

# Postadaptation orientation discrimination

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An orientational difference of only 0.3–0.5 deg can be discriminated between two gratings or two lines, although psychophysical channels and cortical cells both have comparatively broad orientation bandwidths of 10–25 deg. One proposed explanation for the fineness of orientation discrimination is that, while detection is determined by the most excited orientation-tuned neural elements, superthreshold orientation discrimination is determined by difference signals between these elements [Westheimer *et al.*, *J. Opt. Soc. Am.* **66**, 332 (1976)]. This implies that, if stimulus orientation is changed slightly, the most important elements for discriminating this change will be those whose relative activity changes most, even though the excitation of these elements may be comparatively weak. In accord with this prediction, we found that adapting to a high-contrast grating degraded discrimination for test gratings inclined at about 10–20 deg to the adapting grating while having little effect on the detection of these inclined gratings. For test gratings parallel to the adapting grating, discrimination was improved, but detection was degraded. Either an opponent-process or a line-element model can account for these effects of adaptation. An opponent model can also explain our findings that subjects do not confound orientation change with contrast change and that suprathreshold orientation discrimination is almost independent of contrast, varying by only  $\pm 10\%$  from about 3 to about 25 times contrast threshold. A discrimination model must incorporate reliable storage of spatial frequency, because discrimination was not affected by increasing the interval between grating presentations from 1 to 10 sec. In spatial form vision the relation between postadaptation detection and discrimination is formally similar along the dimensions of orientation and of size, and these two independent spatial discriminations can be modeled in formally similar ways, for example, in terms of orientation opponency and size opponency among multiple local elements, each of which is tuned to a different orientation and/or size.

## INTRODUCTION

Many authors have been struck by the remarkable sharpness of orientation discrimination: the verticality of a short (30-min-of-arc) line can be judged with an accuracy of 0.3 deg,<sup>1,2</sup> a 0.15–0.3-deg difference between the orientations of two lines can be discriminated,<sup>3–6</sup> and an orientational difference of only 0.3–0.5 deg can be discriminated between two gratings.<sup>7,8</sup> For 30-min-of-arc lines, an orientation difference of 0.3 deg corresponds to a maximum spatial difference of less than the cone-to-cone separation, so that orientation discrimination is a form of hyperacuity.<sup>1,2</sup>

The acute 0.15–0.5-deg orientation-discrimination threshold contrasts sharply with the comparatively broad 10–20-deg orientation bandwidth of psychophysical channels<sup>9–16</sup> and with the 14–26-deg bandwidths of most orientation-tuned cortical cells.<sup>17,18</sup> Here we attempt to provide data linking discrimination and detection. Our rationale is as follows. The psychophysical hypothesis that, at an early stage of visual processing, visual information passes through elements with limited receptive fields that are tuned to both orientation and spatial frequency is substantially based on the experimental findings that, after one views a high-contrast grating, contrast-detection threshold is selectively elevated for test gratings whose orientations and spatial frequencies are close to those of the adapting grating.<sup>10,19,20</sup> Therefore we used the same selective adaptation procedure to link discrimination and detection.

We report that adapting to a high-contrast grating improves orientation discrimination while degrading contrast detection for test gratings parallel to the adapting grating. For test gratings inclined at 10–20 deg to the adapting grating, adaptation degrades orientation discrimination but has little effect on detection. Thus adaptation affects both detection and discrimination, but the changes are dissociated along the or-

ientation dimension. The most strongly excited elements determine detection, whereas other, more weakly excited elements determine discrimination. These findings are consistent with the idea that the relative activity of orientation-tuned elements determines orientation discrimination.

## METHODS: EXPERIMENTS 1 AND 2

Sine-wave gratings of mean luminance 17 cd m<sup>-2</sup> were generated on a cathode-ray tube (CRT) (Tektronix model 608 with green phosphor) by electronics of our own design. The stimulus field was circular with a dark surround and, from the 145-cm viewing distance, subtended 3.5 deg. The display was controlled by a microcomputer: Contrast, spatial frequency, and grating orientation were under program control. Mean orientation was vertical for all gratings.

During the test interval, two gratings were presented in succession. A test interval consisted of a 0.6-sec period of zero contrast followed by a grating contrast that ramped upward for 0.2 sec, remained constant for 0.2 sec, and then ramped back to zero for 0.2 sec. There was an interval of zero contrast lasting  $T$  sec; then contrast ramped upward for 0.2 sec, remained constant for 0.2 sec, and ramped downward for 0.2 sec, followed by a 0.2-sec interval of zero contrast before the adapting grating replaced the test grating.

We did not use a fixed reference grating. Instead, when we measured discrimination at a mean orientation of  $\theta$  deg, one of the pair of test gratings had an orientation of  $(\theta - \Delta\theta)$  deg and the other,  $(\theta + \Delta\theta)$  deg. The two gratings were presented in random order. The subject's task was to judge which of the two test gratings had the more clockwise orientation. The method of constant stimuli was used with feedback. A new stimulus was delivered 1–2 sec after the subject's response.

In Experiment 1 the interval  $T$  between pairs of grating

presentations was set at either 1 or 10 sec. Contrast was 50%, and spatial frequency was 12 cycles/deg. The contrast of successive grating presentations was randomly varied by up to  $\pm 2$  dB. In Experiment 2 grating contrast was held constant in any given run but was varied in different runs. The interval between grating presentations was 1 sec. Two naive and one experienced subject were used.

### METHODS: EXPERIMENT 3

In Experiment 3 an adapting grating, generated on a Joyce CRT, was optically superimposed upon the test grating. The adapting grating had the same spatial frequency as the test and covered a circular area of 9-deg diameter. It had a contrast of either 0 or 100% with a mean luminance of  $78 \text{ cd m}^{-2}$ . The adapting grating was counterphase modulated at 0.8 Hz (i.e., 1.6 contrast reversals/sec). Data were obtained for 12- and 5-cycle/deg gratings. The contrast of the test grating was set at five times preadaptation contrast threshold when preadaptation orientation discrimination was measured and at five times postadaptation contrast threshold when postadaptation orientation discrimination was measured. The interval between grating presentations was 1 sec.

Subjects fixated a small cross in the center of the adapting grating for 5 min. Then the adapting grating and the fixation cross were removed during the test interval, the adapting grating was replaced for 10 sec, there was another test interval, and so on. The method of constant stimuli was used with no feedback. We calculated orientation discrimination by fitting a cumulative normal distribution to the data points.

In each run 13–15 values of  $\Delta\theta$  were presented with different values of  $\Delta\theta$  randomly interleaved, and each stimulus condition was repeated 10 times. A run lasted about 35 min. Preadaptation discrimination thresholds were measured similarly, except that the adapting grating had zero contrast. Threshold elevations were taken as  $100[(T_A - T_B)/T_B]\%$ , where  $T_A$  and  $T_B$  were the postadaptation and baseline (i.e., preadaptation) thresholds, respectively.

Two experienced subjects were used. A control experiment carried out on both subjects was designed to measure any change in eye torsion that might occur during the test interval. A few seconds before the end of the adaptation period a narrow vertical bar oriented parallel to the adapting grating was superimposed upon the grating. The bar was illuminated by a single intense xenon flash to leave an afterimage on the retina that would indicate any subsequent change in eye torsion.

### RESULTS: EXPERIMENT 1

In Experiment 1 we investigated whether discrimination was affected by changing the length of time  $T$  sec between the end of the first grating presentation and the start of the second grating presentation. For one subject, mean discrimination threshold was not affected when  $T$  was increased from 1 to 10 sec; mean thresholds differed by only 4%. At the 99% confidence level, thresholds did not differ by more than 36% (180 repeats of each of 7 orientation differences, analyzed in blocks of 10 repeats). For the other subject, mean thresholds were slightly different at  $T = 1$  sec and  $T = 10$  sec. Mean thresholds differed by 37%; there was 90% confidence that thresholds

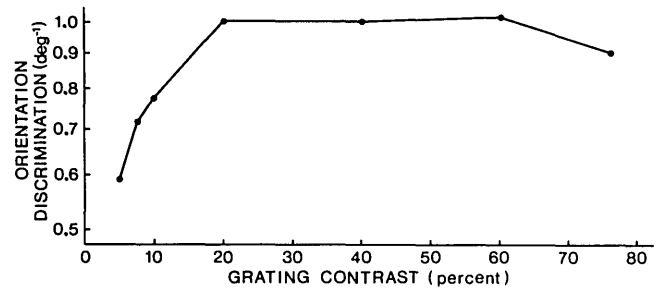


Fig. 1. Orientation discrimination versus grating contrast. Ordinates plot reciprocal of discrimination threshold. Each point is the mean of twenty 4-min runs. Mean orientation was vertical, and spatial frequency was 12 cycles  $\text{deg}^{-1}$ .

were different (120 repeats of each of 7 orientation differences, analyzed in blocks of 10 repeats).

### RESULTS: EXPERIMENT 2

Figure 1 shows that contrast had only a small effect on orientation discrimination over a broad range of contrasts. Discrimination varied by only  $\pm 10\%$  from about 3 times threshold to at least 25 times threshold, although it degraded sharply as grating contrast approached threshold. In this respect orientation discrimination resembles spatial-frequency discrimination.<sup>21,22</sup>

### RESULTS: EXPERIMENT 3

The continuous line in Fig. 2 plots preadaptation discrimination thresholds. They were lowest (0.8 deg) for approximately vertical gratings, although they were slightly skewed toward clockwise orientations. Discrimination thresholds increased progressively as test-grating orientation departed from vertical, reaching 3–4 deg for test gratings inclined at 33 deg. The dashed line in Fig. 2 plots postadaptation discrimination thresholds. Figure 3 brings out our main finding on the relation between postadaptation and preadaptation discrimination thresholds. Threshold elevations and reductions were plotted as positive and negative ordinates, respectively, in Fig. 3. Discrimination thresholds (continuous line) were most elevated at an angle of about 11–17 deg from the adapting grating. When the test grating was parallel to the adapting grating, discrimination thresholds were *reduced*. This reduction was confirmed on a second subject. For comparison purposes, the dashed line in Fig. 3 confirms previous reports<sup>10,19</sup> that contrast-detection threshold elevations were greatest when the test and adapting gratings were parallel and fell to half of this value with the test grating at an angle of about 8 deg to the adapting grating.

The effects of adaptation on discrimination were not large. We maximized them by using an adapting grating that not only had 100% contrast but was also considerably brighter than the test gratings. Postadaptation effects seemed to be clearer when test contrast was low rather than high, possibly because the effects are caused by a change in the balance of orientation-tuned element sensitivities, and this imbalance is negated by saturation at high test contrasts. Adaptation seemed to have less effect on discrimination when test and adaptation gratings had 5- rather than 12-cycle/deg

frequencies, although we made fewer measurements at 5 cycles/deg.

One subject plus a third naive subject confirmed the main finding by using a different experimental procedure. The test grating was always vertical. Postadaptation thresholds were compared after adaptation to a vertical grating and after adaptation to a grating oriented 20 deg counterclockwise from vertical. Test-grating contrast was 75% in each case. The naive subject ran more than 3000 trials on each of the two conditions. Discrimination threshold was lower after adaptation to a vertical than to an inclined grating (*t* test > 95% confidence) even though contrast-threshold elevation is highest at the adapting orientation so that the test grating was

less visible after adaptation to a vertical grating. For the other subject also, threshold was lower after vertical than after oblique adaptation (*t* test > 95% confidence). This confirms the main finding of Fig. 3.

**DISCUSSION**

**Two Orientations Compared by Successive Fixations or Within a Single Fixation**

In everyday vision the orientations of two contours may be compared by successively fixating, first on one and then on the other, so that the two contours stimulate the same retinal region at different times. This corresponds fairly closely to a psychophysical procedure of temporal two-alternative forced choice (2AFC). Alternatively, the orientations of two contours may be compared during a steady fixation, so that the two orientations stimulate different retinal regions at the same time. This procedure corresponds fairly closely to a psychophysical procedure of spatial 2AFC. It has yet to be established whether these two procedures give substantially different estimates of orientation discrimination. The two procedures may even involve different discrimination processes, one a local process that requires the patterns to be compared to stimulate the same retinal region and the other process one that compares two spatially separated targets. In addition, when the two gratings are presented to the same location in quick succession, the temporal 2AFC procedure used in most studies of orientation discrimination can include a stimulus for apparent rotary motion, whereas the spatial 2AFC procedure does not, and there is strong evidence that the visual pathway contains mechanisms specifically sensitive to motion<sup>23</sup> and possibly even to rotary motion.<sup>24</sup> In principle, therefore, the characteristics of orientation discrimination in everyday vision may depend on whether successive fixation or steady fixation is used (and, in laboratory studies, whether temporal or spatial 2AFC is used). This study is restricted to temporal 2AFC.

One way of describing orientation discrimination is in terms of the following four physiological operations: (1) neurally encode the orientation of the first grating, (2) store the neural representation of orientation, (3) neurally encode the orientation of the second grating, (4) compare the neural representations of the two orientations.

One remarkable aspect of orientation discrimination, its high acuity, is well known. No less remarkable, though, is that discrimination threshold changes only slightly or not at all when the interval between the two grating presentations is increased from 1 to 10 sec. This implies not only that the neural representation of the first grating's orientation is sufficiently precise to sustain a 0.15–0.5-deg discrimination threshold but also that this neural representation is stored with little decay in its precision over time to at least 10 sec.

**Orientation Discrimination and Contrast Detection: Opponent-Process and Line-Element Models of Discrimination**

Our main findings are that (1) adapting to a high-contrast sine-wave grating improves orientation discrimination at an orientation parallel to the adapting grating while simultaneously degrading contrast detection; (2) adaptation elevates discrimination thresholds at angles of about 11–17 deg to ei-

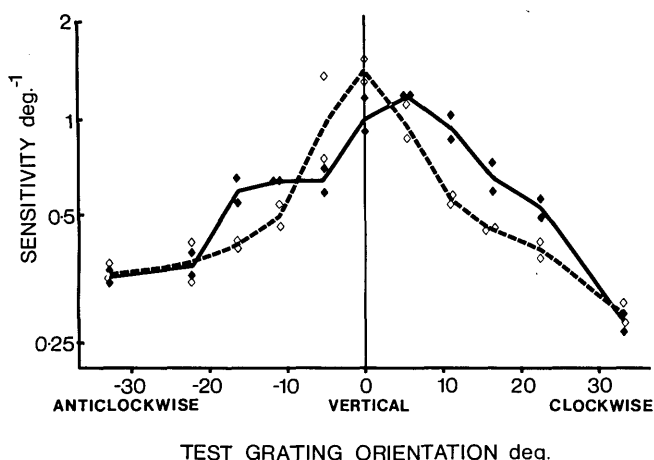


Fig. 2. Acuity of orientation discrimination for different azimuths. Ordinates plot reciprocal of discrimination threshold. Continuous line and dashed line plot preadaptation and postadaptation data, respectively. Each point represents a 35-min run.

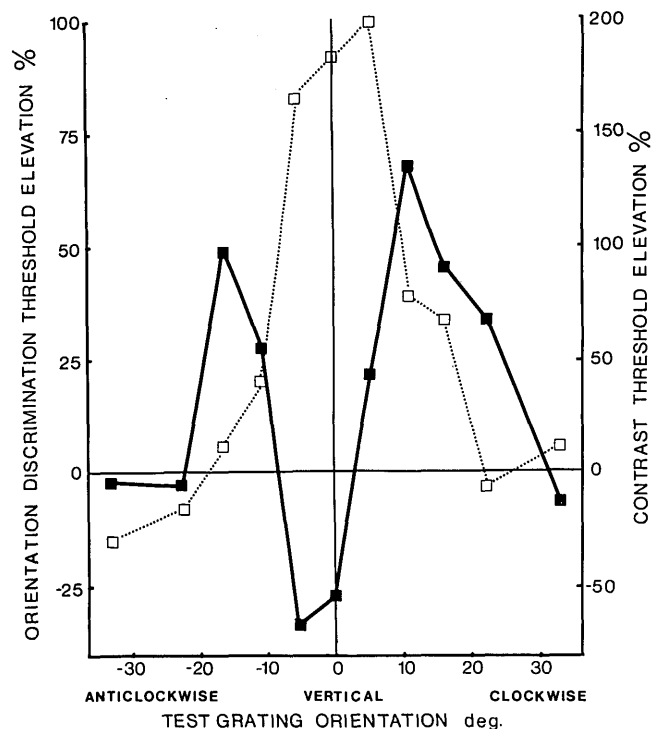


Fig. 3. Postadaptation threshold elevations for orientation discrimination (continuous line) and for contrast detection (dotted line). The adapting grating was vertical (0 on abscissa).

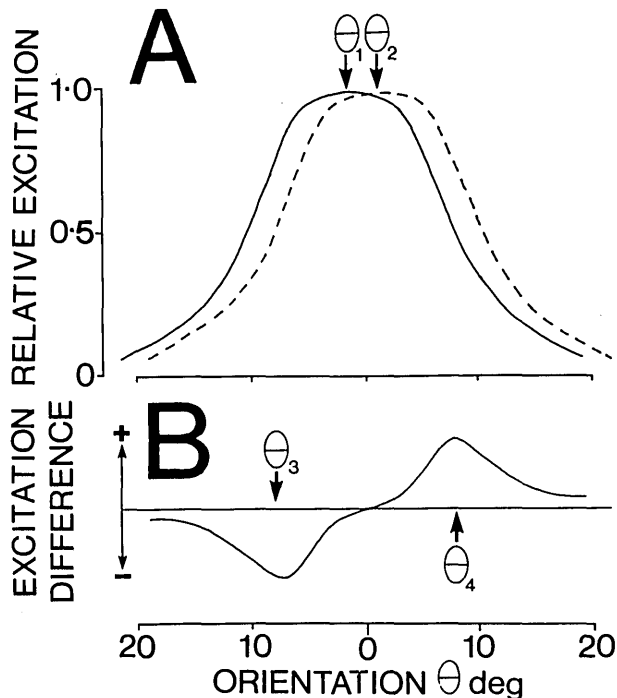


Fig. 4. Detection and discrimination. A, The notional excitation pattern over many orientation-tuned elements produced by a grating at orientation  $\theta_1$  (continuous line) and the slightly different pattern produced by a grating at orientation  $\theta_2$  (dashed line). Zero on the abscissa is vertical. B illustrates the difference between the two excitation patterns in A. The difference is greatest at orientations substantially displaced from the peaks of the excitation curves.

ther side of the adapting orientation, where detection threshold is comparatively little affected.

It has been suggested that contrast detection is determined by the most-excited elements in an ensemble of elements tuned to both orientation and spatial frequency and that adaptation elevates detection thresholds by reducing the excitability of the most-excited elements.<sup>14,20,25,26</sup> Following this line of thought, our finding that adaptation improves discrimination while degrading detection implies that the activity of the most-excited elements detracts from a subject's ability to discriminate the orientations of two clearly visible gratings.

Our finding that discrimination thresholds are most elevated at an appreciable angle to the adapting grating rather than parallel to the adapting grating can be explained by assuming that discrimination is determined by elements whose excitations are comparatively weak. This can be understood as follows.

A suprathreshold grating will excite many orientation-tuned elements to greater or lesser extents. Figure 4A illustrates a notional pattern of relative excitation over many elements. This excitation pattern would be produced by a grating of near-vertical orientation  $\theta_1$  (continuous line), and the slightly displaced excitation pattern (dashed line) would be produced by a subsequently presented grating of slightly different orientation  $\theta_2$ . Figure 4B illustrates that the difference between the two excitation patterns is greatest at orientations inclined to the vertical and that near the vertical the difference is zero. The polarity of the difference curve is inverted if the  $\theta_1$  grating is presented after the  $\theta_2$  grating, so that in principle the difference curve can provide sufficient

information for one to decide whether the second grating was clockwise or anticlockwise to the first grating and thus mediate orientation discrimination.

The improvement of discrimination at the adapting orientation can be explained in terms of signal-to-noise ratio. Adapting to a vertical grating reduces the relative height of the excitation curve for near-vertical gratings ( $\theta = 0$ ) in Fig. 4A without much altering the area under the difference curve in Fig. 4B. Therefore the area under the difference curve is larger in relation to the total area under the excitation curve after adaptation than before adaptation. We suppose that adapting to orientation  $\theta_3$  or  $\theta_4$  would reduce the area under the difference curve relative to the total area under the excitation curve, thus degrading discrimination at the quite different orientation  $\theta = 0$  while having little effect on detection at  $\theta = 0$ .

First consider the idea that orientation discrimination can be explained in terms of the excitation change in a single orientation-tuned element, e.g., the element preferring orientation  $\theta_4$  in Fig. 4B. For single elements that confound a change in grating orientation with a change in grating contrast this idea can be rejected, because we found that orientation discrimination was not significantly degraded when the contrast of successive presentations was randomly varied to the extent that the contrast of successive presentations could differ by a factor of 2. On the other hand, an orientation change and a contrast change could, in principle, be confounded by comparing the change in excitation of two or more elements that are tuned to different orientations (e.g., around  $\theta_3$  and  $\theta_4$  in Fig. 4B) but whose contrast dependencies are identical. This relative-activity idea can explain our main findings in the following way. Figure 5 illustrates the idea that, although the most sensitive element (c) may be the most important for detecting a grating, it plays little part in discriminating small changes in the orientation of that grating. From the point of view of discrimination, its output constitutes noise of greater strength than the signals from the weakly stimulated elements that are most important for discrimi-

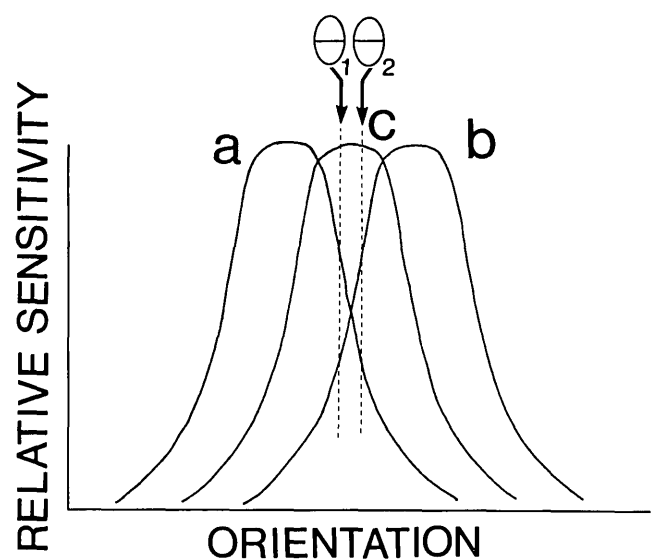


Fig. 5. When the orientation of a stimulus grating changes slightly from  $\theta_1$  to  $\theta_2$  (marked by arrows), the response of the most active of the hypothetical orientation-tuned elements (c) changes negligibly, but there is a substantial change in the relative activations of elements a and b.

nation. After adaptation to a vertical grating, the sensitivity of the vertically tuned element is reduced relative to other elements, thus improving the signal-to-noise ratio of the discrimination signal for near-vertical gratings: a change in grating orientation about the vertical produces a larger fractional change in the total signal from all elements after adaptation than before adaptation. The two elements whose relative outputs change most are the two whose orientation-tuning curves have a greater difference in slope than any other pair at the test orientation (a and b in Fig. 5). In terms of the four-operation description of adaptation set out earlier, our suggestion is that adaptation changes the encoding stages [operations (1) and (3) above] by altering the properties of the visual pathway so that a given change in grating orientation produces a smaller change in the neural output of the opponent elements.

The idea that the most important elements for discrimination are those whose relative outputs change most when a grating's orientation is changed can reconcile the 0.15–0.5-deg acuteness of orientation discrimination with the comparatively broad 10–20-deg bandwidths of orientation-tuned channels<sup>9,10,12</sup> and 14–26 deg bandwidths of orientation-tuned cortical neurons.<sup>17,18</sup>

By analogy with color theory, two ways of formulating this idea are as an opponent-process model or as a line-element model. These two formulations are equivalent in a linear system<sup>27</sup>; in color, at any rate, it has been difficult to find psychophysical data that favor one above the other. Westheimer *et al.*<sup>1</sup> proposed an opponent-process model of orientation discrimination. They suggested that "orientation discrimination is based on neural signals that result from interactions between elements of an ensemble."<sup>1</sup> They compared orientation discrimination with color discrimination "in the sense that Hering's theory of color vision postulates difference signals between pairs of just three classes of elements."<sup>1</sup> Figure 5 indicates how their opponent-process hypothesis can account for our finding that adaptation degraded discrimination at about 15 deg from the adapting orientation. Improved postadaptation discrimination can be incorporated into this model in terms of improved signal-to-noise ratio; the opponent elements driven by a and b will change most, while opponent elements receiving an input from c will receive a strong signal that does not change when grating orientation changes. We suggest that noisy fluctuations in the strong signal from c will produce noisy fluctuations in the outputs of those opponent elements that receive input from c, and this will tend to mask the discrimination signal from the opponent element whose inputs come from b and c. Adaptation will reduce the sensitivity of c and thus improve the signal-to-noise ratio at the output of the opponent elements.

Both opponent-process and line-element models of discrimination have been proposed to explain how signals provided by broadly tuned elements can provide a basis for several acute discriminations<sup>15</sup> including color,<sup>27</sup> motion in depth,<sup>28</sup> and stereoacuity<sup>29,30</sup> as well as the spatial discriminations of size<sup>21,31–33</sup> and orientation<sup>1</sup> that have been called hyperacuties<sup>2</sup> because they can be finer than the intercone separation.<sup>2,3,4</sup> (Other hyperacuties might be explained at least partly along the same lines.<sup>35</sup>) According to this kind of model, discrimination is not directly limited by the tuning bandwidths of the elements. Two important limitations on

the acuity of discrimination are as follows: the shapes of the tuning curves, since this determines the strength of the discrimination signal, and the noise levels of both the elements feeding the opponent stage and the opponent stage itself. As discussed above, acute discrimination is favored if an element's tuning curve attains locally high slopes to each side of the peak, especially if the high slopes are located close to the peak. For a given curve shape, the lower the noise, the more acute the discrimination that can be achieved. Further to this point, a possible advantage of opponent processing can be that noise common to the elements feeding the opponent stage can be suppressed to some extent, for example, in the way that a differential amplifier rejects noise common to its two inputs (see Appendix A). In this context it is of interest that the firing of pairs of cortical neurons can be highly correlated.<sup>36</sup>

Different models of orientation discrimination can be tested against our findings that discrimination is not much different at low and high contrasts (from about 3 times to about 25 times threshold) and that a subject's ability to discriminate an orientation change of only 0.5 deg or so is not confused by a simultaneous 2:1 change of contrast or by a simultaneous change of spatial frequency. These findings weigh against a single-element model and constrain relative-activity models of orientation discrimination: The relative activity of orientation-tuned elements must be computed in such a way that it remains approximately constant when contrast (or spatial frequency) is changed without changing orientation. Appendix A compares the predictions of two versions of the opponent-process model. At, and very close to, psychophysical threshold, presumably only the most sensitive element is active, so that in this special case discrimination can no longer be determined by the relative activity of many elements. From Fig. 3 we suppose that the thresholds of elements a and b in Fig. 5 will not be reached until contrast is about 1.5 to 2.0 times threshold for the most-excited element c in Fig. 5, so that the contrast of the test gratings must be at least twice detection threshold before maximum discrimination is attained.

Wilson attempted to predict our discrimination-threshold elevations on the basis of his line-element model of discrimination, working "blind." We told him our experimental conditions but not our findings. His estimates of the bandwidth and the symmetry of channel-tuning curves were based on his own masking data. He predicted a 46% improvement of discrimination for vertical gratings and a 54% symmetrical threshold elevation at 12 deg either side of vertical, in striking agreement with the data of Fig. 3.<sup>37</sup>

### Perceived Orientation and Orientation Discrimination

The hypothesis that the most important orientation-tuned elements for discrimination are those whose relative outputs change most when a grating's orientation is changed is an idea that can also be reconciled with data on perceived orientation. One proposed explanation for the so-called tilt aftereffect<sup>38,39</sup> is that the perceived orientation of a grating is determined by the weighted mean of all excited channels.<sup>40,41</sup> Adaptation distorts the pattern of subsequent excitation, shifting the weighted mean away from the adapting orientation. Although this is a model of perceived orientation, it can be extended to discrimination if we assume that the orientations of two test gratings can be discriminated when there is a sufficiently large difference between the weighted means of the

excitation patterns that they produce. Elements whose orientation-tuning curves peak near the orientations of the test gratings will tend to stabilize the position of the weighted mean and thus degrade orientation discrimination. This can be understood as follows. The most-excited element will exert the strongest influence on the weighted mean, but because the test gratings fall on the locally flat peak of the tuning curve of the most-excited element, a small change in orientation will not much change the element's excitation. Elements tuned to orientations inclined to the test gratings will have a greater tendency to shift the weighted mean because the test gratings will fall on a steep part of their tuning curves. On the other hand, elements that prefer orientations much different from the test-grating orientation will be weakly excited, so that they can exert little influence on the weighted mean. Thus the most important elements for discrimination will be decided on the basis of two factors: curve slope and sensitivity. Adaptation to a vertical grating will increase the influence on the weighted mean of weakly excited elements tuned to oblique orientations so that a given change in the orientation of a near-vertical test grating will shift the weighted mean along the orientation axis a greater distance after adaptation than before adaptation. By similar reasoning, vertical adaptation will reduce the shift of the weighted mean produced by a given change in test grating orientation about some oblique angle, thus accounting for the data of Fig. 3.

#### Orientation Discrimination and Spatial-Frequency Discrimination

Finally, we draw attention to the analogies between orientation discrimination and spatial-frequency discrimination. The chief effect of adapting to a grating of  $S$  cycles/deg is to increase the just-noticeable spatial-frequency difference between parallel gratings for test gratings centered on about  $2S$ . There is a smaller reduction of spatial-frequency discrimination at  $S/2$  cycles/deg, and discrimination is slightly improved at the adapting frequency  $S$  cycles/deg.<sup>32</sup> Threshold elevations for contrast detection and for spatial-frequency discrimination have the same orientation tuning. These effects can be explained if discrimination is determined not by the most active elements that determine detection but by comparatively weakly excited elements; adaptation improves size discrimination by reducing the excitability of the most-active elements whose signals, from the point of view of discrimination, are noise. The effects of adaptation on spatial-frequency discrimination between sine-wave gratings<sup>32</sup> can be explained if, for a given orientation, spatial-frequency discrimination is determined by the relative activity of multiple elements tuned to different spatial frequencies but all tuned to the same given orientation and all driven from the same point in the visual field.<sup>42,43</sup> The orientation and the size selectivity of these elements correspond to the well-known receptive-field-tuning properties of cortical cells. An opponent-size mechanism could explain why spatial-frequency discrimination is not significantly degraded when the contrast of successive presentations is randomly varied by up to 2:1<sup>32</sup> and why spatial-frequency discrimination is approximately independent of contrast from about twice threshold level to about 30 times above threshold.<sup>21</sup> As is discussed above, an opponent-size mechanism could reduce the effect of noise common to elements feeding the opponent stage (see Appendix A). We conclude that in spatial form vision the rela-

tion between postadaptation detection and discrimination is formally similar along the dimensions of orientation and size and that these two independent<sup>7</sup> spatial discriminations can be modeled in formally similar ways, for example, in terms of orientation opponency and size opponency<sup>31,32</sup> among several elements, each of which is tuned to a different orientation and/or spatial frequency.

#### APPENDIX A: TWO OPPONENT-PROCESS MODELS OF ORIENTATION DISCRIMINATION COMPARED IN RESPECT TO INDEPENDENCE OF CONTRAST AND TO NOISE REJECTION

The visual system's problem is to compute orientation to an accuracy of 0.5 deg or better from the outputs of neural elements, each of which is rather broadly tuned to orientation with half-height bandwidths of about 14–26 deg. Two additional requirements are that a change of orientation be computed independently of a simultaneous change of contrast and of spatial frequency.

If the output of any given element depends on orientation, but not on contrast, then our finding that subjects do not confound an orientation change with a contrast change follows straightforwardly. A pertinent finding is that one kind of orientation-tuned cortical cell behaves in just this way; firing frequency is approximately independent of contrast over a range of at least 10–80% contrast.<sup>44</sup> If the output noise level of such neurons is sufficiently low, it would not, in principle, be necessary to postulate interactions among orientation-tuned cells in order to explain how discrimination thresholds can be as low as 0.3–0.5 deg.

If the output of any given element depends on both orientation and contrast, then the single-element model just discussed fails the requirement that orientation be computed independently of contrast. Furthermore, a single element tuned to both orientation and spatial frequency would confound a change in these parameters. However, for such multiply tuned elements, orientation can be unconfounded from contrast and from spatial frequency by comparing the outputs of two or more elements that are tuned to different orientations but are identically tuned to contrast and to spatial frequency.

Let  $A$  and  $B$  represent orientation-tuned elements with overlapping orientation-tuning curves that respond best to orientations  $\theta_1$  deg and  $\theta_2$  deg, respectively. (Alternatively,  $A$  and  $B$  might each include several elements with a range of preferred orientations.) Suppose that  $A$  and  $B$  feed signals of strengths  $a$  and  $b$  to an opponent element  $D$  whose output  $z$  is a function of the relation between  $a$  and  $b$ . We suppose that  $z$  determines orientation discrimination. An increase of  $a$  relative to  $b$  causes the output of element  $D$  to change, signaling a change of orientation in the  $\theta_2 \rightarrow \theta_1$  direction and vice versa.

Alternative ways of encoding the orientation of a stimulus grating are by computing the difference<sup>1</sup> ( $a - b$ ) and by computing the ratio  $a/b$ . At a physiological level, a mechanism sensitive to the ratio of two inputs is not implausible; neurons that are sensitive to the ratio of two stimulus velocities have been found in the cat's visual cortex.<sup>45,46</sup> Here we compare the difference-signal and ratio-signal models of discrimination in the context of known properties of cortical neurons. Sclar and Freeman's<sup>44</sup> findings are particularly

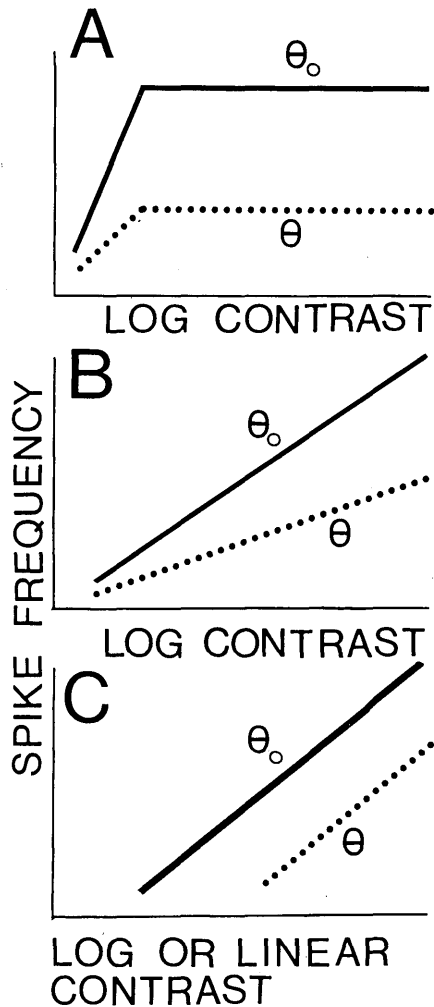


Fig. 6. Contrast dependency of four idealized kinds of neuron. A, Firing rate saturates at low contrast. Saturated response is largest at orientation  $\theta_0$  and less at any other orientation. B, Firing rate proportional to log contrast. Contrast gain (i.e., slope of curve) is largest at orientation  $\theta_0$  and less at any other orientation. C, Firing rate either is proportional to log contrast or varies linearly with contrast. Threshold depends on orientation, but slope does not. Sclar and Freeman<sup>44</sup> describe neurons whose properties resemble A and B rather than C.

relevant. They found that orientation-tuned cortical cells fell into two classes. The first, mentioned above, saturated at a low contrast (Fig. 6A). For the second class, firing frequency was proportional to log contrast over a broad range of contrasts, as had been noted previously,<sup>47-51</sup> but Sclar and Freeman added that the slope of the contrast plot depended on the orientation of the grating stimulus so that the orientation tuning of such cells was consequently almost independent of contrast (Fig. 6B). Let the outputs of two such cells be  $a_\theta$  and  $b_\theta$  when stimulated by a grating of orientation  $\theta$ . Then

$$a_\theta = C_\theta(\log c - \log c_{a=0})$$

and

$$b_\theta = K_\theta(\log c - \log c_{b=0}).$$

According to the ratio-signal model of discrimination, the output of discrimination stage  $D$  is given by

$$z = a_\theta/b_\theta = C_\theta/K_\theta,$$

if  $\log c \gg \log c_{a=0}$  and  $\log c \gg \log c_{b=0}$ , so that the discrimination signal  $z$  is independent of contrast if outputs  $a$  and  $b$  are sufficiently above threshold. This agrees with the experimental data. The difference-signal model, on the other hand, is not consistent with the psychophysical data if we assume that neural firing is proportional to log contrast, because the difference-signal model predicts that the discrimination signal  $z$  should increase with log contrast.

However, the ratio model is not necessarily preferred over the difference-signal model for elements whose contrast dependencies are other than those illustrated in Fig. 6B. For example, the ratio- and difference-signal models are both indifferent to contrast over the 10–80% saturated range of contrasts for Sclar and Freeman's first class of cells (Fig. 6A). For elements whose outputs follow Fig. 6C, then the difference-signal model predicts that discrimination will be independent of contrast over a broad range of contrasts, while the ratio-signal model fails: However, cortical neurons reported so far do not generally behave as shown in Fig. 6C.

Now we consider the effect of noise on discrimination. Opponent processing has the feature that noise in the first-stage outputs  $a$  and  $b$  can be partially or even completely suppressed by the opponent element. If discrimination is limited by noise in outputs  $a$  and  $b$ , suppression of part of this noise allows the possibility of more acute discrimination. On the other hand, this point has little importance if discrimination is limited by noise at the opponent stage. Unfortunately, few or no physiological data are available on the three crucial points: the degree of correlation between the noise level of adjacent orientation-tuned neurons; the dependence of noise level on the firing frequency of orientation-tuned neurons; the balance between the noise levels of orientation-tuned neurons and more-central orientation-opponent elements. If the level of common noise in adjacent neurons tuned to different orientations is independent of firing level, then a difference-signal element will eliminate this common noise. On the other hand, variance has been reported to increase with firing frequency,<sup>48,49</sup> so a ratio-signal element might be more effective in reducing common noise. Similar considerations presumably apply to opponent-size models of spatial-frequency discrimination.<sup>31,32</sup>

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35. Comparing postadaptation thresholds for discrimination and detection might be useful in studies of hyperacuity other than orientation discrimination. For example, if, as has been suggested,<sup>2</sup> orientation discrimination is involved in vernier acuity, the findings reported here imply that adapting to a grating parallel to the vernier lines would enhance vernier acuity, whereas adapting to a grating inclined to the lines would degrade vernier acuity, the most effective inclination depending on gap width.
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42. This idea can also account for acute discrimination of small changes in the separation of two closely separated blurred lines. However, for two narrow lines whose separation is considerably more than the line width, the idea of opponency between elements of different receptive field size that receive input from the same retinal point does not seem to be adequate. In this case a possible discrimination mechanism involves opponency between elements that receive inputs from different retinal locations. One such element would receive inputs from two small retinal areas located a distance  $x_1$  apart; we suppose that the element would respond strongly when both areas were simultaneously stimulated. A second similar element would receive inputs from two small retinal areas located distance  $x_2$  apart. The relative activity of these two elements would be acutely sensitive to a small change in the separation of two thin stimulus pages and would distinguish an increase from a decrease of separation. We suppose that these two kinds of opponent mechanism coexist and that one or other dominates in different stimulus situations.
43. As it stands, this hypothesis does not account for the finding that spatial-frequency discrimination is the same between parallel and orthogonal gratings.<sup>7</sup> However, it is not necessary that it should be. Our hypothesis covers only the encoding and comparison processes of discrimination [operations (1), (3), and (4) above] and is not intended to describe the storage process [operation (2)]. A hypothesis of storage might appropriately address the question of discrimination between orthogonal gratings.
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