF. The flat OSFs in Figure 1 are obviously contrary to this expectation. Accordingly, we were initially inclined to dismiss the model as fundamentally unsound. Such a conclusion is unwarranted, however; a more careful evaluation of factors that could influence the form of the OSF shows why a flattening of the functions could have occurred under our particular experimental conditions even if the number-of-neurons theory, with its predictions about the effects of spatial frequencies, is essentially correct.

Basically, our reasons for suggesting that the present experiment did not provide a critical test of the theory derive from the possibility that De Valois, Albrecht, and Thorell's (1982) distribution of cells as a function of spatial frequency was not representative of the cells involved in the discriminations made in our study. The reasons for this do not revolve around possible differences between humans and macaques. Indeed, we are persuaded that the two visual systems are essentially comparable, and we will treat them as such for the purpose of this analysis (see De Valois, Morgan, & Snodderly, 1974). Nor do we think the result could reasonably be attributed to the possibility that the psychophysical method we used lacked sensitivity and was therefore unable to reflect the neural distributions. In fact, the latter possibility can be dismissed for the following reason: A comparison of the macaque's neural meridional anisotropies (Figure 5 in De Valois, Yund, & Hepler, 1982) with that animal's neural cellular distributions as a function of spatial frequency (Figure 6 in De Valois, Albrecht, & Thorell, 1982) shows much more pronounced neural frequency differences for the latter case than for the former. The model, therefore, actually predicted a spatial frequency effect that would be larger than the oblique effect. Because the data for all subjects showed a pronounced oblique effect despite the small corresponding neural anisotropy in the macaque, there seems to be no doubt that the method used was sufficiently sensitive to reflect the much larger spatial-frequency-dependent differences in numbers of neurons.

Nonetheless, there is a very good reason for questioning our initial assumption that the cellular distributions in De Valois, Albrecht, & Thorell (1982) can be regarded as representative of the cells involved in orientation dis-

Figure 1. Results of Experiment 1. Orientation sensitivity (slope of the psychometric function) as a function of spatial frequency for 3 observers. Each data point represents the mean of four slopes obtained at each orientation. The bars represent ± 1 SE. The reciprocal of the slope (right vertical axis) can be treated as the just noticeable difference (JND).

criminations under our experimental conditions. De Valois et al. employed large rectangular gratings, whereas the gratings in our experiments were disk-shaped and relatively small (2.5° in diameter). We chose disks to avoid the cues to orientation produced by straight edges between the stimulus and the background. However, the following considerations suggest that the disks, while solving one problem, might well have created another. Because the center cycle of a disk-shaped grating is longer than the cycles to the left and right, and because orientation discriminations are known to improve with stimulus length (Orban, Vandenbussche, & Vogels, 1984; Westheimer, 1981), a threshold in the present experiment was not necessarily determined by the entire grating. It may have been determined by the grating's center cycle, which has a broad Fourier spectrum. If this were the case, the recruitment of neurons with tuning functions peaking at spatial frequencies considerably removed from the frequency of the grating could be expected, with a resultant flattening of the OSF.

To explore this possibility, we performed a second experiment, in which we compared orientation discrimination thresholds using the six grating stimuli employed in Experiment 1 and six corresponding bar stimuli, each consisting of its grating's center cycle.

EXPERIMENT 2

Method

The basic experimental design, daily procedure, and method of analyzing the data were similar to those employed in Experiment 1. However, each replication required twice as many running days, because each experimental day with a grating was followed by a similarly designed experimental day with a bar. The bar stimuli were constructed from a set of photographic transparencies of sinusoidal gratings by masking all cycles save the center one with black tape. Two of Experiment 1's subjects (Observers A and B) were used again in Experiment 2. Three replications of the basic design were completed by Observer B; Observer A, whose data were more variable, completed four replications.

Results

The results of Experiment 2 can be seen in Figure 2, which is a plot of orientation sensitivity (slope of the psychometric function) versus spatial frequency for the bars and the gratings at two ROs, 90° and 45° . At all spatial frequencies and at both ROs, orientation sensitivity for both subjects was similar for bars and gratings. As was the case in Experiment 1, there was a large oblique effect and no systematic effect due to spatial frequency.

A four-way analysis of variance for each subject confirmed the highly significant oblique effect (for Observer A, $F(1) = 71.67$, $p < .001$; for Observer B, $F(1) = 118.47$, $p < .001$) and yielded no significant effects due to the grating-bar variable [for Observer A, $F(1) = 2.74$, $p = .1$; for Observer B, $F(1) = .59$, $p = .447$]. Similarly, there were no significant effects due to spatial frequency [for Observer A, $F(5) = 2.4$, $p = .04$; for Observer B, $F(5) = 1.38$, $p = .24$].

Figure 2. Results of Experiment 2. Orientation sensitivity as a function of spatial frequency or bar width for 2 observers.

Discussion

The results of Experiment 2, which show no systematic differences between orientation sensitivity measured with sinusoidal gratings and orientation sensitivity measured with bars consisting of the gratings' center cycles, are compatible with our suggested explanation for the independence of orientation sensitivity and spatial frequency under our experimental conditions. That is, the results are consistent with the idea that sensitivity was not determined by the grating as a whole but rather by the grating's center cycle, with its broad Fourier spectrum. Information from the cycles to left and right of center appears to play no important part in the discrimination.

The questions we raised about the effect of the disk-shaped grating in the present experiment also apply to the results of Caelli, Brettel, Rentschler, and Hilz (1983), the only other researchers who have obtained data on this very basic question. They also used small disks as stimuli for measurements of discrimination thresholds in the two-dimensional spatial frequency domain. Their OSFs were similar to ours in general form, although a slight decrease in sensitivity occurred at the highest frequency. However, at all spatial frequencies, Caelli et al.'s thresholds were

greater than the thresholds in the present experiment by almost an order of magnitude (e.g., their subjects required a difference of approximately 3° to discriminate between two orientations near the 90° meridian, whereas ours required a difference of about $.6^\circ$). Recognizing that their thresholds were considerably larger than those obtained by other experimenters who had used bars or slits, not gratings, Caelli et al. (p. 132) suggested that the distributed nature of the grating might result in reduced orientation sensitivity. However, even if their effective stimulus had been a full grating (not the single center cycle, as the preceding analysis suggested), their explanation for the larger thresholds could not be correct, because we obtained much smaller thresholds with similar stimuli. In our opinion, Caelli et al.'s psychophysical procedure (method of adjustment) was probably the cause of the coarse measurements, although the relatively low contrast they used may have been a contributing factor.

CONCLUSIONS

From our analysis of the results of the present experiments and the results of the related research of Caelli et al. (1983), we conclude that interpretation of the presently available data on orientation sensitivity as a function of spatial frequency is complicated by the artifact introduced by the use of small gratings. In effect, the stimulus actually used for making the discriminations was not really a grating at all. Accordingly, resolution of the theoretical issues raised in this paper must be deferred until further measurements become available.

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NOTES

1. Bouma and Andriessen's (1968) model was designed to account for meridional differences in orientation sensitivity and also for various constant errors of orientation perception. Only the former are considered in this report.
2. In Figure 6 of their paper, De Valois, Albrecht, and Thorell (1982) presented frequency distributions for four classes of cells: foveal X, foveal Y, parafoveal X, and parafoveal Y. Although the four distributions are by no means identical, they all show the high- and low-frequency roll-offs on which our analysis is focused. For simplicity, we make no distinction between them.
3. The contrast calibration was furnished by Arthur Lange and Charles Strohmeier, from whom the gratings were purchased.

(Manuscript received March 29, 1985;
revision accepted for publication November 26, 1986.)