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Size Interactions in the Perception of Orientation

SENSORY EXPERIENCE, ADAPTATION, AND PERCEPTION

FESTSCHRIFT FOR IVO KOHLER

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ABSTRACT

To dissociate the roles of small and large receptive fields in the processing of line orientation, we devised a sawtooth line stimulus where local tilt of the sawtooth segments could be varied independently of overall tilt of the line. Perceived orientation of the overall line varied with the tilt of the segments in a biphasic manner. For small segment tilts (peaking between 5–15°) overall orientation was shifted in the direction of the segment tilt, whereas for greater segment tilts (peaking between 30–45°) there was a larger perceived shift in the opposite direction. The results suggest an interaction between orientation-specific neurons with small receptive fields and those with large receptive fields.

To explain these effects, we developed a model which illustrates that peak orientation shift for a population of large receptive fields is proportional to the slope of the population response profile for small receptive fields. Within this framework, small receptive fields show both excitatory and inhibitory influences on larger receptive fields, and it is possible to estimate the magnitude and orientation selectivity of these influences. The model can account for two powerful illusions of orientation, the Fraser and the Zöllner illusions.

INTRODUCTION

The perception of straightness and orientation in straight lines has been of interest since the earliest years of visual investigation. Purkinje (1819) observed that after prolonged inspection, straight lines were perceived as breaking into

differently oriented segments, and many well-known illusions of the 19-century deal with deviations from perceived straightness (e.g., Zöllner, 1862; Hering, 1879/1942). Purkinje's (1819) observation is of particular interest, because it suggests that straight lines might be processed in terms of small segments whose orientation may be dissociated from that of the line as a whole.

The discovery of orientation- and size-selective cells in the visual cortex offers a fresh approach to the problem. For any given retinal region, there exist many cortical units with different receptive field sizes as well as different preferred orientations (Hubel & Wiesel, 1962). When a long straight line is projected onto the retina, orientation-selective cells with both large and small receptive fields will be stimulated (Fig. 31.1a). Because there is a congruence between local and global orientation in straight lines, the orientation associated with maximum response is the same for populations of neurons with small and large receptive fields. (Figs. 31.1b and Fig. 31.1d).

On the other hand, if the stimulus line is broken up into equal segments, with a local orientation different from that of the configuration as a whole (Fig. 31.2), the distribution of responses will differ for cells with small and large receptive fields. Thus, each group of cells would provide conflicting information as to line orientation (Fig. 31.2b and Fig. 31.2d).

To determine the interactions between orientation signals from cells with large and small receptive fields, we measured the effect of local segment angle
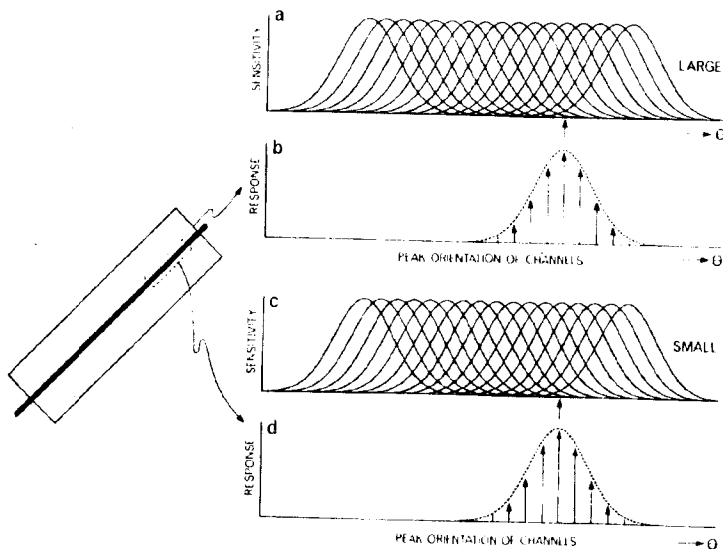

FIG. 31.1.   Single line stimulus and two sizes of cortical receptive field that will be preferentially stimulated by the oriented lines. a) Population sensitivity of a class of cells having large receptive fields. b) response of population a to single line stimulus. c and d) Same as in a and b except for small receptive fields.
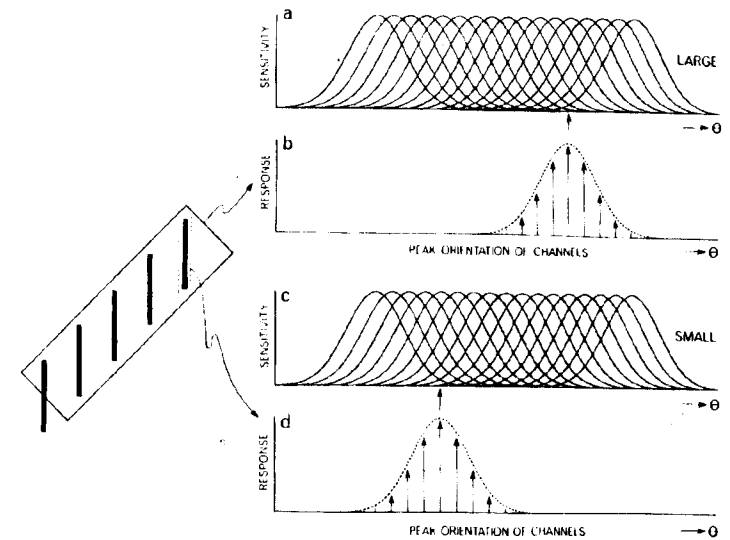
FIG. 31.2.   a) Interrupted sawtooth stimulus used in this study. Note that in contrast to Fig. 1, the optimal orientation for large and small cortical receptive fields is different, and response profiles are shifted relative to each other (compare b and d).

on overall perceived orientation of a segmented line. This approach differs from previous studies of the Zöllner illusion (Gibson & Radner, 1937; Wallace, 1964; Carpenter & Blakemore, 1973; Oyama, 1975), which were concerned with interactions of orientation mechanisms for stimulus elements in *different* (but adjacent) retinal locations. In contrast, our stimulus is designed to examine interactions between orientation mechanisms for stimuli of different sizes in the *same* retinal location.

To anticipate our results, a demonstration of the basic findings are shown in Fig. 31.3. When the angle of tilted segments is small, the overall line appears to
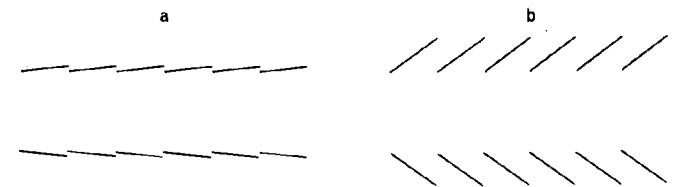

FIG. 31.3.   Two pairs of parallel segmented lines where local orientation differs from the global orientation. a) Line segments are tilted by a small amount, causing a slight shift in perceived orientation of the segmented lines in the same direction as segment tilt. b) Same, except the segments are tilted by a much larger angle. In this case, perceived tilt of the segmented lines is in the opposite direction.

tilt in the same direction as the tilt of individual segments (Fig. 31.3a), while the reverse can be seen when the angle of the individual segments is larger (Fig. 31.3b).

A similar result was reported by Oyama (1975) in the classical Zöllner paradigm; although for most inducing tilts the test line was tilted in the opposite direction to the inducing lines, for small tilts the test line appeared to be tilted in the same direction as the inducing lines. While this result is interesting, it is potentially contaminated by assimilation from spread of excitation within the retina, rather than by interactions between cortical neurons. This supposition is in accord with another of Oyama's (1975) experiments, in which tilted segments were set at different distances from the test line. An assimilation effect at small tilts disappeared for separations greater than 6 arc min, although negative induction at large tilt angles was relatively unaffected by the distance to the test line.

METHODS

Either one or two segmented lines were generated on the face of an oscilloscope screen using an electronic function generator. Angle and number of segments per line could be controlled by varying the amplitude and frequency of a sawtooth waveform. Because the fast phase of the sawtooth was extremely rapid, it was possible to adjust the luminance of the trace so that only the tilted segments were visible. The lines subtended $10°$ in length and, unless otherwise noted, had a luminance of 1 cd/m^2 in a room with dim illumination. The screen had a circular surround and thus could not have been used as an orientation cue. Angle of the segments was related to the amplitude (A) and frequency (f) of the sawtooth by the following expression:

$$\theta = \tan^{-1} (k\ A\ f), \text{ where k is a scaling constant.}$$

The angles used were limited to a range of $\pm 60°$, since beyond this range the sawtooth lines were wider than the gaps between them.

To measure the effect of segment angle two experiments utilized a cancellation procedure and one a matching procedure. In Experiment I, two horizontal configurations with oppositely tilting segments were presented (see Fig. 31.3) and the observer adjusted the angle between these configurations until they appeared parallel. For Experiment II, only one segmented vertical line was visible in an otherwise dark room. The observer had to set the segmented line to perceived verticality without the aid of any visual comparison. (Vertical orientation was used here because it has the best absolute orientation discrimination; Howard, 1981). In Experiment III, the observer set a straight, non-segmented comparison line to be parallel to a single segmented line, again in a horizontal orientation. One experienced and two naive observers were tested.

RESULTS

Experiment I: Pairs of Segmented Lines

In this experiment, two segmented lines with oppositely directed segments were varied in overall orientation until the observer judged them to be parallel. The number of segments was maintained at six and the distance between the centres of the two lines was $4°$. The observer was instructed to move fixation freely over the display and to set the orientation of the global lines to be parallel, without attending to particular positions, and especially avoiding attention to the theoretical line joining the two end points. Four adjustments were made at each segment orientation.

The effect of segment angle on perceived orientation of the overall line is plotted in Fig. 31.4a. Note that there is a biphasic change in orientation of the overall line as the angle of segments is increased. This can be seen for all three observers in varying amounts. Between $5–20°$ there is a small but reproducible shift of orientation towards the angle of individual segments, whereas at larger angles (peaking between $33–45°$), there is a much larger shift in the global orientation in the opposite direction. Similar results for the classical Zöllner illusion have been reported by Oyama (1975).

We were concerned that if judgments were made with regard to the theoretical line joining the extreme tips of the segmented line, judged orientation of the global line would be biased towards the tilt of the terminal segments. This might explain the first part (but not the second part) of the biphasic curve. We therefore conducted the same experiment with the outer halves of the terminal segments removed (see inset, Fig. 31.4b). In this condition the terminal points of the segmented pattern defined a line which always remained parallel to the overall pattern, regardless of the angle of the segments. Figure 31.4b shows that adding this restriction does not diminish the effect. Consequently, the data are in accord with the observer's impression that the judgment can be made without regard to the terminal points.

Experiment II: Single Segmented Line

Because the previous experiments used a pair of oppositely tilted lines, it is possible that the results could be contaminated by an interaction between the tilted segments of one line and corresponding regions of the other line $4°$ away (see Discussion). To deal with this issue, we repeated the experiment with a single vertical segmented line in a dark room where no other visual orientation cues were available. Residual stray light in the room was kept below visibility by light-adapting the observer between trials. Thus, the only available orientation references were gravitational and proprioceptive.

For observer KN the results (Fig. 31.5) are similar to those obtained with the pairs of segmented lines in Experiment I. The curve has the same biphasic
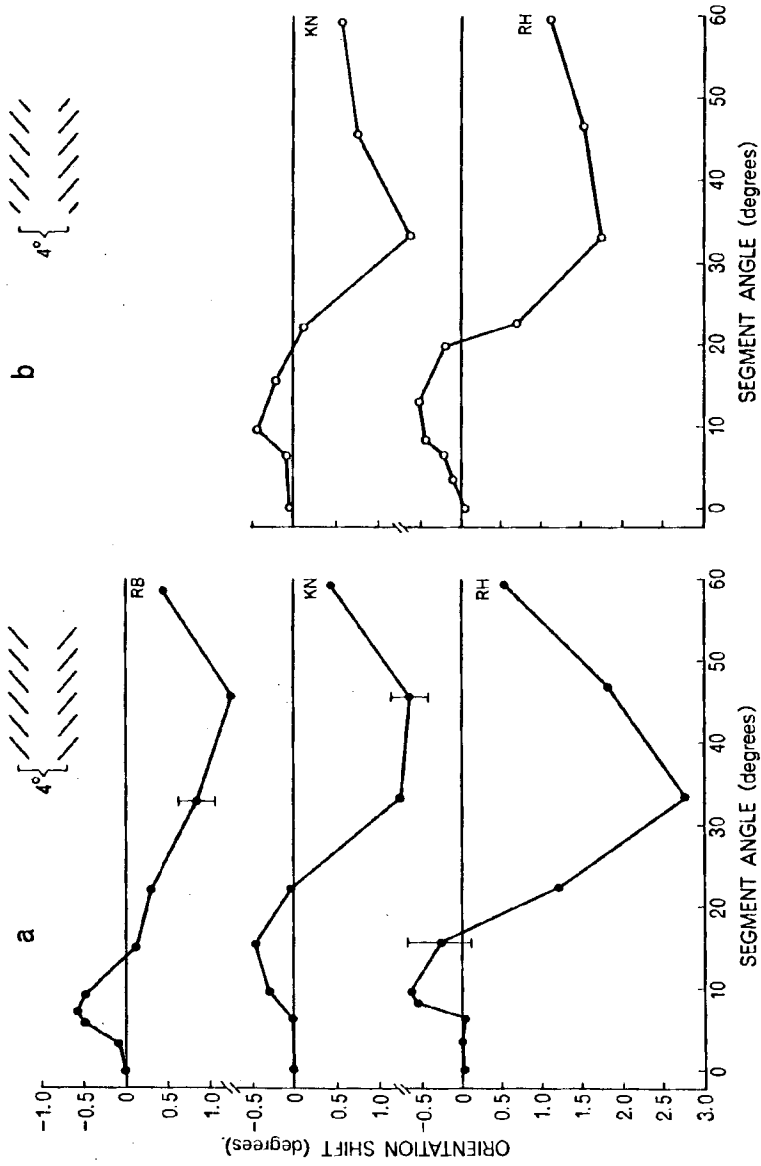
FIG. 31.4. a) Effect of segment tilt on perceived orientation. Minus values indicate that the overall line appears to be tilted in the same direction as the segments, whereas plus values indicate the opposite. b) Similar data obtained with the outer halves of the terminal segments removed, thereby excluding any cues as to the end point of the lines. The distance between the lines was 4°.
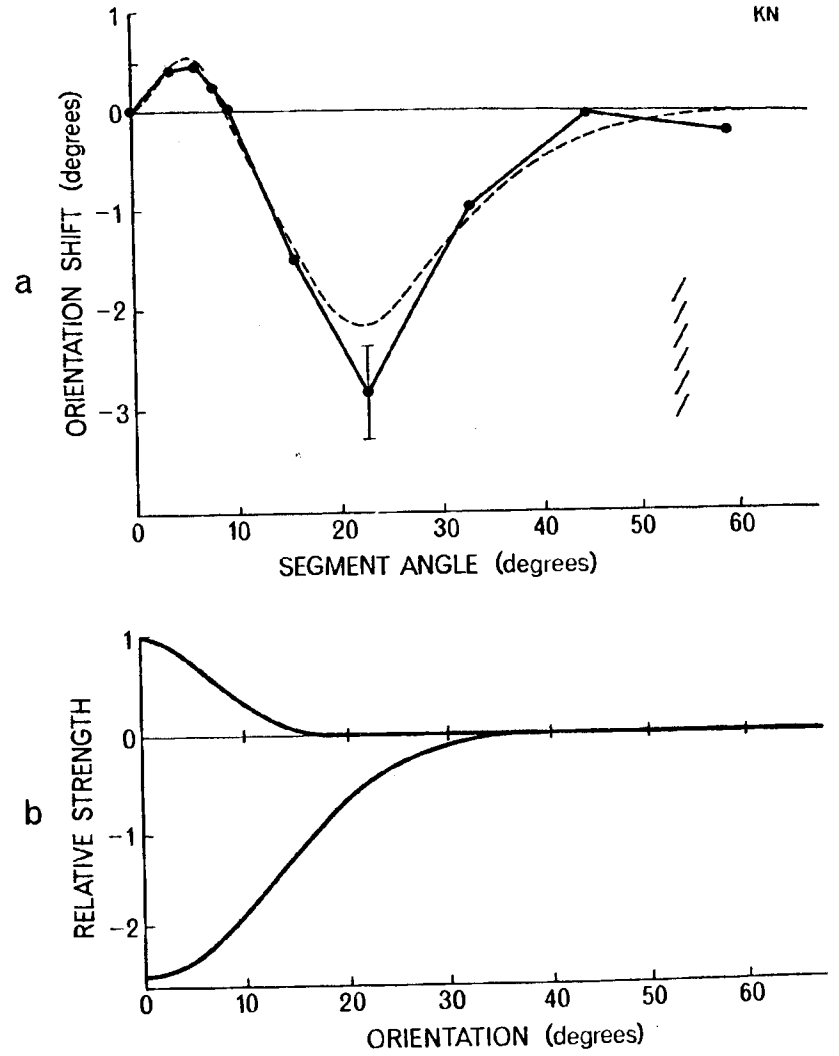

FIG. 31.5. a) Perceived orientation of a single segmented line in an otherwise dark room. The fact that these results are similar to those using pairs of segmented lines (see Fig. 4) indicates that the previous results are not due to spatial interactions between the configurations. b) Relative magnitude and orientation tuning of hypothetical excitatory and inhibitory signals from a population of small receptive fields impinging upon a similar array of large receptive fields. Dashed curve in (a) shows the computed fit of this theoretical model to the observed perceptual shifts (see Theoretical Model).

relationship with segment tilt, although each aspect of the curve occurs at slightly lower inducing tilts than in Experiment I. By providing a control for contour repulsion effects between segments, this experiment supports the view that orientation rather than position is the determining sensory variable for both positive and negative induction effects. The small differences in peak orientations relative to Fig. 4 suggest that there may be a small degree of interaction between the two segmented lines in Experiment I, which is eliminated in the single segmented configuration. The latter is therefore considered to be the purer case of size/orientation interactions, and the one that is modeled in the Theoretical section.

Experiment III: Effect of Segment Spatial Frequency

The relation obtained between segment angle and perceived orientation of the segmented line suggests an interaction between size and orientation mechanisms; signals from smaller receptive fields can affect those from larger receptive fields. Therefore, we examined the effect of size directly. The strength of both positive and negative tilt induction was measured as a function of the spatial frequency of
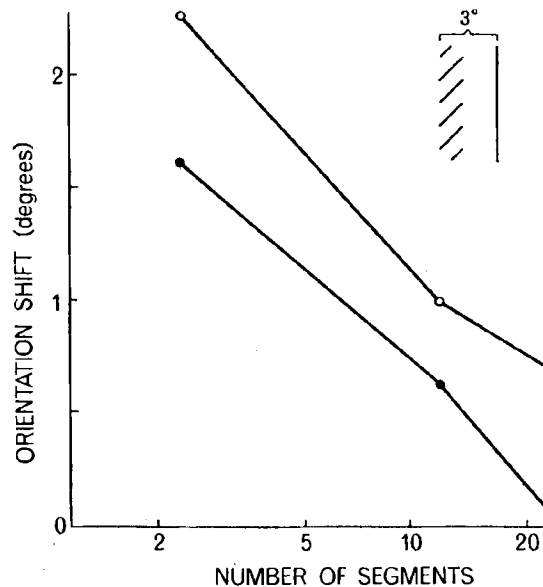

FIG. 31.6.   Effect of number of segments on the magnitude of the positive (filled circles) and the negative (open circles) effects for observer KN. Both magnitudes are plotted as positive to aid comparison of the slopes. The stimulus had segment angles of 15° for the positive effect and 40° for the negative effect.

the segments (reciprocal of segment length in degrees, or number of segments per degree of visual angle).

For this experiment, the tilt angles of the segments that yielded the greatest positive and negative effects in Experiment I were selected and the number of segments was varied. For KN these peak values were about 15° for the positive and 40° for the negative effect. As in the second part of Experiment I, the outer halves of the endmost segments were removed to avoid end effects. The observer set the global orientation of the segmented line so that it appeared parallel to a straight comparison line placed 3° away. Figure 31.6 shows the effect of spatial frequency on both positive and negative induction effects. The major finding is that perceived tilt increases directly with length of the segments. Greatest amounts of induction occur at 5° per segment, where there are only two complete segments. Oyama (1975) reported related results for the classical version of the Zöllner illusion, in which tilted segments were adjacent to a straight test line, but for his data the length effect saturated at a segment length of about 2°, whereas in Fig. 31.6 the length effect continues up to at least 5°.

DISCUSSION

The results indicate that local orientation of a series of line segments affects the orientation of the "line" formed by those segments. For segment angles from 0° to about 20° (depending on the observer), the global orientation is tilted in the same direction as the local tilt. On the other hand, beyond about 20° the opposite result occurs. In this case, the results are analogous to the apparent contour repulsion seen in figural aftereffects (Köhler & Wallach, 1944), but the present data show "repulsion" with respect to orientation rather than distance.

The results are similar in many respects to those of previous investigators (see Introduction), with the difference that in our stimulus the orientation interactions must be occurring between cells responding to different sizes of oriented stimuli, rather than between cells responding at different retinal locations.

Relation to Fraser and Zöllner Illusion

The biphasic nature of the tilt response appears to relate two illusions of orientation which have not been previously considered under the same rubric, namely, the Fraser (1908) and Zöllner (1862) illusions. In the Fraser illusion, segments with a small angle of tilt induce a perceived global tilt in the same direction, as is the case for small angles of tilt in our sawtooth line. This result is an important control for the possible artifact that local retinal interactions may be responsible for the small angle assimilation effects reported in previous studies (Oyama, 1975).

In the Zöllner illusion, segments with a large angle of tilt usually induce the opposite direction of tilt in an overlaid test line. We have shown that it is not necessary to have a separate test line. The global orientation of the line formed by the segments themselves is similarly affected by the segment tilt.

It may be noted that the original Fraser illusion (and our equivalent tilted letter illusion, Fig. 31.7) is more powerful than the segmented line version (Fig. 31.3). This is probably due to relatively weak stimulation of cells with large receptive fields (as in Fig. 31.2) in the original illusion, as a result of the presence of both dark and light patches in the summation region of such receptive fields. With this qualification, both the Fraser and Zöllner effects can be considered manifestations of the interaction between oriented receptive fields of different sizes processing the same stimulus.
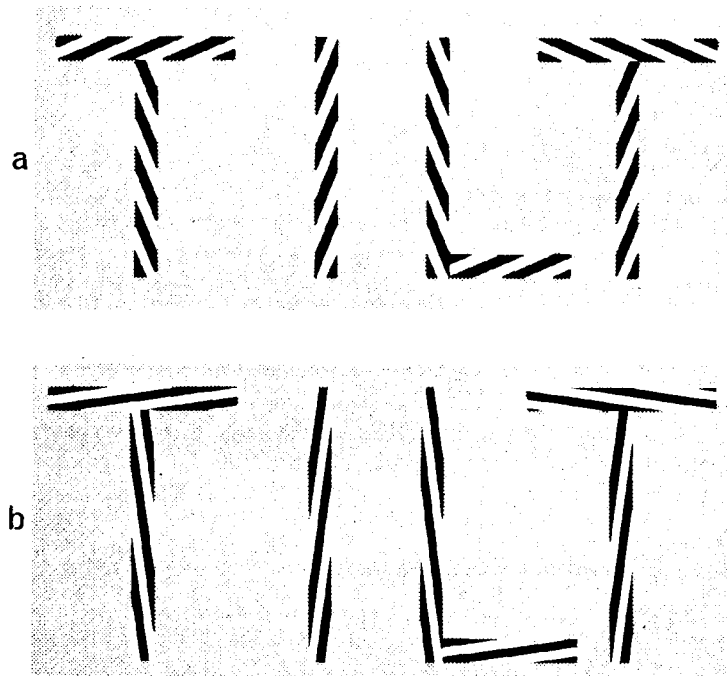

FIG. 31.7.   Zöllner (a) and Fraser (b) effects illustrated by segmented letters. In the Zöllner illusion the apparent orientation of each bar of the letters is in the opposite direction as the segments, which are tilted at 30° to the horizontal and vertical bars. The tilt direction alternates in alternate letters. For the Fraser effect the segment tilt is at 10° to the bars. Note the opposite directions of perceived tilt in the two cases.

Theoretical Model

In order to understand the tilt induction data in terms of psychophysical and neurophysiological information on orientation selectivity, they should be placed in the framework of a general model for the perceptual shifts. Our model is based on the idea that the induced shift is a function of the rate of change of inducing signal across the relevant perceptual dimension (which is orientation in the present case, but the analysis is generally applicable to any perceptual dimension).

To begin, we assume a population response of orientation channels similar to that suggested by Blakemore (1970), Anstis (1975), and Howard (1981), based on much neurophysiological (Hubel & Wiesel, 1962, 1968) and psychophysical (Campbell & Kulikowski, 1966) evidence. Each local region of visual space is processed by a set of cortical neurons with overlapping receptive fields, each tuned to a narrow range of orientation by means of the relationship of excitatory and inhibitory subfields. The half-bandwidth of these orientation tunings is from 12–15°, assuming a Gaussian envelope for each tuning. For a stimulus of a given orientation, the pattern of excitation across this array of orientation channels is assumed to be proportional to the sensitivity of each channel at the stimulus orientation. The pattern of excitation across a population of channels, therefore, is also Gaussian with the same bandwidth as that of the individual channels.

In this study, we have explored the dimension of size as well as orientation specificity. Consequently, we must consider separate arrays of orientation channels for different sizes of stimulus. What is the form of the interaction from small to large receptive field arrays of orientation channels, beyond the level of interactions that determine the orientation specificity of each channel? This higher level interaction might be purely excitatory (i.e., a form of direct crosstalk), it might be purely inhibitory, or it might be a combination of both excitation and inhibition. (The question of corresponding interactions from the large to the small orientation channels is not considered in this chapter, because the observers judged only the orientation of the global configuration, not the local segments.) For simplicity, only two size tunings of orientation array were considered, but the argument would apply equally across a range of sizes. In that case, the interactions would be some function of the size difference between the tunings of arrays (as suggested by Fig. 31.6).

We now analyze how tilt is affected by the interaction between arrays. Suppose there is an added pattern of excitation from the small orientation channels to the large orientation channels. In the simplest case, this added excitation might have a uniform slope (Fig. 31.8b). Such a slope will alter the resultant excitation pattern so as to shift the peak in the direction of increasing amplitude of the added signal (Fig. 31.8c). We assume that perceived orientation of the stimulus is determined by the position of the peak of the distribution of excitation. Clearly, the degree of peak shift will depend on the slope of the added excitation. If

a

EXCITATION

b

ADDED EXCITATION

c

RESULTANT EXCITATION

-30 -20 -10   0   10   20   30

RELATIVE ORIENTATION (degrees)

d

PEAK SHIFT (degees)

20

10

0

-10

-20

-3 -2 -1   0   1   2   3

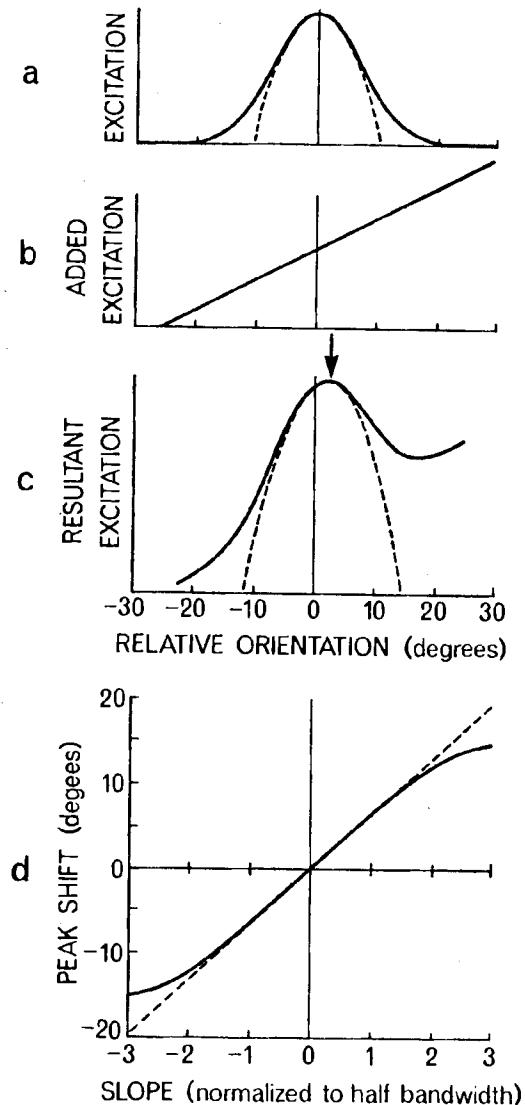SLOPE (normalized to half bandwidth)

FIG. 31.8.   a) Theoretical analysis of orientation interactions assuming Gaussian (continuous lines) or parabolic (dashed lines) sensitivity profiles for the population response of orientation selective mechanisms. For a linear distribution of added excitation from the interaction input (b), the peak of the resultant excitation (arrow) shifts towards the higher added excitation (c). The bottom panel (d) shows that for a parabolic population response profile, the peak shift is a linear function of the slope of added excitation (dashed line). For a Gaussian profile of population response (continuous line) the profile is approximately linear up to 2 times the half bandwidth.

the slope were zero, there would be no peak shift, whereas a steep slope would induce a large peak shift.

How can the degree of peak shift be quantified? For purposes of mathematical simplicity consider that the population response profile is parabolic (dashed lines in Fig. 31.8) with a linear slope of added excitation. In this case the peak shift is directly proportional to the slope of added excitation, as derived in the Appendix. For a more realistic Gaussian distribution the peak shift is close to that of the parabola for shallow slopes and progressively deviates from proportionality as slope is increased. The amount of peak shift as a function of slope is shown for the parabola (dashed line) and the Gaussian (continuous line) in Fig. 31.8d. These relations are general, but the degree of peak shift for the case of orientation channels with a full bandwidth of 24° is shown on the ordinate of Fig. 31.8d. It can be shown that even for the Gaussian, peak shift is a linear function of added slope within 10% for peak shifts up to 10°, which exceeds the range of induced tilts obtained in most studies of orientation interactions.

Suppose the added excitation is also Gaussian. Since the addition of two complex distributions is analytically unwieldy, we determine merely the degree of departure from the simple linear slope model. The pattern of added excitation being Gaussian rather than a linear slope will cause some further distortion in the peak shift function. However, this distortion can be neglected to the extent that a Gaussian distribution of added signal approximates a parabola. This is a good approximation for small peak shifts, as shown in Fig. 31.8d.

This analysis of orientation interactions shows that the peak shift of the combined excitation pattern should be approximately proportional to the slope of the added excitation but of the opposite sign, because the shift is measured in terms of effect on the global orientation. Thus, in the orientation domain, the expected degree of peak shift should correspond to the inverse of the first derivative of the added excitation distribution.

Three possible effects of the added signal from the small orientation channels on the peak for the large orientation channels are diagrammed in Fig. 31.9. If the interaction signal were purely excitatory, with a Gaussian distribution (Fig. 31.9a), the peak shift would first increase and then decrease back to zero tilt as the orientation difference between the small segments and the global line increased from zero (Fig. 31.9b). (The opposite function for orientation differences in the other direction is indicated by the dotted line).

Thus for excitation only, the expected tilt function is a single-humped, positive curve (solid curve in Fig. 31.9b). Similarly, for inhibition only (Fig. 9c), the first derivative gives an expected tilt function in a single-humped negative curve (solid curve in Fig. 31.9d). Neither case resembles the biphasic curve that was obtained in Fig. 31.3 and Fig. 31.4 for the measured data. In order to match this form, one needs the presence of both excitatory and inhibitory interactions, as shown for the response function in Fig. 31.9e and for its derivative, the expected tilt function in Fig. 31.9f. This last function is a good match to the qualitative features of the measured data. An example of the theoretical fit to one set of data

a
POPULATION EXCITATION
FUNCTION

b
PREDICTED EXCITATION
PEAK SHIFT

c
POPULATION INHIBITION
FUNCTION

d
PREDICTED INHIBITION
PEAK SHIFT

e
COMBINED POPULATION
RESPONSE FUNCTION

f
PREDICTED COMBINED
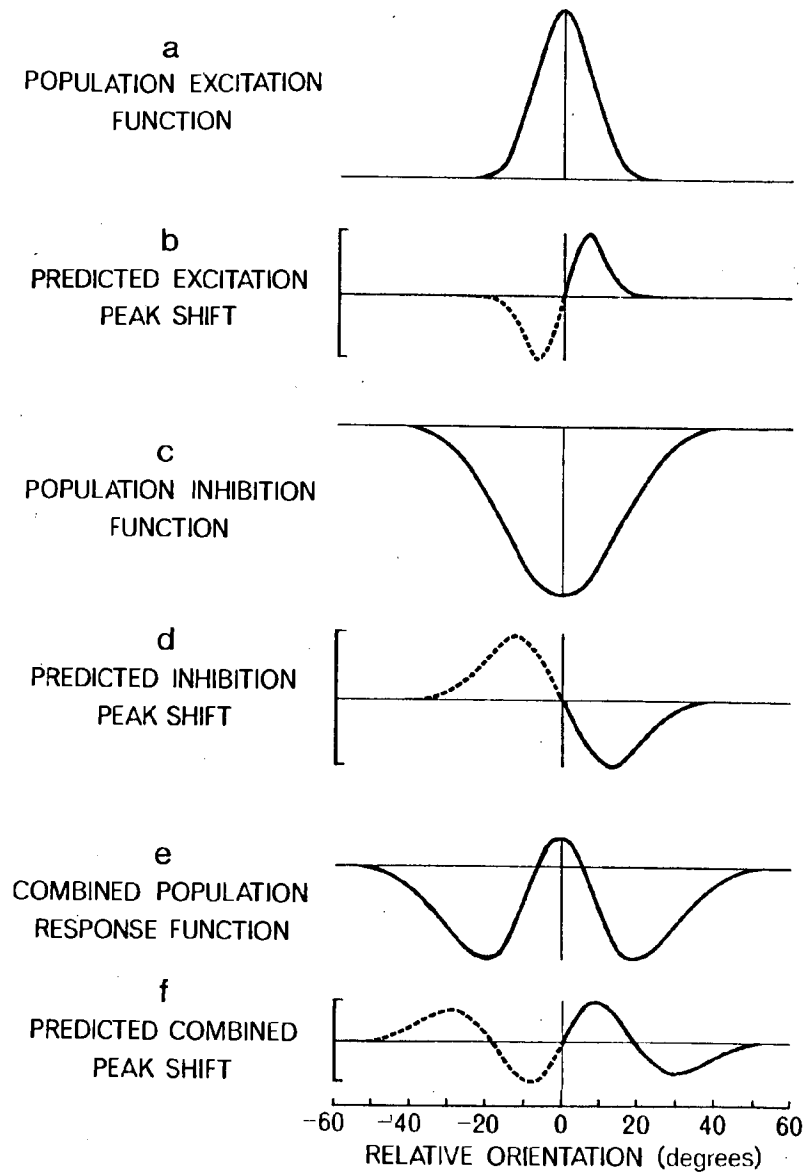PEAK SHIFT

RELATIVE ORIENTATION (degrees)

FIG. 31.9. Predicted peak shift (b, d, and f) for different types of population interaction: Purely excitatory (a), purely inhibitory (c), or a combination of the two (e). Note that peak shift changes sign from positive (upward) to negative (downward) with type of interaction.

is shown in Fig. 31.5 (dashed line), derived as in Fig. 31.9. The parameters used for this curve are a half bandwidth of 8° for the excitation function and 16° for the inhibition function, with relative amplitudes of 1:2.5 (as depicted in lower panel of Fig. 31.5). Although the fit is quite good, it should be mentioned that the four parameter fit allows other choices of parameter values with similar results. Thus, while the model is an acceptable description of the data, it should not be regarded as a unique solution.

CONCLUSION

This analysis suggests that the "assimilation" effect of the Fraser illusion is due to excitatory "crosstalk" between arrays of cells with small and large receptive fields and different orientation preferences. The Zöllner illusion, on the other hand, is a result of the inhibitory interactions between these same arrays of cells. The analysis is consistent with physiological recordings showing the existence of both size and orientation selectivity (Hubel & Wiesel, 1962), as well as interactions between orientation selective neurons (Blakemore & Tobin, 1972; Nelson & Frost, 1978). Furthermore it adds weight to previous psychophysical evidence for the interaction of orientation signals (Carpenter & Blakemore, 1973; Magnussen & Kurtenbach, 1981). It appears that the signals conveying orientation information are segregated as to size, although the effect of size is graded rather than abrupt, as was shown in Fig. 31.6. Furthermore, the analysis suggests that the inhibitory interaction has about twice the strength of the excitatory interaction. Thus, the segmented line approach may provide new insight into the mechanisms processing orientation, and suggest an analytic approach for use in other perceptual domains.

ACKNOWLEDGMENTS

APPENDIX

Derivation of Proportionality of Peak Shift to Slope of Added Excitation

If the population response profile (y) with respect to orientation (θ) is parabolic, it has the equation:

$$y = a - b\theta^2 \tag{1}$$

where a is an amplitude constant and b is the steepness parameter.

Adding an excitation signal with a constant slope (m), gives a resultant response profile of

$$y = a - b\theta^2 + m\theta \tag{2}$$

The peak of this distribution (θ) will occur at the orientation where its slope is zero, that is,

$$\frac{dy}{d\theta} = 0, \theta = \hat{\theta} \tag{3}$$

This occurs when

$$\frac{d(a - b\theta^2 + m\theta)}{d\theta} = 0 \tag{4}$$

$$m - 2b\theta = 0 \tag{5}$$

From equation 5 the peak orientation (θ) is directly proportional to the slope of added excitation

$$\hat{\theta} = \frac{m}{2b} \tag{6}$$

as shown by the dashed line in Fig. 30.8d. Similarly, for a Gaussian excitation profile the resulting distribution is

$$y = e^{-b\theta^2} + m\theta \tag{7}$$

The slope is zero when

$$-2b\theta e^{-b\theta^2} + m = 0 \tag{8}$$

when θ is small, $e^{-b\theta^2} \approx 1$

$$\text{and } \hat{\theta} = \frac{m}{2b}, \text{ as before.} \tag{9}$$

Therefore, the peak shift for a Gaussian direct excitation function approximates that of a parabola when θ is small, as shown by the full line in Fig. 30.8d.

We next show that if the *added* excitation has a parabolic profile, peak shift is proportional to the orientation difference ($\Delta\theta$) between the population profiles.

If the equation for the added excitation is

$$y = c - k(\theta - \Delta\theta)^2 \tag{10}$$

The resultant response distribution is

$$\begin{aligned} y &= a - b\theta^2 + c - k(\theta - \Delta\theta)^2 \\ &= a + c - b\theta^2 - k\theta^2 + 2k\theta\Delta\theta - k\Delta\theta^2 \end{aligned} \tag{11}$$

For which

$$\frac{dy}{d\theta} = -2b\theta - 2k\theta + 2k\Delta\theta \tag{12}$$

When $\frac{dy}{d\theta} = 0$, $\theta = \hat{\theta}$

and hence

$$2(b + k)\hat{\theta} = 2k\Delta\theta$$

$$\hat{\theta} = \frac{k\Delta\theta}{b + k} \tag{13}$$

Thus the peak orientation shift ($\hat{\theta}$) is directly proportional to orientation difference ($\Delta\theta$) between the two populations of orientation detectors, for any fixed values of the widths of response profiles (b and k). More importantly, it should be noted that the slope (m_θ) of a parabolic added excitation is directly related to distance ($\Delta\theta$) from the peak.

Consider that, for $y = c - k\theta^2$

$$m_\theta = \frac{dy}{d\theta} = -2k\theta \tag{14}$$

When $\theta = \Delta\theta$, $m_\theta = -2k\Delta\theta$

or

$$\Delta\theta = -\frac{m_\theta}{2k} \tag{15}$$

We can substitute this into equation 13, giving

$$\hat{\theta} = \frac{-m_\theta}{2(b + k)} \tag{16}$$

Thus the peak shift ($\hat{\theta}$) is directly proportional to the slope of added excitation, at the peak of the direct excitation function. Since this result was obtained both for a linear slope (equation 6) and a continuously varying function (equation 16), it will be taken as a general result for well-behaved profiles of added excitation, as long as the direct excitation profile approximates a parabolic form (see Fig. 30.8d).

In summary, the mathematical derivations indicate that the *peak shift* of the resultant excitation function may be considered to be directly proportional to *local slope* of the added excitation function at the peak, for the class of well-behaved orientation tuning functions:

$$\hat{\theta} \propto m_\theta$$

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