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ORIENTATION SELECTIVITY IN CATS AND HUMANS ASSESSED BY MASKING

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Abstract—A two-alternative, spatial forced-choice procedure was used to measure contrast thresholds for detection of sinusoidal gratings that appeared within one-dimensional random noise. The orientation of the noise was symmetrically varied relative to the orientation of the test grating to derive estimates of orientation tuning at two spatial frequencies for both cats and humans. For cats, orientation tuning (half-width at half-strength) averaged 23 deg while for humans tuning averaged 28 deg. Both species displayed narrower tuning at the higher spatial frequency. In addition, evidence is presented that estimates of orientation tuning may be narrower when only one orientation of noise is presented, due to "off-channel" detection strategies. These estimates of orientation tuning are discussed in terms of the orientation selectivity of cortical neurons.

Cat vision Orientation tuning Grating detection Oblique effect Masking

INTRODUCTION

One of the hallmarks of neurons in cat visual cortex is orientation selectivity (Hubel and Wiesel, 1962): with few exceptions, each neuron responds maximally to a particular contour orientation, with the neuron's response decreasing with deviations from this preferred orientation. Moreover, these orientation selective cortical neurons are arranged in columns, such that cells in neighboring columns exhibit similar, though not identical, orientation preferences. It is generally thought that the orientation selectivity of cortical neurons arises from two sources, the pattern of afferent input from geniculate cells (Hubel and Wiesel, 1962) and intracortical inhibitory connections between neighboring neurons (Blakemore and Tobin, 1972; Daniels and Pettigrew, 1975).

Several lines of evidence point to the existence of neural elements within the human visual system selective for contour orientation. For instance, selective adaptation experiments have found that exposure to contours of a given orientation subsequently increases the difficulty of detecting low contrast contours of that and similar orientations (Gilinsky, 1968; Blakemore and Nachmias, 1971). Similarly, masking studies have found that a low contrast grating is more difficult to detect when it appears superimposed upon a higher contrast, "masking" grating of similar orientation (Campbell and Kulikowski, 1966; Phillips and Wilson, 1984). Further evidence for orientation selectivity comes from subthreshold summation experiments, wherein contours too weak to be seen on their own can facilitate detection of low contrast contours of similar orientation (Kulikowski *et al.*, 1973). Taken together, these perceptual effects strongly support the premise of orientation selective neurons in human vision.

It is tempting to presume that human orientation selective neurons are comparable to orientation selective neurons studied physiologically in the cat. This presumption would be substantiated if it could be shown that orientation selectivity in cat and human vision is similar. Toward this end, the present study employed a masking paradigm to evaluate orientation selectivity psychophysically in cats and to compare the degree of selectivity with that measured in humans tested under comparable conditions.

METHODS

For both cats and humans, a two alternative, forced-choice staircase procedure was used to measure contrast thresholds for detection of sinusoidal gratings. The same displays were used for both and will be described in a single section; procedural details specific to cats and to humans will then be outlined separately.

Apparatus

The observer (cat or human) viewed a pair of matched CRTs (Tektronix 634; P31 phosphor) situated side by side. The viewing distance was 30 cm for the cats and 100 cm for humans. The face of each CRT was masked to a circular area which, at their respective viewing distances, was 16 deg visual angle in diameter for cats and 4.8 deg for humans; the center-to-center distance between CRTs was 18.5 deg for cats and 5.5 deg for humans. The use of circular masks minimizes the contaminating effects of edges on the spatial frequency spectrum of the patterns, by continuously changing the truncation phase of each cycle of the sinusoidal test pattern (Kelly, 1970).

Conventional electronic techniques were used to generate rasters on both CRTs. Before application to the X and Y amplifiers of the CRTs, the signals used to generate the rasters were passed through a sine/cosine multiplier (Picasso Image Generator, rev. 5) which, under computer control, was used to vary the orientation of the raster within 1/3 deg accuracy. One-dimensional, dynamic visual noise could be displayed on both CRTs by feeding the output of an audio noise generator through an electronic filter into the z-axis amplifier of the CRTs. The electronic filter was used to delimit the spatial frequency content of the noise to a one octave-wide band. A sinusoidal test grating could be displayed on either CRT. Presentation of this test grating did not change the average luminance of the display (8 cd/m2). Using programmable attenuators under computer control, grating contrast ($[L_{max}—L_{min}]/[L_{max} + L_{min}]$) and noise contrast (measured in terms of rms voltage—see Stroymeyer and Julesz, 1972) could be varied independently in 1 dB steps.

The noise, which appeared on both CRTs, consisted of *two* orientations symmetrically placed with respect to the test orientation (see Fig. 1). Using an electronic switch, these variations in test and noise orientation were achieved by interleaving successive display frames in the following manner. Frame n displayed one noise orientation, frame $n + 1$ the test grating, frame $n + 2$ the second noise orientation, frame $n + 3$ the test grating, with this sequence repeating. At the overall frame rate of 100 Hz, the repetition frequency for the test grating ws 50 Hz, a value too high for flicker to be perceived. The repetition frequency for each noise orientation was 25 Hz, but since the noise was dynamic (i.e. the bars comprising the noise continuously shifted in phase) flicker associated with this repetition frequency was not apparent. The contrast of the noise in frame n was identical to the contrast of the noise in frame $n + 2$. It should be stressed that the photograph of stationary noise in Fig. 1 does *not* represent the actual stimulus conditions employed in our experiments. Specifically, the "beat" patterns created by adding stationary noise to a stationary grating were not present with the dynamic noise.

Procedures: cats

Specifics of the two-alternative, forced choice behavioral procedure for measuring contrast thresholds in cats are given in detail elsewhere (Blake and Petrakis, 1984). In brief, during daily testing sessions the cat was comfortably housed in a restraining box with a porthole located at one end. By extending its head through this porthole the cat could view a pair of CRT displays. Situated in front of the cat and just below its line of sight were two response keys, one in front of each CRT. Midway between these two response keys was a small metal tube through which controlled amounts of food could be delivered.

On each trial, the computer presented the sinusoidal test grating on one of the two CRTs, with the choice of CRT varied randomly over trials. The grating was introduced gradually over 500 msec, to avoid abrupt transients, and was accompanied by an auditory tone alerting the cat to the grating's presence. The grating remained present until the cat made a response. The cat was trained to touch its nose against the response key, left versus right, in line with the CRT displaying the test grating. The cat received a small food reward following correct responses. Following incorrect responses, however, the cat received no food and had to wait several seconds before the next trial; hence its next opportunity to receive food was delayed. Responses between trials further delayed the onset of the next trial.

To measure contrast thresholds, the contrast of the test grating was systematically varied over trials according to a staircase rule that converged onto the 71% correct level of performance (Wetherill and Levitt, 1965). Initially, contrast was varied in 3 dB steps, but once near threshold step size was reduced to 1 dB. A staircase was terminated following 15 reversals, and the last 6 were averaged to yield an estimate of threshold for that staircase. At least three threshold estimates were obtained for each stimulus condition.

Results were obtained from two well-trained, adult female cats. These animals were on a 23 hour food deprivation schedule and were allowed to eat only during daily testing sessions. Both animals maintained at least 90% normal body weight on this schedule. Owing to complications unrelated to the experimental procedure, one of these cats became ill and died during the very last part of the experiment. For the nine months of testing prior to her illness, however, this cat's performace was equivalent to that of the other animal.

Procedures: humans

The human observer viewed the same CRT displays while seated within a darkened booth; a chin-rest served to fix the viewing distance. Grating presentation and the mechanics of the staircase procedure were exactly the same as those used for the cats, except that staircases were terminated after the twelfth reversal. Observers indicated their responses by pressing one of two buttons. Feedback was provided by following incorrect responses with a longer intertrial interval than that following correct responses. At least two staircase estimates of threshold were obtained for each stimulus condition.

Three human observers participated in this experiment. Two were experienced observers (the authors) while the third was naive. All had normal or corrected-to-normal visual acuity.

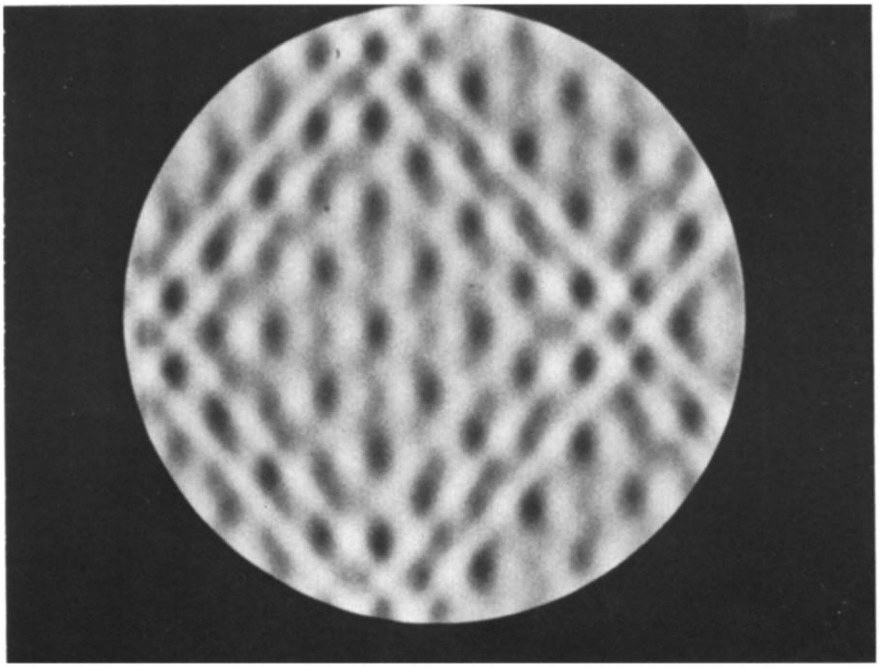

Fig. 1. A photograph illustrating the kind of display used in these masking experiments. A vertical, sinusoidal grating appears embedded within a one-octave band of noise whose contours are oriented 30 deg clockwise and 30 deg anti-clockwise from vertical. For photographic purposes, the noise was stationary, but in the actual experiments it was dynamic.

RESULTS

Rationale

The general aim in this study was to measure the decrease in masking (the reduction in the amount of threshold elevation produced by the noise) as the function of the difference in orientation between test grating and noise. When test and noise orientations are identical, we expect grating detection to be impaired. But when the test grating stimulates mechanisms maximally responsive (i.e. tuned) to orientations other than those activated by the noise, the strength of masking should be reduced. In general, the magnitude of masking furnishes an index of the breadth of orientation tuning of the mechanism utilized for grating detection: as the orientation of the noise deviates more and more from the preferred orientation of the detecting mechanism, the strength of masking will be reduced proportionately. Noise orientations completely outside the detecting mechanism's range of responsiveness should produce no impairment in grating detection.

Growth of masking with noise contrast

We were interested in comparing selectivity for cat and human vision at two orientations (vertical and oblique) and for gratings of low spatial frequency and gratings of high spatial frequency. To make these comparisons, it was necessary to utilize for all conditions noise contrast values producing an equivalent level of masking for the condition where test grating and noise orientations were identical. This insured that any differences in the fall-off of masking could be attributed to differences in orientation tuning of the underlying detecting mechanism.

As a first step, therefore, we measured for each stimulus condition contrast thresholds over a range of noise contrast values, including unmasked thresholds (i.e. thresholds for detection of the test grating in the absence of masking noise). These results were plotted in the form of masking functions, with threshold elevation expressed as the ratio of the masked to the unmasked threshold (a value referred to as "relative threshold elevation"). Representative examples of these masking functions are shown in Fig. 2. For human observers the slopes of these functions averaged 1.04 at the lower spatial frequency and 0.89 at the higher spatial frequency; for cats slopes at low and high spatial frequencies averaged 0.82 and 0.73, respectively. (Correlations for best fit were consistently above 0.90.) Incidentally, for both cats and humans standard errors for unmasked and masked thresholds averaged about 0.05 log-units, a relative threshold elevation value of 1.1.

From these masking functions, we determined for each condition the noise contrast level producing a relative threshold elevation of 7.0 (a value equivalent to a 0.84 log-unit elevation in contrast threshold). This noise level was then used in all subsequent measurements for that condition.

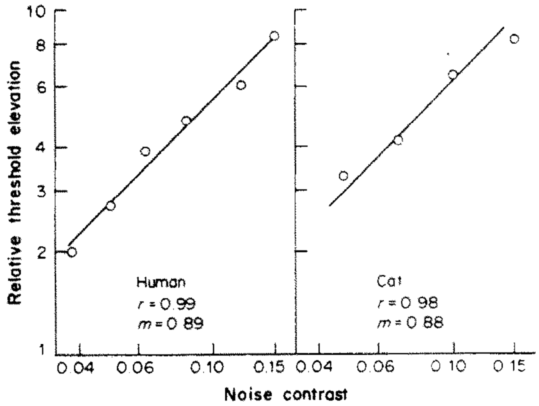

Fig. 2. Representative results for human and cat showing growth in masking (masked threshold divided by unmasked threshold, expressed in terms of relative threshold elevation) with noise contrast. For these data, test and noise orientations were equivalent. Masking functions of this sort were measured for each stimulus condition, and best fit straight lines were derived for each function. For each condition, we determined the noise contrast level producing a seven-fold increase in threshold and used this noise level in the subsequent orientation tuning measurements.

Fall-off in masking with noise orientation

For each stimulus condition, we measured contrast thresholds over a range of masking noise orientations. As illustrated in Fig. 1, the noise consisted of two orientations that deviated symmetrically on either side of the test orientation. We used this type of display, rather than a single orientation of noise, to discourage observers from utilizing an "off-channel" detection strategy. Viewing just a single noise orientation, an observer might optimize performance by relying on a mechanism whose preferred orientation corresponded to some value other than that of the test grating. Noise orientations presented symmetrically on *both* sides of the test orientation encourage the observer to utilize the same mechanism for detecting the test grating, namely the mechanism optimally responsive to the test orientation. It is this mechanism whose orientation selectivity we sought to assess.

Orientation selectivity was measured at two test orientations, vertical and oblique, and at two spatial frequencies. Realizing that cats and humans are sensitive to different ranges of spatial frequencies (Blake *et al.*, 1974), we chose spatial frequencies from comparable regions of the contrast sensitivity function. The low spatial frequency was 0.35 c/deg for cats and 1.25 c/deg for humans and the high spatial frequency was 1.0 c/deg for cats and 8.0 c/deg for humans.

Representative results for cats and for humans are presented in Fig. 3–6. Each graph shows the fall-off in masking with angular deviations from the test orientation. (The threshold elevations at 0 degrees angular deviation are not exactly equivalent for all conditions, because it was impossible to match noise

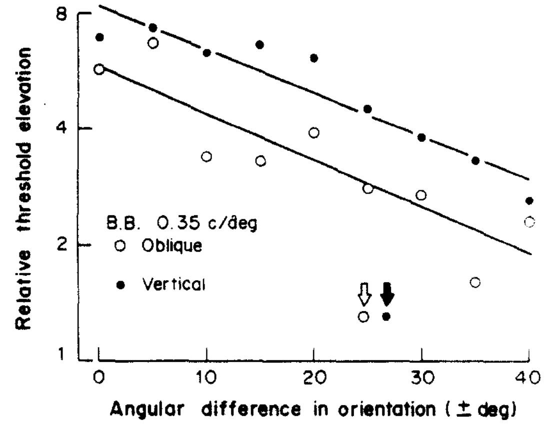

Fig. 3. Fall-off in masking with angular separation between test orientation and masking orientation. The separate symbols show results for two different orientations, vertical and oblique. The test spatial frequency was 0.35 c/deg. The arrows along the abscissa denote the angular value at which masking fell to half-strength. These half-width values were determined from straight lines fit to the masking functions. Data shown are for cat B.B.

contrasts perfectly.) Regression analysis was used to fit a straight line to each masking function; the resulting correlations averaged −0.9 for both species. From this best fit line, the breadth of orientation tuning was defined as that angular deviation where masking fell to half strength. In the figures, half-width values are denoted by arrows pointing to the abscissa.

Several aspects of these results are notable. First, for both cats and for two of three humans tuning was broader at the lower of the two spatial frequencies tested. For humans, half-width values averaged 30 deg at the lower spatial frequency and 25 deg at the higher spatial frequency; for cats, these values averaged 25 and 20 deg, respectively. Second, for the cats there was no tendency for tuning at vertical to be narrower than tuning at oblique; if anything, the trend was in the opposite direction. For humans, however, tuning at vertical was somewhat narrower than tuning at oblique for the higher spatial frequency gratings, averaging 23 deg for vertical and 27 deg for oblique*. Of course, this difference is relatively small, and one of the three observers (the individual whose data appears in Fig. 3) did not show this trend at all.

Average half-width values for cats and humans are summarized in Table 1. We have also estimated half-width values using a procedure that takes into account differences in the slopes of the masking functions (recall Fig. 2) across conditions. For each condition we determined the angular difference between test and mask necessary to produce a reduction in masking equivalent to that produced by reducing noise contrast by 6 dB. The resulting half-width values were within 2 degrees of the values shown in Table 1.

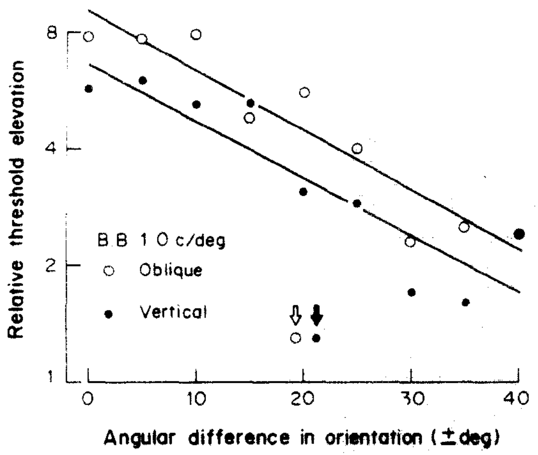

Fig. 4. Same as Fig. 3, except the test spatial frequency was 1.0 c/deg. Data shown for cat B.B.

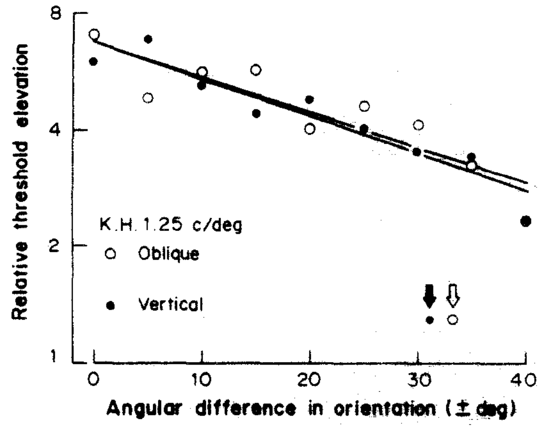

Fig. 5. Same as Fig. 3, except the test spatial frequency was 1.25 c/deg. Data shown are for human K.H.

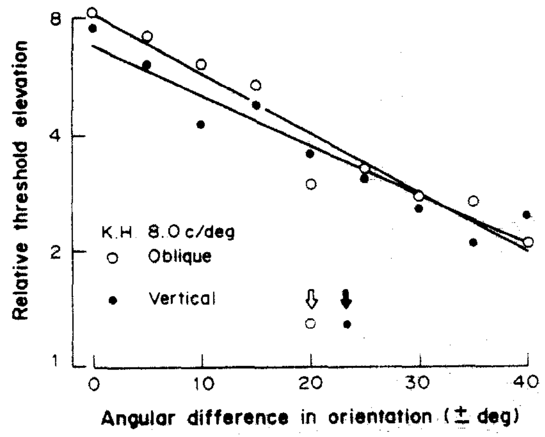

Fig. 6. Same as Fig. 3, except the test spatial frequency was 8.0 c/deg. Data shown are for human K.H.

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*The unmasked thresholds also revealed an oblique effect at the higher spatial frequency in humans (i.e. sensitivity to vertical was greater than sensitivity to oblique); this effect averaged 5 dB among our three observers. No evidence for a threshold oblique effect was observed in the cats at either spatial frequency tested.

Table 1. Average half-width values, defined as the angular difference between test grating and mask at which masking fell to half strength. Results are for vertical and oblique gratings at both low and high spatial frequencies

	Vertical		Oblique	
	Low	High	Low	High
Cat	28	20	22	20
Human	30	23	31	27

Evidence for "off-channel" looking

As explained earlier, we employed symmetrically oriented noise (see Fig. 1) to discourage observers from employing an "off-channel" detection strategy. To elucidate this idea of off-channel detection, suppose an observer is required to detect a vertically oriented grating. In the absence of masking noise, it stands to reason that the observer would rely on that mechanism most sensitive to vertical. Now, suppose the observer is asked to detect that some vertical grating embedded within noise oriented, say, clockwise. Under this condition, the signal-to-noise ratio may actually be greater within a mechanism maximally responsive to an orientation some degrees anticlockwise from vertical. Now imagine that the observer actually utilized this anticlockwise mechanism for detecting the vertical grating, an optimum detection strategy, The resulting contrast threshold would *not* represent the sensitivity of the mechanism of interest (i.e. that mechanism maximally responsive to vertical). As a consequence, the amount of masking would be reduced, the masking function would be shallower, and the estimate of tuning hence narrower. This narrow tuning would *not* represent the orientation selectivity of the mechanism of interest (i.e. that mechanism tuned to vertical). A similar line of reasoning has been developed to account for the narrowness of tuning of frequency selective channels in audition (Patterson and Nimmo-Smith, 1980; O'Loughlin and Moore, 1981).

Based on the arguments advanced above, if an observer were indeed to utilize off-channel detection under conditions of noise masking, orientation tuning estimates should be narrower when measured using asymmetric noise (which would allow off-channel detection) than when measured with symmetrically oriented noise (which eliminates the benefit of off-channel detection). This prediction is based on the reasonable assumptions that: (i) orientation tuning in the underlying detection channel is symmetrical; and (ii) the effects of noise within a single mechanism are additive. To test this prediction, the following experiment was performed.

For one observer, the fall-off in masking was measured as the function of noise orientation. In one condition (symmetric noise), the noise consisted of two orientations; as in the previous experiment, this was achieved by interleaving two orientations every other raster frame. When the orientation of the noise was different from the test, the two noise orientations were symmetrically positioned with respect to the test grating. In the other conditions (asymmetric noise) the noise was oriented either clockwise or anticlockwise with respect to the test orientation; this single orientation was produced in exactly the same manner, only new interleaving the *same* orientation every other raster frame. In all conditions, each raster frame displayed noise whose average contrast was 0.107, a value yielding about a seven-fold increase in contrast threshold when test and noise orientations are identical. The test orientation was always vertical. Details of the staircase procedure used to measure thresholds are the same as before.

Once again best-fit straight lines were computed and estimates of orientation tuning (i.e. half-width at half-height) were derived for each condition. When the noise was oriented either clockwise or anticlockwise with respect to the test orientation (asymmetric noise), the results were equivalent: estimates of orientation tuning were 18 degrees for both conditions. (This equivalence, by the way, supports the above assumption that orientation tuning is symmetrical). When the noise was oriented symmetrically around the test, tuning was broader, with a half-height of 24 deg. This pattern of results is consistent with the idea that an observer may employ an off-channel detection strategy under conditions of masking. Further evidence for off-channel detection is presented in the following paper (Blake *et al.*, 1985).

DISCUSSION

Our motivations for performing these experiments were to compare orientation selectivity in the cat assessed psychophysically with the tuning of neurons in cat visual cortex, and to compare these psychophysical estimates of orientation selectivity in cats with selectivity estimates from humans tested under the same conditions. We will consider these two issues in turn.

Comparison of cat psychophysics and cat physiology

For the cats, the angular difference in orientation at which masking fell to half-strength averaged 23 deg. How does this value compare to physiological estimates of orientation tuning of cells in cat visual cortex? A number of investigators (Watkins and Berkley, 1974; Campbell *et al.*, 1968; Rose and Blakemore, 1974; Orban and Kennedy, 1981; Payne and Berman, 1983; and others) have quantitatively assessed orientation selectivity (though never using noise masking), and everyone agrees that the range of orientations over which a neuron responds varies widely from cell to cell. Some neurons are very narrowly tuned, responding over a range no larger than 15 angular degrees; at the other extreme, some cells respond to a range of orientations spanning 100 degrees or more. Moreover, physiological estimates of orientation half-widths average anywhere from less than 15 to more than 30 deg, depending on cell type (simple vs complex), retinal eccentricity and other variables. It is not very surprising (nor particularly significant), then, that our behavioral estimate of orientation selectivity, 23 deg, falls within the range measured physiologically.

A logically stronger psychophysiological linking hypothesis (Teller, 1984) takes the form of the following question: do psychophysical and physiological estimates of orientation selectivity vary in a comparable fashion with some stimulus manipualtion? To the extent that they do, one is more inclined to believe that the physiological property plays a crucial role in the psychophysical phenomenon. With this in mind, recall from the behavioral data that orientation selectivity was narrower at the higher spatial frequency. Are cortical cells responsive to higher spatial frequencies more narrowly tuned for orientation than cells responsive to lower spatial frequencies? It is commonly found that simple cells are more narrowly tuned than complex cells (Rose and Blakemore, 1974; Watkins and Berkley, 1974; Payne and Berman, 1983), and for a given retinal eccentricity simple cells tend to have smaller receptive fields and, therefore, to respond to higher spatial frequencies. More to the point, Watkins and Berkley (1974) found a strong correlation between receptive field size and orientation selectivity: neurons with smaller receptive fields were more narrowly tuned for orientation*. This finding dovetails nicely with our behavioral result that orientation tuning is narrower at higher spatial frequencies.

Some physiologists find that in and near the area centralis cells preferring vertical far outnumber those preferring oblique (e.g. Payne and Berman, 1983). Others report that simple cells preferring vertical are more narrowly tuned for orientation than simple cells preferring oblique (Rose and Blakemore, 1974). Recall from the footnote on p. 1464, though, that we found no evidence in cats for sensitivity differences between vertical and oblique, a finding consistent with previous behavioral work (Bisti and Maffei, 1974; Vandenbussche and Orban, 1983) and that we also found no differences in tuning between these two orientations. So in this respect, the correspondence between physiology and visual performance is poor. Perhaps cells preferring oblique, though fewer in number, are just as senstitive as those preferring vertical, accounting for the absence of sensitivity differences between these two orientations. It is noteworthy, too, that orientation discrimination assessed behaviorally in cats is better at vertical than at oblique (Vandenbussche and Orban, 1983), consistent with the narrower tuning of cells preferring vertical (Rose and Blakemore, 1974). Evidently, the orientation selective mechanisms in cats isolated using noise masking, which show no oblique effect, are not identical to those utilized for orientation discrimination, which do show an oblique effect.

Comparison of cat psychophysics and human psychophysics

Using procedures other than masking, previous studies of orientation selectivity in humans have found half-width values of 3 deg (subthreshold summation—Kulikowski *et al.*, 1973) and 7 deg (selective adaptation—Blakemore and Nachmias, 1971). These values are considerably narrower than those found in the present experiment. Previous studies that have used some form of masking procedure, however, found half-width values much closer to the present results (Campbell and Kulikowski, 1966; Phillips and Wilson, 1984). Phillips and Wilson (1984) have argued that differences in tuning estimates derived from these various procedures can be reconciled by taking into account spatial probability summation. In addition, our results indicate that off-channel detection can influence estimates of orientation tuning. None of the previous studies of orientation selectivity in human vision have explicitly controlled for this influence.

One notable result from our study is the similarity of orientation tuning in cats and in humans: the numerical estimates of angular half-width were within 5 deg†. Moreover, for both species, tuning was narrower at higher spatial frequencies. We were careful to test cats and humans under comparable conditions, including the selection of spatial frequencies from equivalent regions of the contrast sensitivity functions. Furthermore, the slopes of the masking functions (i.e. the growth in masking with noise contrast) were only slightly shallower for cats, compared to humans. Therefore, the similarity in orientation tuning for cat and for human is no accident and probably reflects the involvement of comparably tuned neural elements in cat and human vision. It is tempting to conclude that these neural

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*Cortical cells in macaque striate cortex are similar to cat cortical neurons in terms of their orientation selectivity (Schiller *et al.*, 1976; Poggio *et al.* 1977), and they exhibit narrower tuning at higher spatial frequencies (DeValois *et al.*, 1982).

†Using an aperture to delimit the size of oriented patterns introduces spectral energy at orientations other than those represented in the stimuli. In particular, orientation bandwidth varies inversely with aperture size, which in turn, could influence estimates of orientation tuning. This effect of aperture size, however, is inversely related to spatial frequency. We calculated the orientation bandwidths of our displays, taking into account spatial frequency and aperture diameters, and determined by how much our empirical estimates of tuning might be in error because of changes in the orientation bandwidths of the stimuli. At the lower spatial frequency (where the effect of aperture size is greater), the estimated error was 4% for cats and 1.7% for humans; at the higher spatial frequency, the estimated error was 0.8% for cats and 0.08% for humans. In other words, our empirical measures overestimate tuning by only a very small amount which is in fact within the standard error of the actual threshold estimates. We feel justified, therefore, in comparing orientation tuning at low and high spatial frequencies for cats and for humans.

elements correspond to the orientation selective cortical cells so thoroughly studied by physiologists.

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