SUMMARY AND CONCLUSIONS

1. Neurons in the visual cortex respond selectively to stimulus orientation and spatial frequency. Changes in response amplitudes of these neurons could be the neurophysiological basis of orientation and spatial frequency discrimination. We have estimated the minimum differences in stimulus orientation and spatial frequency that can produce reliable changes in the responses of individual neurons in cat visual cortex. We compare these values with orientation and spatial frequency discrimination thresholds determined behaviorally.

2. Slopes of the tuning functions and response variability determine the minimum orientation and spatial frequency differences that can elicit a reliable response change. These minimum values were obtained from single cells using receiver operating characteristic (ROC) analysis.

3. The average minimum orientation and spatial frequency differences that could be signaled reliably by cells from our sample were 6.4° (n = 22) and 21.3% (n = 18), respectively. These values are ~0.20 of the average full tuning width at one-half height of the cells.

4. Although these average values are well above the behaviorally determined thresholds, the most selective cells signaled orientation and frequency differences of 1.84° and 5.25%, respectively. These values are of the same order of magnitude as the behavioral thresholds.

5. We show that, because of slow fluctuations in a cell's responsivity, ROC analysis overestimates response variability. We estimate that these slow response fluctuations elevated our estimates of single cell "thresholds" by, on average, 30%.

6. Our data point to an approximate correspondence between orientation and spatial frequency discrimination "thresholds" determined behaviorally and those estimated from the most selective single cortical cells. Interpretation of this quantitative correspondence is considered in the DISCUSSION.

INTRODUCTION

A primary goal of the neurophysiological study of sensory pathways is to establish a neural basis for perception. Barlow (2) has argued that this problem is best approached by examining the response properties of, and interactions between, individual neurons. Consistent with this notion, contemporary neurophysiological models of visual function relate perception to the response properties of individual neurons. This and the accompanying paper (37) examine a neurophysiological model of perceptual discrimination that is based on the response characteristics of individual orientation and spatial frequency tuned neurons in the striate cortex.

The relationship between the spatial selectivity of individual cells and the spatial discrimination abilities exhibited behaviorally is poorly understood. For example, psychophysical orientation and spatial frequency discrimination thresholds can be <0.5° and 0.1 octaves, respectively (1, 9, 22, 47). Cortical cells, on the other hand, appear by comparison to be relatively broadly tuned and can respond, on average, over ~90° and 3 octaves (8, 15,
Seemingly, a large discrepancy exists between behavior and single cells. However, recent models propose that small orientation and spatial frequency changes are coded via changes in the response of the relatively broadly tuned neurons (23, 32, 33, 34, 47, 48, 49). According to this type of model, discrimination is not limited by the width of the tuning function but by the minimum change in stimulus orientation or spatial frequency that can elicit a response change.

The average magnitude of a response change in tuned cortical cells following orientation or spatial frequency changes will be determined by the magnitude of the stimulus change and the slope of the tuning function. However, because the responses of cortical neurons are highly variable (13, 39, 40), the minimum stimulus change that can cause a response change becomes a statistical issue. That is, orientation and spatial frequency discrimination thresholds may be limited by the minimum stimulus change that can cause a statistically reliable response change.

The discrimination models listed above assume that the cortical neurons have sufficiently steep slopes to their tuning functions and sufficiently low response variability to produce statistically reliable response changes to behavioral threshold orientation and spatial frequency changes. However, it has been suggested that they are too broadly tuned (46) and too noisy (45) to achieve this degree of reliability. The present paper examines this particular issue quantitatively for neurons in the striate cortex of the cat. We have evaluated the minimum orientation and spatial frequency differences that will cause statistically reliable response changes in individual area 17 neurons. Our results show that cells produce reliable response changes for changes in stimulus orientation or spatial frequency that are considerably less than their tuning width. Indeed, some cells produce statistically reliable response changes to very small changes in orientation and spatial frequency.

METHODS

Extracellular recordings were made from single units in the primary visual cortex (area 17) of normal adult cats. Details of the surgical procedure have been presented elsewhere (38). Initial surgery was performed under halothane anesthesia. Following the cannulation of a cephalic vein, anesthesia was continued, for the rest of the surgery, with an intravenous infusion of Surital (thiamylal sodium). During recording, animals were paralyzed with Flaxedil (gallamine triethiodide) and artificially respirated with a mixture of 75% N₂O-25% O₂. Rectal temperature and end-tidal CO₂ level were monitored and maintained at ~37.5°C and 4.5%, respectively. The cornea were protected by contact lenses incorporating 4-mm-diam artificial pupils. Corrective lenses were placed in front of each eye to arrange conjugacy between stimuli and retinae.

Action potentials, recorded extracellularly with tungsten-in-glass electrodes (27), were amplified and monitored using auditory and visual display systems. Receptive fields were mapped and orientation and direction selectivity were established qualitatively by manually controlled bright bars projected onto a tangent screen. Following this initial mapping, response properties were examined with computer-controlled drifting sinusoidal luminance gratings presented on a large (30 × 22") bright (300 cd/m²) green raster display (Joyce Electronics, P 31). Optimal orientation, spatial frequency, and temporal frequency were determined qualitatively through the dominant eye. Then, using optimal spatial and temporal frequencies, we examined orientation tuning quantitatively. Gratings of different orientations were presented in a random sequence, while the computer compiled peristimulus time histograms for each orientation. Tuning functions based on the mean firing rates were constructed. A similar procedure was followed to map the cell's spatial frequency tuning.

These initial coarsely mapped tuning curves (e.g., 8 data points) were followed by a more detailed analysis. Typically, only one side of a cell's tuning function was studied in detail. Eight to twelve orientations or spatial frequencies ranging from the peak to the limit of the tuning function were presented in steps as small as 1.4° (orientation) or 0.025 cycles per degree (c/deg) (spatial frequency). In order to obtain accurate descriptions of the response distributions associated with each stimulus (see Figs. 1D and 2D), responses to 80 cycles of each grating were obtained for the majority of cells. The number of spikes generated by each cycle of grating drifting across the receptive field constitutes the measure of response amplitude that is examined statistically. The stimulus gratings were presented in 20 four-cycle blocks or 10 eight-cycle blocks. Each block was presented in a randomly interleaved sequence. When mapping spatial frequency tuning, the temporal frequency was held constant, i.e., the velocity was varied.

For some cells we used a second technique analogous to the two-alternative forced choice (2AFC) method used in psychophysical experiments (5). This experiment was similar in purpose to the pre-
viously described experiment. However, it is not affected by slow fluctuations in responsivity known to occur in cortical neurons (13, 39). Stimuli of 0.5-s duration were presented in pairs, one after the other, separated by a 0.5-s interval during which the screen was blank but of the same mean luminance as the gratings. A reference stimulus was selected from the previously determined detailed tuning functions. All stimulus pairs contained the reference stimulus. The other interval in the pair contained one out of several (6–9) different stimuli. These “test” stimuli differed in orientation or frequency from the reference by varying amounts. Each combination of reference and test stimulus was presented 40 times, and for each presentation the sequence of test and reference was randomized. The responses from this experiment were analysed for each individual presentation and compared in two different ways.

1) The probability that, within a pair (1 S-s time interval), one stimulus would elicit a greater response than the other was calculated. The number of presentations where the test stimulus produced a greater response than the reference were computed for each test-reference combination. Of the presentations where test and reference elicited identical responses, half were added to this number.

2) Response distributions were constructed from all 40 presentations of each test and reference stimulus and subjected to ROC analysis (see below).

RESULTS

The results are presented in four sections. First, we describe the orientation and spatial frequency selectivity and response variability of individual cortical neurons. These data form the basis of the subsequent statistical analyses. Second, we describe a method for determining the minimum orientation or spatial frequency differences capable of eliciting reliable response changes from an individual neuron. Third, we compare thresholds determined from individual cells with behavioral orientation and spatial frequency discrimination data. Finally, we evaluate the effects of slow response fluctuations on our single cell data.

Response selectivity and variance of individual neurons

Using interleaved presentations (see METHODS), we determined both the response mean and variance of each cell to grating stimuli spanning a range of orientations and spatial frequencies. Examples of orientation and spatial frequency tuning data from two complex cells are given in Figs. 1 and 2, respectively. Peristimulus time histograms were compiled for each stimulus condition (Figs. 1A and 2A). These histograms represent the action potentials elicited during each of 128 8-ms intervals. They were accumulated over 20 and 10 2-s presentations in Figs. 1 and 2, respectively. Mean firing rates (spikes/second) for each orientation and spatial frequency are plotted as tuning functions in Figs. 1B and 2B. These functions have full-widths at half-heights of 46° and 1.72 octaves, respectively, which are typical of complex cells in area 17 of the cat (20, 29). Although this type of plot provides a description of the cells’ average response characteristics, it ignores the cycle-to-cycle variability in response amplitude. Cortical neurons characteristically exhibit high response variability. In fact, the averaging of spikes over many repetitions and the random interleaved sequencing became a standard technique precisely to counter this variability (20). Previous investigations (13, 20, 39, 40) have reported that the response variance of cortical cells is roughly proportional to their mean firing rate. Constants of proportionality from 1.0 to 5.0 have been observed for the interleaved presentation technique used in these experiments. We have plotted this relationship in Figs. 1C and 2C using the same log-log format employed by previous investigators (13, 40) who have shown that the relationship

\[
\log V = K \log M + C
\]

where \(V\) = variance, \(M\) = mean firing, and \(K\) and \(C\) are constants, provides an accurate fit to the data. This relationship appears to hold irrespective of what stimulus parameter is altered to change the response strength (13, 37, 40). In Fig. 2C the slope of the best-fitting straight line is \(-1\), and the \(Y\)-intercept (at \(M = 1\)) indicates that the variance is \(\sim 1.5\) times the mean response of this cell. Because of the high spontaneous activity and small range of mean response amplitudes, the relation between variance and mean firing in Fig. 1 is less obvious, but again most of the observed variance was between 1.5 and 2.0 times the mean response.

Although the response mean and variance may seem adequate descriptions of the cells’ signal-to-noise characteristics, the shapes of the response distributions produced by repeated presentations of the same stimulus are not
FIG. 1. Responses of an area 17 complex cell to drifting sinusoidal gratings are shown. A: peristimulus time histograms are shown for gratings of 9 different orientations. The spontaneous activity (Spa) is shown in the lower histogram. Each histogram represents the cumulative neural responses in each of 128 8-ms bins accumulated over 20 randomly interleaved 2-s repetitions. B: mean firing rate is plotted as a function of orientation (degrees). The mean firing rates (spikes/second) were computed by averaging the responses in each histogram in panel A (mean Spa is given by the open arrow). C: response variance is plotted against mean firing rate in double logarithmic coordinates. D: distributions of responses for the 9 stimulus orientations and the Spa. Histograms show the number of stimulus cycles that produced firing of various strengths (spikes/cycle). Each histogram represents the distributions of the responses to 80 cycles of the grating (drift frequency, 2 Hz). Arrows indicate mean firing rate.

specified by these variables. If the distributions are Gaussian and have equal variance, standard parametric statistics can be employed to estimate the probability of one stimulus eliciting a greater or lesser response than another (e.g., 3, 18). However, it is clear from our data
that neither condition is met by the response distributions of cortical cells (see also 13,40). This can be seen directly in Figs. 1D and 2D where response distributions for these two sets of data are shown. Here, for a given stimulus dimension (i.e., orientation in Fig. 1 and spatial frequency in Fig. 2), the number of occurrences of a given response amplitude (number of spikes per stimulus cycle) are plotted. As the stimulus is changed from one that,
on average, produces little response, to the one that elicits the maximum response, there is an accompanying increase in the width of these distributions. The shape of the response distribution also changes. It may appear approximately Gaussian at higher response levels, but it becomes skewed at low amplitudes (see e.g., the lowest and highest spatial frequencies in Fig. 2D). Consequently, any statistical analysis of the response properties of striate neurons must not rely on assumptions of Gaussian distribution or fixed variance.

The distributions in Figs. 1D and 2D serve to illustrate how response variability can limit resolution for both orientation and spatial frequency. For example, consider the cell shown in Fig. 1. A change in stimulus orientation from 135 to 125° (a change ~20 times the human behavioral threshold of 0.5°) produces two response distributions that largely overlap. Therefore, although this cell will tend, on average, to produce larger responses to a stimulus oriented at 125° than to one oriented at 135°, the converse will be true in many instances. Consequently, if response amplitude of this neuron was used to determine which of two orientations (135 or 125) had been presented, many decision errors would occur.

Quantitative determination of the minimum orientation and spatial frequency differences that can be signaled as response changes by individual neurons

From the kind of data provided in Figs. 1B and 2B, it is possible to determine the orientation or spatial frequency changes necessary to produce a certain prespecified criterion change in average firing rate. Such an approach was taken by De Valois et al. (14) when studying wavelength discrimination with monkey LGN cells. However, the chosen response criterion is necessarily arbitrary and the effects of response variability are not taken into account by such an analysis.

Because of the variability in each neuron’s response, estimating the smallest orientation or spatial frequency differences that can elicit a response change becomes a statistical problem. That is, instead of determining the stimulus change necessary to elicit a criterion response, we determine the minimum stimulus change that results in a statistically reliable response change. However, because the response distributions have neither Gaussian nor fixed variance, a statistical analysis that assumes neither is required. Receiver operating characteristic (ROC) analysis meets these requirements. Given the response distributions elicited by two stimuli, it can be used to estimate the probability that an ideal observer can correctly discriminate between the two stimuli using only the response amplitudes as a cue. This probability value is directly comparable to that generated in 2AFC psychophysical experiments. Therefore, ROC analysis results can be directly compared with behavioral data.

The ROC method compares two response distributions of the kinds shown in panels D of Figs. 1 and 2. The four different stages in the analysis are illustrated in Fig. 3. First, for a given pair of distributions, a series of criterion response amplitudes are adopted (indicated by arrows in Fig. 3A). For each criterion, two values are determined from the distributions. First, if the response (spikes/cycle) to a particular stimulus cycle exceeds the criterion, a decision is made that this response is caused by the stimulus, which on average elicits a greater response (orientation 1 in this case). By counting the number of cycles of this stimulus that elicit responses greater than the criterion, a proportion of correct identifications (hits) is determined. Second, because of the overlap of the response distributions, responses elicited by the second stimulus (orientation 2) will exceed the same criterion and therefore be attributed to the first (false alarms). The proportion of false alarms is given by the number of stimulus cycles that result in a response that exceed the criterion in the response distribution for orientation 2. Consider the two response distributions shown in Fig. 3A. By setting the criterion high enough there will be few hits, but no false alarms. As the criterion is lowered, the proportion of hits will increase and eventually reach 1. The proportion of false alarms will also increase and reach 1, although, for the distributions used in this example, they will always be smaller than the proportion of hits. In Fig. 3B we plot the proportion of hits versus the proportion of false alarms for all 10 criteria identified by arrows in Fig. 3A. The resulting function is called the ROC curve. The characteristics of this curve are described in detail by Green and Swets (17) and its application to neuronal responses by Cohn et al. (12).

The ROC method of analysis is applied to
FIG. 3. A: distributions of firing rates (spikes per cycle) are shown for 2 gratings that differ in orientation by 8°. Each distribution was accumulated for 80 cycles of the gratings drifted across the receptive field. The histograms are equivalent to those of Figs. 1D and 2D and depict the number of cycles that produced a given response amplitude (spikes/cycle). The arrowheads indicate the 10 response criteria used in the receiver operating characteristic (ROC) analysis of these distributions. B: the ROC curve plots hit versus false alarm rates for the 10 response criteria shown in A. C: ROC curves obtained from comparing response distributions associated with stimuli that differed in orientation by various amounts: 3° (filled dots), 6° (open circles), 9° (filled squares), 13° (open triangles), and 18° (crosses). For these ROC curves, one stimulus, the reference (R), was held constant and was compared with stimuli of more and more different orientations (1-5) as shown in the inset. D: the area under the ROC curves in C is plotted as a function of orientation difference (degrees). The area under the ROC curve corresponds to the maximum probability of correctly discriminating the 2 orientations based solely on the responses each elicit (see text).

a series of response distribution pairs. For example, in Fig. 3C, we compare response distributions generated by stimuli of different orientations (orientations 1 through 5) with that generated by a reference stimulus (R) (see inset tuning function). A family of ROC curves is produced, one for each comparison (R and 1, R and 2, etc). As the response distributions differ more and become less overlapping, the resulting ROC curves bow further away from the positive diagonal. In order to better understand the significance of this it may be helpful to consider two extreme cases: 1) comparing a distribution with itself and, 2) comparing two completely nonoverlapping distributions. When comparing a distribution with itself, the proportion of hits will equal the proportion of false alarms for whatever criterion we select. Therefore, the resulting ROC curve will be the positive diagonal (hits equal false alarms). For two nonoverlapping distributions, as an initially high criterion is decreased, the proportion of hits will rise up to 1 before any false alarms are encountered. Further drop in
the criterion will not affect the hit rate, but the false alarm rate will increase and eventually reach 1. The ROC curve resulting from this analysis will follow the left and upper boundary of the ROC plot.

A decision process based on two identical distributions would perform at chance level. In the case of nonoverlapping distributions, it would be possible to discriminate the two conditions correctly on every trial, i.e., whichever of the two stimuli elicits the greatest response on a trial is identified as the stimulus that on average elicits the greatest response. When considering the ROC curves in these two cases we find that the areas under the curves, 0.5 and 1, correspond to the expected proportion of correct responses on a 2AFC discrimination task for these two situations.

Finally, we plot the areas under each ROC curve as a function of the stimulus differences associated with each comparison (Fig. 3D). If the stimulus difference is small (e.g., the difference between stimuli 1 and 2), the probability of correct discrimination will be close to 0.5. This probability increases monotonically with stimulus difference. These "neurometric functions" from individual cortical cells can be compared with behaviorally determined psychometric functions that plot the probability that a real observer can discriminate between two stimuli as a function of magnitude of the stimulus difference.

It has been suggested that spatial frequency and orientation discrimination depend on cells that respond maximally to stimuli other than the ones to be discriminated (33, 34). We have examined this claim empirically by means of ROC analysis. Data from two cells are shown in Fig. 4, A and B. The top halves of each figure show detailed orientation tuning functions from two area 17 cells. One cell (Fig. 4A) is somewhat broadly tuned for orientation (one-half width at one-half height of 25.4°) and was therefore sampled at relatively large intervals (9.8°). The other cell (Fig. 4B) is more finely tuned (one-half width at one-half height of 5.0°) and was sampled at small intervals (1.4°). For each cell we have plotted the probabilities of signaling orientation differences correctly at various positions along the tuning function. These are shown in Fig. 4, C and D. Each panel shows three functions. Every sampled orientation was used as a reference. For a given reference orientation, ROC analysis was performed by comparing the reference distribution with the distribution associated with the adjacent orientation (filled circles), the second (open circles) and the third orientation (open triangles) from the reference. As orientation differences increase, the areas under the ROC curves, and, correspondingly, the probabilities of correctly signaling the stimulus differences also increase. The second major effect comes from changing the position along the tuning function. For all three curves and both cells the highest probabilities are found on either side of the peak of the tuning functions. The probabilities near the peaks and at the extreme flanks fall to near chance levels (i.e., 0.5). The central dip reflects the high variability and the flattening of the tuning functions near their peaks. A similar flattening is found at the peak of spatial frequency tuning functions, and our ROC analysis showed an associated dip in the probability of detecting a frequency change.

Figure 4, C and D show that the probability of detecting a given stimulus difference varies with position along the tuning function. Rather than adopt some rule for selecting reference stimuli, we compared all response distributions with all others. For each cell we obtained a family of neurometric functions; each curve having a different reference. Examples of such families are shown in Fig. 5. Figure 5, A and C show neurometric functions for differences in stimulus orientation (degrees) and B and D give functions for spatial frequency differences (percent of the lower frequency in each pair). With many cells there was a range of reference stimuli that produced similar neurometric functions. Two such cells are shown in Fig. 5, A and B. However, for other cells, optimal discrimination was observed only with a single reference stimulus (e.g., Fig. 5D). The outer envelope of a family of neurometric functions such as those shown in Fig. 5 defines the best possible discrimination performance for any given stimulus difference, irrespective of absolute stimulus orientation or spatial frequency. By noting where the envelope function crosses the 0.75 probability level, we obtained a single "discrimination threshold" measure for each cell.

Because of the large number of presentations required, we typically studied only one side of the tuning function in detail. However, both sides of the tuning functions were compared for a few cells. Data for orientation and spatial frequency are given in Fig. 6, A and B,
ORIENTATION AND FREQUENCY DISCRIMINATION

FIG. 4. A and B show detailed orientation tuning functions for one broadly tuned (A) and one narrowly tuned (B) complex cell, respectively. Mean firing rate (spikes/second) is plotted against orientation in degrees (zero = vertical). The dashed line indicates the spontaneous activity level. C and D show, for the same two cells, the probability that a constant orientation difference along the tuning functions can be correctly discriminated (a probability of 0.5 represents chance performance). Probabilities for three orientation differences are shown for each cell: 9.8° (filled dots), 19.7° (open circles), and 29.5° (open triangles) for the broadly tuned cell in C, and 1.4° (filled dots), 2.8° (open circles), and 4.2° (open triangles) for the narrowly tuned cell in D.

respectively. In Fig. 6A we have plotted the minimum stimulus differences necessary to achieve 0.75 correct discrimination performance for clockwise (right) and counterclockwise (left) slopes of the orientation tuning functions. Figure 6B shows similar data for the high- and low-frequency slopes of the spatial frequency tuning functions. For orientation we find that “thresholds” for each slope never differed by more than 20%. On the other hand, “thresholds” associated with the high-frequency slopes averaged about half of those associated with the low-frequency slopes. This reflects the asymmetries of spatial frequency tuning functions observed when plotted on a logarithmic spatial frequency axis (41), i.e., that high-frequency slopes are generally steeper than the low-frequency slopes.

Comparison of behavioral and single cell “thresholds”

Using the high-frequency slope of the spatial frequency tuning functions and either side of the orientation tuning curves, we determined envelope functions to estimate the minimum stimulus differences that can be signaled reliably by each of 22 cells for orientation and 18
FIG. 5. The probabilities that a stimulus difference can be discriminated on the basis of the accompanying response changes are plotted as a function of stimulus difference magnitude. Sets of "neurometric" functions from 4 cells are shown: 2 for orientation (A and C) and 2 for spatial frequency (B and D) differences. Cells A, B, and D are complex and C is simple. Within each panel, individual curves plot probability of correct discrimination for a single reference stimulus. Each panel shows a number of such curves with different reference stimuli all from one side of the tuning function.

FIG. 6. Discrimination thresholds (stimulus differences corresponding to a 75% correct criterion) from both sides of the tuning functions are plotted against each other. Diagonal lines (slopes = 1) mark equal thresholds from both sides of the tuning functions. For orientation (A) we have plotted thresholds determined from the left (counterclockwise) and right (clockwise) slopes. These data are well fit by the diagonal. For spatial frequency (B), thresholds determined from the high-frequency slope are consistently and substantially lower than those determined from the low-frequency slope.
cells for spatial frequency. The distributions of the stimulus differences corresponding to the 0.75 probability criterion are plotted in Fig. 7 as orientation and spatial frequency "thresholds." For orientation, the majority of thresholds are between 2 and 10° (mean = 6.4°). For spatial frequency, all but two fall between 5 and 35% (mean = 21% = 0.28 octaves). In comparison the average tuning widths were 14.4° (one-half width at one-half height) and 1.71 octaves (width at one-half height). Each cell, therefore, is able to signal orientation and spatial frequency differences considerably smaller than the tuning width. Published behavioral orientation and spatial frequency discrimination thresholds for humans [filled arrows (1, 9)], monkeys [open arrow (31)], and cats [inverted triangle (45)] are shown for comparison.

Despite our small samples, we found that some cells are capable of signaling stimulus differences similar to the behavioral thresholds. For orientation, some neurons can signal differences smaller than the lowest reported behavioral thresholds of 2.1° (45) for cats. Furthermore, most cells can signal orientation differences smaller than the earlier behavioral orientation discrimination thresholds reported for cats of ∼5° (4). In the case of spatial frequency discrimination, behavioral thresholds have not been determined for cats. We therefore compared our data with human psychophysics. We found that some cells can signal differences comparable to human discrimination thresholds.

Physiology: long-term variability

ROC analysis allowed us to estimate the discrimination performance of an ideal ob-

![Graph](image-url)
server using the response distributions of individual cells to make decisions about stimuli. However, the ROC method differs from behavioral experiments in one fundamental respect. In a behavioral 2AFC experiment, a decision is based on two simultaneous presentations or two presentations in close succession, whereas the ROC method utilizes response distributions generated over a long recording sequence of ~20 min. This difference would not represent a problem if the system was stationary, i.e., showed some “long-term” variability. Dean (13), Tolhurst et al. (39), and Tomko and Crapper (42) have demonstrated that the firing of single cortical neurons exhibits slow variations over time. The variability demonstrated in Fig. 1, C and D and Fig. 2, C and D may reflect rapid as well as slow variations in response. Therefore, long-term fluctuations may have degraded the performance estimated with the ROC method by inflating the variability.

In order to evaluate the effect of long-term variability on our single cell data, we developed an alternative approach (see METHODS). We estimated the possible discrimination thresholds from the responses of single cells in a way that more closely resembles the psychophysical procedure. In contrast to the ROC method, we compared the number of action potentials from two temporally adjacent stimulus presentations. From 40 presentations we recorded the number of trials that the stimulus, which on average produced the greater response, actually elicited a higher spike activity. This number (plus 50% of trials where both stimuli elicited identical responses) divided by the total number of trials corresponds to the best possible discrimination performance for an observer confined only to observations of the neuron’s response amplitude. Most important is that the temporal sequence used is identical to that of standard temporal 2AFC psychophysical experiments.

Because the decision process is based on comparison of response amplitudes produced by two stimuli within a pair, spanning a 1.5-s time interval, slow changes in responsiveness of a cell will have little effect on these decisions. However, the same data can be subjected to ROC analysis. Therefore, by comparing the results obtained with this method with those obtained from the same data with the ROC method used earlier, we were able to evaluate the effects of long-term variability on the ROC estimates. The two ways of processing the data are illustrated in Fig. 8. In Fig. 8A the response amplitude elicited by the reference stimulus (in this case a 1.2 c/deg grating) and one of the test stimuli (a 0.6 c/deg grating) are plotted in sequence for each of the 40 paired presentations. The responses fluctuate with time, but in a parallel fashion. Within each pair, the lower frequency (open symbols) always produces the higher response. The 40 repetitions of this pair were interleaved with six other pairs and presented at random intervals over a period of 12 min. On average, each pair was presented every 18 s. Figure 8B shows the accumulated response distributions associated with each of these same two stimuli for all 40 trials. These distributions are equivalent to those previously used with the ROC method. Because the two distributions overlap, a performance of <100% correct would be predicted. The ROC analysis gave a probability of correct of 0.88 for this pair of frequencies. However, within each pair, 0.6 c/deg always produces a greater response than 1.2 c/deg (Fig. 8A). Therefore, a decision process based on comparison of responses for each individual stimulus pair could be free of errors.

The effect of long-term variability in elevating the estimated thresholds is also illustrated in Fig. 9. This figure shows two sets of data obtained with the 2AFC stimulus presentation method. Orientation and spatial frequency discrimination data are shown for simple and complex cells in Fig. 5, A and B, and Fig. 5, C and D, respectively. The accumulated perstimulus time histograms for each stimulus pair are shown in panels A and C. These show the accumulated responses over a 2-s period starting with the onset of the reference stimulus. Although the actual order of presentation was randomized, it is shown here reordered for purpose of illustration with the reference stimulus first, followed by a 0.5-s gap and then the variable stimulus. The lowest pair of histograms in each panel was generated with two identical stimuli, i.e., the test and reference stimuli were identical.

As stimulus differences increase, so do the response differences. The left-hand histograms do not change, since each of these are the responses to different presentations of the same
ORIENTATION AND FREQUENCY DISCRIMINATION

FIG. 8. A: the responses to two stimuli differing in spatial frequency (0.6 c/deg, open symbols and 1.2 c/deg, filled symbols) presented 40 times over approximately a 20-min time span. Each stimulus was presented for 0.5 s, and the two stimuli were separated by a 0.5-s period of zero contrast. The order of presentation within the pair was randomized so that 0.6 c/deg was sometimes presented first and sometimes last. Significant fluctuations in firing over the 20-min period are evident, but the responses to 0.6 c/deg is always the stronger. The same data are shown in B where histograms of the response distributions associated with each spatial frequency are plotted. Upper and lower histograms represent the distribution of 0.6 c/deg and 1.2 c/deg, respectively. A large overlap of the distributions can be seen.

reference stimulus. In both cases a reference near the cutoff point of the tuning curve was chosen. Therefore, as orientation or frequency differences increased, the test stimuli approached the peak of the tuning function and the responses they elicited increased accordingly. The resulting neurometric functions are shown in the right-hand portion of the figure. Functions derived from decisions made following the presentation of each stimulus pair (open symbols) consistently lie above those derived from ROC analysis (filled symbols). Both data sets show a monotonic increase in probability of correct discriminations with increasing stimulus difference. For orientation (Fig. 9B), the 0.75 probability threshold obtained with the 2AFC method is 2.7° but 3.7° when determined with the ROC method. For spatial frequency we also found differences between the two methods: 50% obtained with the ROC method and 15% with the 2AFC method. Therefore, when the decision process
FIG. 9. Peristimulus time histograms and neurometric functions are shown for the paired stimulus presentation procedure (see text for details). A and B show data for a simple cell stimulated with gratings of different orientations, whereas C and D show data for a complex cell presented with gratings of different frequencies. In both A and C the left-hand column of the histogram shows accumulated responses to the reference grating that was included in all stimulus pairs. The right portion of the histograms show responses to the variable stimulus. The histograms show responses obtained with ascending differences in orientation (indicated in degrees in A) and frequency (indicated in % in C). B and D plot the probability of correctly identifying the variable stimulus as a function of the orientation (B) or spatial frequency (D) difference. Open symbols represent the probabilities derived from within-pair comparisons, whereas filled symbols show estimates obtained by applying the receiver operating characteristic analysis technique to the same data.

is restricted to each individual pair of presentations, the thresholds for these two cells are reduced by 27 and 70%, respectively.

The 2AFC data were collected from relatively few cells: five cells for orientation and seven cells for spatial frequency. Compared with ROC analysis, the paired-comparison technique gave a lower estimate of threshold from all cells tested, indicating some long-term response variability in all cells. For a threshold criterion of 0.75 probability correct, the average reductions were 25 and 36% for orientation and spatial frequency discrimination thresholds, respectively. We adjusted all the ROC "thresholds" (Fig. 7) with the average of these values in order to compensate for effects of long-term variability. This reduced the average discrimination thresholds of our samples to 4.8° and 13.6%, and the thresholds for the most selective cells become 1.38° and 3.36% for orientation and spatial frequency, respectively. Individual cells differ somewhat in the extent to which they manifest long-term response fluctuations. Since our correction is based on average values, the estimates for the most selective cells may be over- or under-
estimates depending on the actual effects of long-term variability on these particular cells.

**DISCUSSION**

We have attempted to estimate the minimum differences in orientation and spatial frequency that can be signaled as changes in response amplitude by individual neurons in the cat's striate cortex. Our investigation yielded three main results. 1) Single cortical cells can reliably signal orientation and spatial frequency differences considerably smaller than their tuning widths. Some neurons have sufficiently steep tuning curves and sufficiently low response variability to signal orientation and spatial frequency differences that are just detectable behaviorally. 2) Near the peak of the tuning function, the slope is reduced and the variability is at its maximum. Therefore, neurons that respond maximally to a particular stimulus provide little information about orientation or spatial frequency changes in the vicinity of this stimulus. 3) Our results highlight one of the problems of estimating the response variability of individual cells. Methods that accumulate responses from cortical neurons over extended periods are likely to overestimate the response variance (13, 39) and consequently underestimate the reliability with which these neurons can signal small stimulus changes (cf. Figs. 8 and 9).

Caution must be exercised when interpreting the approximate quantitative correspondence between the single cell and behavioral "thresholds". Several important issues must be examined. First, there are factors inherent in our single cell analysis that may have influenced our probability estimates. Responses from cells were studied in anesthetized and paralyzed cats. However, without detailed information on the effect of anesthesia on response amplitude, variability, and selectivity, it is impossible to evaluate the potential effects on our data. Furthermore, we have made several assumptions about the source of information within the neuronal responses. We measured the number of action potentials produced over one stimulus cycle (typically 500 ms). Although we have tried to make the temporal parameters the same as those of representative psychophysical experiments, it is not clear whether information gathered throughout the full 500-ms period contributes to the psychophysical performance or whether equivalent performance could be achieved if the stimuli were confined to a much shorter interval (e.g., 100 ms or less). Although we have summed the spikes over full stimulus cycles, the peak firing rate, onset of the response, interspike interval, clustering of spikes, or some other feature of the response may have been less variable (e.g., 35), more selective (10), or both. Our analysis has discarded all information carried by the distribution of action potentials within the stimulus cycle. This shortcoming appears to be particularly significant for cells whose responses are dominated by their modulation, i.e., simple cells. By discarding any such potential information we may have underestimated the performance possible from the cells' responses.

In addition to these possible systematic errors, our single cell data may have been contaminated by random sampling errors. Using envelope curves to select the highest probabilities systematically (Fig. 5), we may have overestimated performance. Although it is difficult to evaluate this factor, our data suggest that these overestimates are small because there were often several similar neurometric functions obtained with reference stimuli at different points along the tuning functions (cf. Fig. 5, A and B). Conversely, given our limited sample of cells (n = 27) and the observed variability between cells (Fig. 7), it is almost certain that our "best" cells are not the "best" we might have possibly observed.

In addition to the methodological considerations there are a number of theoretical points to consider. In our analysis, we have estimated the performance of an "ideal observer" (12, 17). That is, we have assumed a perfect decision maker that, without error, counts spikes and knows which stimulus on average produces the greatest response. Performance of the decision process in an actual neural system can be degraded by factors such as a failure to count action potentials accurately, failure to remember response amplitudes associated with previous stimuli, or uncertainty along one or more stimulus dimensions (11). For this reason it is possible that the performance of an "ideal observer" having access only to responses from a single neuron
The effect of response variability on a mechanism that compares responses from two or more neurons will depend on the degree of independence of the response variance for each cell. For example, if the response variability of two neurons were independent, the variance of the response difference distributions becomes equal to the sum of the original response distribution variances. Therefore, a stimulus change that produces a reliable response change from each of two individual neurons, may not produce a reliable change in the response difference. However, the response variances of cortical neurons have been shown not to be independent (43, 44). In this case the variance of the difference distribution can be less than that of each neuron individually. Under these circumstances, an orientation or spatial frequency difference too small to produce a reliable response change from an individual cell may produce a reliable change in the response difference between two or more cells. (A similar case can be made for ratios of responses from multiple neurons.) Although correlation of the noise can improve discrimination performance in an individual comparison process, it will reduce the advantages that may be accrued from probability summation across many neurons. Probability summation has been suggested as the reason why behavioral contrast threshold is lower than that of the most sensitive cell (39). However, the close correspondence between single cell and behavioral thresholds suggests that probability summation may play a minor role in orientation and spatial frequency discrimination. The brain may fail to utilize the available information from single cells efficiently. In this case, behavioral performance levels could only be achieved with probability summation.

Although we have measured the smallest orientation or spatial frequency change that can elicit a response change from an individual neuron, identical response changes can be produced by varying a wide range of stimulus parameters (contrast, orientation, spatial frequency, velocity, position, luminance, etc.). Therefore, in isolation, response changes of an individual neuron provide ambiguous information about the stimulus. This inherent ambiguity can be removed by comparing (e.g., subtracting or dividing) the responses of two or more neurons tuned to different but overlapping ranges of the same stimulus dimension (33, 34, 48). The inadequacy of the response changes in individual neurons to explain psychophysical discrimination thresholds is emphasized by the results of two recent studies (5, 7). Spatial frequency discrimination by human observers between parallel and orthogonal gratings result in equal performance. Likewise, orientation discrimination between two gratings of the same spatial frequency and between gratings differing by as much as three octaves is equally accurate. Because of the orientation and spatial frequency selectivity of cortical neurons, two orthogonal stimuli or gratings differing in spatial frequency by three octaves will activate largely different populations of cells. Thus comparison of sequential responses in the same neuron can not be a prerequisite for fine orientation and spatial frequency discrimination.

Our physiological data from cats show that some neurons can signal orientation differences smaller than the cat behavioral thresholds (Fig. 7). Also, in the case of the macaque, Parker and Hawken (30) found some cells that surpassed the behavioral acuity limit of the animals. These results plus previous examples of a close correspondence between behavioral and single cell thresholds (26, 28, 30, 39) eliminate the necessity to postulate massive statistical averaging among cells in order to achieve behavioral resolution. They raise the possibility that threshold behavioral performance depends on relatively few cells.

ACKNOWLEDGMENTS

We thank Joan Slobin for histological and photographic assistance and Ted Cohn for helpful suggestions. Two anonymous referees provided helpful criticism.

This work was supported by National Eye Institute Grant EY-01175 to R. D. Freeman. B. C. Skottun received support from the Norwegian Research Council for Science and Humanities (NAVF).

Present address of A. Bradley: Dept. of Visual Sciences, School of Optometry, Indiana University, Bloomington, Indiana 47405.

Present address of G. Sclar: Center for Visual Science, University of Rochester, Rochester, New York 14627.

Received 3 June 1985; accepted in final form 17 October 1986.
REFERENCES

38. Skottun, B. C. and Freeman, R. D. Stimulus spec-
If you need further assistance, please don't hesitate to ask.