

Mechanisms of Contour Perception in Monkey Visual Cortex. II. Contours Bridging Gaps

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We have studied the mechanism of contour perception by recording from neurons in the visual cortex of alert rhesus monkeys. We used stimuli in which human observers perceive anomalous contours: A moving pair of notches in 2 bright rectangles mimicked an overlaying dark bar. For control, the notches were closed by thin lines so that the anomalous contours disappeared or half of the figure was blanked, with a similar effect. Orientation-selective neurons were studied. With the receptive fields centered in the gap, 23 of 72 (32%) neurons tested in area V2 responded to the moving "bar" even though the stimulus spared their response fields, and when the notches were closed, their responses were reduced or abolished. Likewise, when half of the figure was removed, the neurons usually failed to respond. Neurons with receptive fields within 4° of the fovea signaled anomalous contours bridging gaps of 1°–3.5°. The anomalous-contour responses were compared quantitatively with response field profiles and length-summation curves and found to exceed the predictions by linear-summation and summation-to-threshold models. Summation models also fail to explain the effect of closing lines which add only negligible amounts of light. In V1, only one of 26 neurons tested showed comparable responses, and only with a narrow gap. The others responded only when the stimulus invaded the response field and did not show the effect of closing lines, or failed to respond at all. The contour responses in V2, the nonadditivity, and the effect of closure can be explained by the previously proposed model (Peterhans et al., 1986), assuming that the corners excite end-stopped fields orthogonal to the contour whose signals are pooled in the contour neurons.

This is the second of 2 papers in which we try to relate contour perception to neuronal signals by using anomalous contours. In the preceding paper (von der Heydt and Peterhans, 1989a), we showed that neurons exist in area V2 of the monkey visual cortex that signal orientation and position of a line of discontinuity in a grating as though it were a real line or light–dark edge. Since in this case the anomalous contour and the lines inducing it had

different orientations, we could easily distinguish whether the signals were related to the contour or the inducing elements. In many figures used to demonstrate anomalous contours, however, the contours appear as continuations of the inducing elements (Schumann, 1900; Kanizsa, 1955). Often they form the straight connection of 2 aligned edges in the stimulus, as in the example of Figure 1A, although curved contours can also be produced. One might think that cortical "edge detector cells" are activated by a pair of such aligned edges to give the appearance of a continuous edge even though only their ends are given by stimulation and that this would be the explanation of anomalous-contour perception. However, this explanation is not satisfactory. On the one hand, vivid perception of anomalous contours can be induced by orthogonal lines (Ehrenstein, 1941; cf. von der Heydt and Peterhans, 1989a). On the other hand, the cortical edge detector hypothesis, as an explanation based on linear spatial filtering, predicts the perception of anomalous contours in many figures where they are not perceived (for example, Fig. 1B). Indeed, a spatial filter unit that is activated by a pair of sectorized disks as in Figure 1A will not be shut off when the thin arcs are added. Another instance where the simple edge detector explanation fails is the effect of occluding part of the figure. If one of the sectorized disks in Figure 1A is occluded by a sheet of paper, the adjacent anomalous contours seem to disappear completely, but the edge detector would still be activated to 50%. These considerations led us to study cortical neurons with stimulus configurations that are critical for the perception of anomalous contours.

Materials and Methods

The methods of this study were identical to those described in the previous paper (von der Heydt and Peterhans, 1989a) except for the visual stimuli. Briefly, single units were recorded extracellularly in semi-chronic experiments with monkeys (*Macaca mulatta*). The animals had learned to fixate their gaze on a small target in the center of a stereoscopically viewed electronic display on which various test stimuli were also presented. The stimulus patterns are described below (see Results). Stimulus–response relationships were analyzed during the periods of fixation. In order to compare the responses of a neuron to various stimulus patterns, the patterns were presented alternately in blocks of 8 repetitions, generally until each had been tested in 3 or more blocks. The 8 repetitions were distributed over several periods of fixation, 4 on the average, separated by pauses of 2 sec or more. The dot displays shown in the figures are reproductions of the photographic records taken during the experiment. Each block is marked by a vertical bar at the left, and forward and backward sweeps are shown in left and right halves, respectively, the backsweep with reversed time axis (right to left). The stimulus insets in the figures are photographs of the stimuli used in the experiments. Note, however, that black in the figures corresponds to a background of 10 cd/m² luminance and white to 16–20 cd/m² (unless otherwise noted), and that thin lines have been enhanced for ease of reproduction.

Received Sept. 29, 1988; accepted Oct. 24, 1988.

We wish to thank Vappu Furrer-Isoviita and Bernadette Disler for technical assistance, and Elisabeth R. Strickler for histological work. Günter Baumgartner suggested the use of illusory-contour figures and the effect of closure for studying cortical processing at the neuronal level. The manuscript benefited from comments from Peter O. Bishop, Walter H. Ehrenstein, Stephen Grossberg, and 2 anonymous referees. This work was supported by the Swiss National Foundation Grant 3.939.84.

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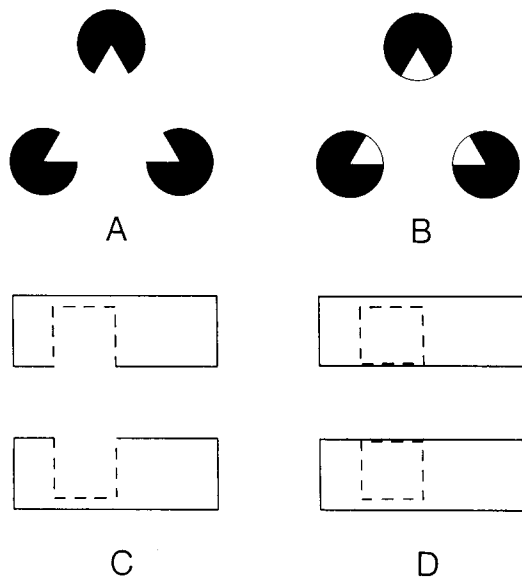


Figure 1. Anomalous contours. *A*, A white triangle overlaying 3 black disks can be perceived. Anomalous contours appear in the gaps between the sectored disks, and the triangle looks slightly brighter than the surround. *B*, When the sectors are closed by lines, contours and brightness difference disappear. *C* and *D*, Schematic of the stimuli used in this study. The outlined shapes were lighter than the background. The outer borders were kept stationary while the borders marked by *dashed lines* were moved sideways to and fro. Panel *C* gave the impression of a dark rectangle moving over 2 light rectangles and anomalous contours crossing the gap could be perceived. Intersecting lines (*D*) abolished this perception, similar to that in *B*.

Results

Figures 1, *C*, *D* illustrate the type of stimuli we used. The 2 outlined shapes were homogeneous in luminance and lighter than the background. The borders drawn with continuous lines were kept stationary and those marked with dashed lines were moved to and fro sideways. Looking at such a display, one perceives a dark rectangle hovering over 2 bright rectangles. The rectangle in front also looks darker than the background. When the 2 notches are closed by thin lines as in Figure 1*D*, the dark rectangle is no longer perceived, or appears to be moving behind, rather than in front of, the horizontal strip separating upper and lower parts. In any case, closing off the notches abolishes or very much reduces the perception of the anomalous contours bridging the gap and annuls the apparent brightness difference. This is similar to the perception of an overlaying triangle in Figure 1*A* and its disappearance in *B*. Some difference results from the movement in our display. Movement seems to strengthen the percept of the overlaying object. In a stationary display, the overlaying object can be perceived only if it has a certain minimal width; with movement, even narrow bars are consistently perceived as crossing the gap. The size of the stimuli (Fig. 1*C* and *D*) was varied by scaling in the length dimension. The length of the “bar” was $\frac{1}{10}$, the width of the gap $\frac{1}{3}$, of the overall size. A gap width of 120 min arc (2°) was typically used. At this size, the stimulus produced a vivid illusion in near-foveal vision.

We started the investigation of a unit by determining the best shape, orientation, and movement of a conventional stimulus, i.e., a light or dark rectangle. Preferences for light versus dark and edge versus bar were recorded, as well as the effects of

varying length and (in the case of bars) width of the stimulus. Ocular dominance and sensitivity to binocular disparity were also checked. The stimuli were usually binocular with zero disparity, but monocular stimulation or binocular stimulation with horizontal disparity was used if necessary. Neurons that preferred light bars exclusively were not studied further because we could only produce dark illusory figures. For neurons that responded better to an edge than to a narrow dark bar, the preferred edge was centered over the response field and the bar made wide enough to make the response equal to the edge response. Sometimes the nonpreferred edge was left out completely (see Fig. 2*C*). This stimulus looked as if the end of a dark object would overlay a light object with its opposite end remaining invisible. The response fields were mapped as usual. The preferred stimulus, bar or edge, at optimum orientation, was first centered lengthwise, and the lateral limits of response were marked. Then, while oscillating laterally in the most sensitive region, the stimulus was slowly withdrawn to either side in the length direction until the responses ceased. The positions of the ends of the bar or edge were then marked as the length limits of the response field. In practice, the whole procedure is an iterative process. We do not assume that there is anything particular about the response field beyond the criteria by which it is defined. It is just the minimum region in the visual field outside which no responses can be evoked by rectangular shapes of light. If only this class of stimuli would exist, a response of the cell would tell us that a line or edge within a certain range of orientations was present in the cell’s response field. The limits of the response field must be distinguished from the limit of length-summation observed when stimuli of various lengths are tested. Length-summation often exceeds the response field. We avoid speaking of the “classical receptive field” since this term is used with different meanings by different authors (see von der Heydt, 1987). Examples of quantitative determinations of the length limits will be presented below. We have studied a total of 106 orientation-selective cells with the stimuli of Figure 1, *C*, and *D*: 26 in area V1, 72 in area V2, and 8 near the border between these areas (± 0.5 mm).

Prestriate cortex

Figure 2 shows 3 examples of cells recorded in V2. Cells A and B responded best to dark bars; cell C preferred a light–dark edge. These stimuli are shown in the insets in row 1. A cross marks the position of the fixation target. The ellipses indicate the response fields (note that a response field can be elongated either in the length or in the width dimension). The dot displays show the neurons’ responses to back-and-forth movements of the stimuli and, in row 4, traces of spontaneous activity. The numbers below are the mean spike counts per motion cycle or an equal interval without stimulus. When a central strip including the response field was blanked, producing the illusion figures, the cells still responded regularly (row 2), but when intersecting lines were added, the responses were strongly reduced (row 3). The blank strips were 120 min arc wide, the intersecting lines only 2 (*A*, *C*) and 6 min arc (*B*). If one tries to explain the responses to the illusion figures by contrast summation of edge detectors, one must assume that these detectors summate over a length of more than 120 min arc. However, adding the pair of lines could then have only a very small effect since the lines removed contrast only over a few minutes of arc. Indeed, cells A and B responded similarly to illusion figures with blank strips

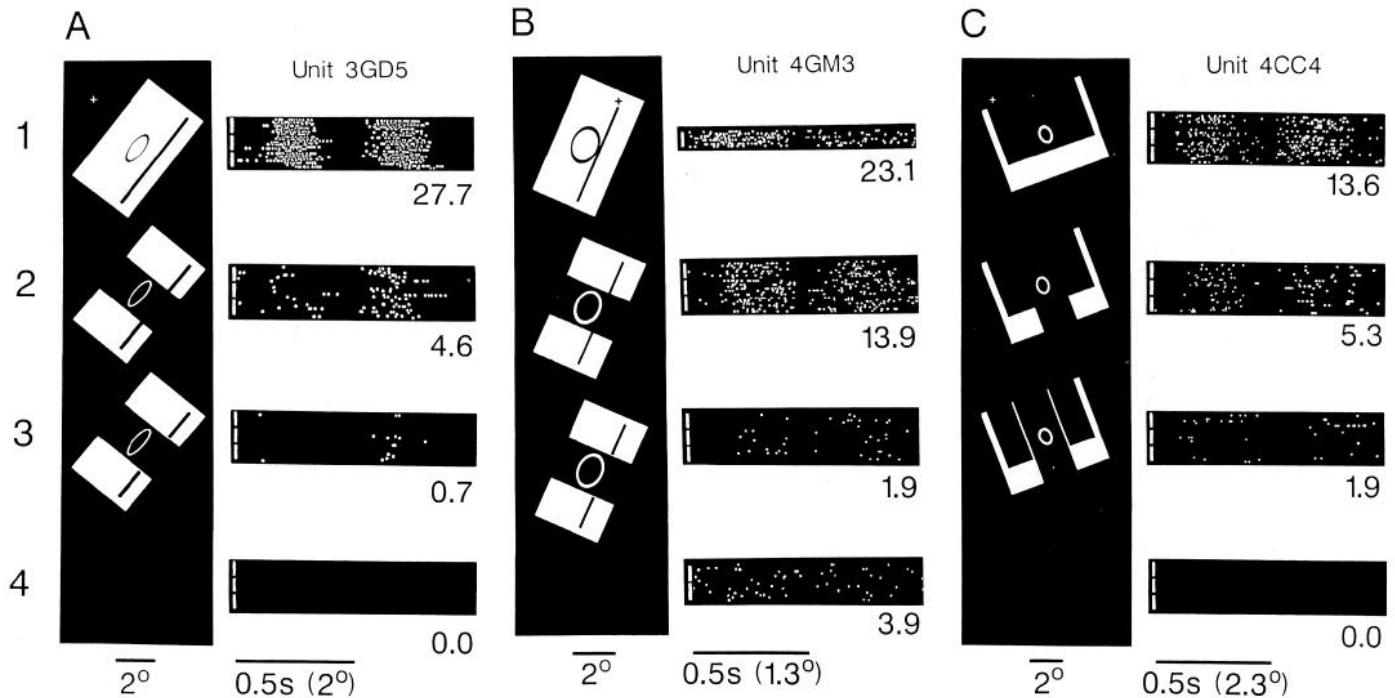


Figure 2. Responses of 3 neurons of area V2 to movement of anomalous contours. The stimuli are shown in the insets. Ellipses mark the response fields, crosses the position of the monkey's fixation point. The responses are represented by rows of dots, for the forward sweep of movement in the left halves of the displays, for the backward sweep in the right halves, with reversed time axis. The scale bars below the dot displays mark the duration of the forward sweep; sweep amplitudes are indicated in parentheses. Neurons *A* and *B* preferred dark bars and neuron *C*, dark-light edges, as shown in row 1. One can see that the neurons responded when the response fields were blanked out (row 2), but when thin intersecting lines were added, the responses were abolished (row 3). The figures below the spike traces are mean spike counts per stimulus cycle; row 4 shows corresponding samples of spontaneous activity. The blanked strips were 120 min arc wide; the intersecting lines, 2 (*A*, *C*) or 6 min arc (*B*). Bar widths were 10 (*A*) and 8 min arc (*B*).

of 120 and 160 min arc (see Fig. 6*B*), and an extension of the gaps by 4 or 12 min arc left the responses practically unchanged.

Twenty-three of 72 cells in V2 (32%) responded to these illusion figures and showed reduced responses when the intersecting lines were added (26/80 if the border region is included). Figure 3 shows a scatter plot of the strengths of the responses to the illusion figure and to the control figure with intersecting lines for 61 cells of V2. After subtracting spontaneous activity, the responses to either figure were divided by the response to the corresponding bar or edge. For cells with end-stopping ($n = 14$), the bar/edge responses at the optimum lengths rather than the corresponding lengths were used. Thus, the vertical position of a dot indicates the relative strength of the illusory-bar response, and its horizontal distance from the 45° line the effect of the intersecting lines. Filled squares represent the cells that showed consistent responses and reduction effects. (We have used additional criteria: The reproducibility of the responses and the reduction effect, and their invariance against change of the gap width.) The strength of the responses to the illusion figure was between 9 and 210% of the corresponding bar or edge responses (median, 38%), and the addition of the lines reduced it by 12–120% (median, 37%). The reduction was always much stronger than the effect predicted from varying the gap width. In 3 cases, the activity was reduced below the spontaneous level. With the exception of the 3 end-stopped cells represented by asterisks, the responses plotted in Figure 3 were obtained with stimuli outside the response field. A further 11 cells that failed to respond under this condition are not included in Figure 3 because the responses were not recorded. Those end-stopped

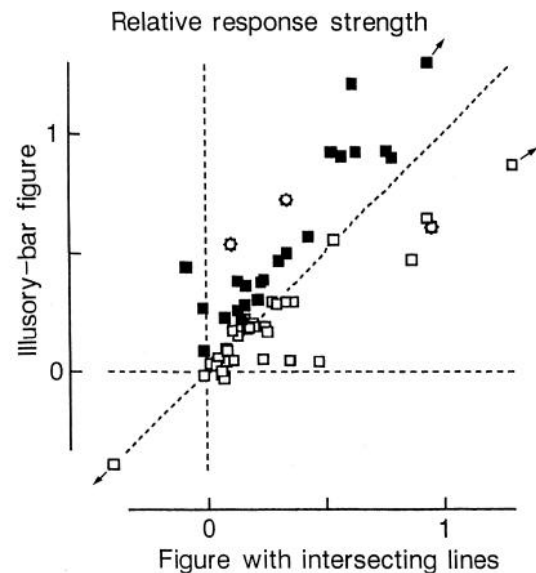


Figure 3. Joint representation of the strengths of responses to the illusory-bar figure and the figure with intersecting lines in 61 cells of V2. For each cell, the responses to the 2 figures were divided by the response to the corresponding bar or edge, or the bar/edge of optimum length. Negative values indicate suppression of activity below the spontaneous level. The vertical axis represents the relative strength of the illusory-bar responses, the horizontal distance from the 45° line the effect of adding the intersecting lines. Black squares indicate responses that we related to the perception of anomalous contours. Asterisks represent end-stopped cells that presumably signaled local features rather than the illusory bar.

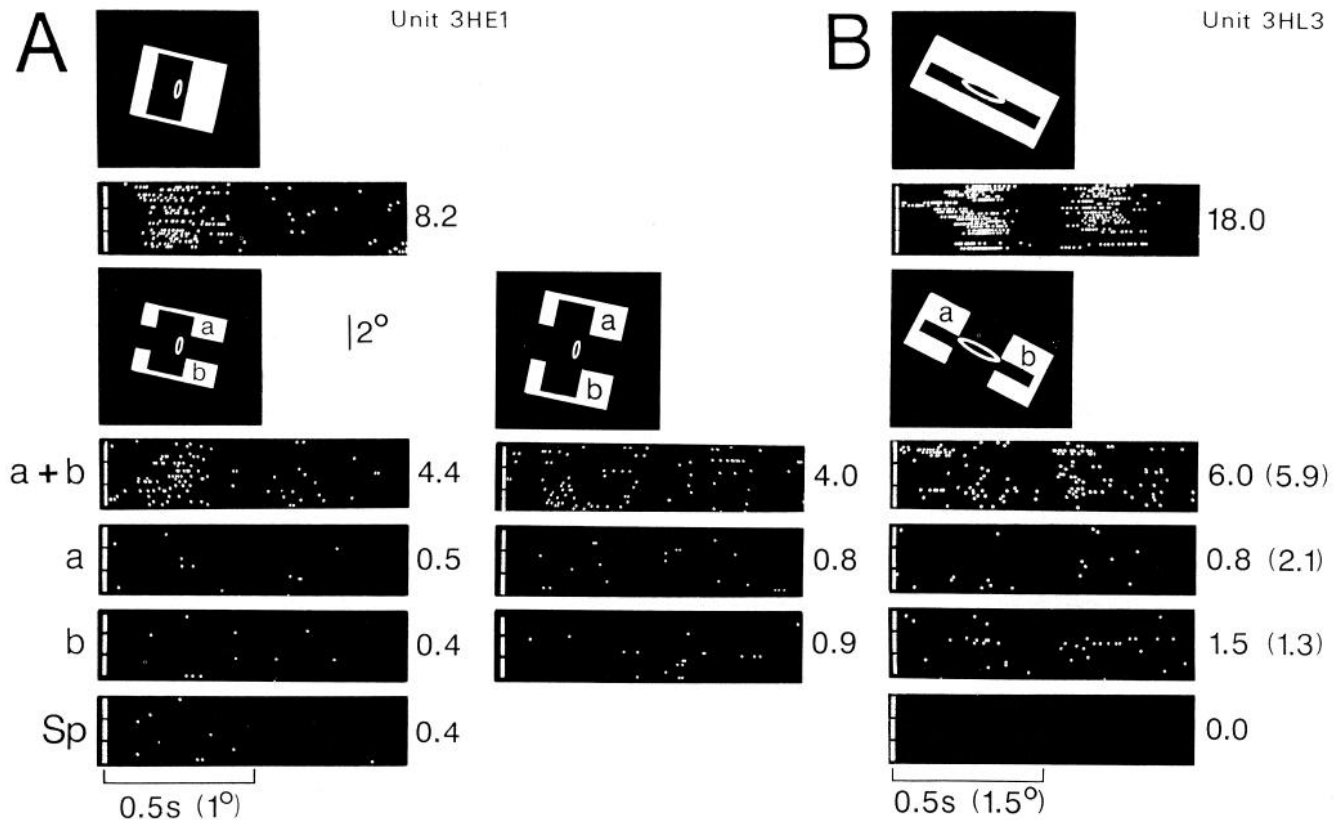


Figure 4. Effect of presenting the complete illusion figure and its parts separately in 2 neurons of area V2. Representation of stimuli and responses are described in the legend of Figure 2. The *top row* shows the responses to the preferred conventional stimulus; row *a+b*, the responses to the illusory-bar stimulus; rows *a* and *b*, the activity evoked by the half-figures; and *Sp* the spontaneous activity. The mean spike counts per stimulus cycle are indicated to the *right* of the response traces. Neuron *A* was tested with gap widths of 80 and 120 min arc; incremental luminance was 60%. Neuron *B* was tested with 160 min arc gap width, and 40 and 250% incremental luminance; the figures in *parentheses* correspond to the higher contrast. The response to the whole was greater than the sum of the responses to the halves.

cells were strongly activated by the illusion figure if the bar-ends invaded the response field, but half of the figure then produced a comparable response. We assume, therefore, that these responses signaled local features.

Other end-stopped cells, however, did respond to stimuli outside the response field and showed the effect of the intersecting lines. This is particularly interesting; stimuli confined to “inhibitory end-zones” evoked responses in these cells. We have seen 2 such cases with end-stopping greater than 50%, one of which is shown in Figure 6D below.

We have obtained responses with gaps up to 260 min arc (4.3°). In this case, the receptive field was centered at 3° eccentricity. The other receptive fields were located between 0.7° and 4.5° of the fovea (mean, 2.5°). Nearly all these cells had normal, convex response fields that were not unusually large (see ellipses in Figs. 2 and 4, and position-response functions in Fig. 5, *A*, *C*). One cell had an unusual receptive field, in which an edge evoked responses in 2 regions that were spatially separated along the preferred orientation. It responded to the illusion figure better than to edges or bars.

The perception of contours bridging a gap weakens or breaks down when one “pier” of the “bridge” is taken away. Figure 4 shows the result of such an experiment in 2 cells of V2. Both responded to edges, as shown at the top, and also signaled the corresponding edges of illusory bars. The row labeled *a+b* shows these responses, and the rows below the activity when either

half of the stimulus was presented alone (*a*, *b*) and a corresponding sample of spontaneous activity (*Sp*). It can be seen that the responses with the whole figure were greater than the sum of the responses to either half. In fact, the halves did not activate neuron A above its spontaneous level. Again, the width of the gap between the 2 halves was not critical; responses to figures with 80 and 120 min arc gap width are illustrated in Figure 4A. One might think that the responses to the illusion figure were due to stray light falling into the response field and moving along with the real edges and that the light coming from only half the figure might just not reach threshold. We therefore tested neuron B of Figure 4 with the normal, moderate contrast (40% luminance increment) and with a 6-fold higher increment (250%; Fig. 4B, numbers in brackets). The response to the illusion figure was unchanged and again much greater than the responses to either half of it. Thus, stray light cannot be the explanation.

The demonstration that either half of the stimulus alone did not produce a response (Fig. 4) confirms that the edges inducing the anomalous contour were, in fact, outside the cell’s response field. We have often determined the extent of the response field by recording the responses to an edge or bar moving across the field at different positions (Fig. 5, *A*, *C*). From the resulting position-response function one can predict how much a cell would respond to illusion figures with various widths of the blank strip if it would sum the excitation produced by the 2

edges or bars of the stimulus. These predictions are plotted in *B* and *D* of Figure 5 with filled symbols. The open symbols represent the actual responses to the illusion figures. They are clearly above the predicted curve for the various sizes of figures, again showing the nonlinearity of the anomalous-contour responses.

Part of the nonlinearity might be due to the threshold of the spike-generation process. A "negative baseline" is often assumed to account for nonlinearities of cortical neuron responses (see Henry et al., 1969; Schumer and Movshon, 1984). In order to test this explanation, we have derived predictions from the cells' length response functions. In a mechanism of linear summation with threshold, the difference between the responses to stimuli of different lengths is a measure of the excitation produced by the extra length. Specifically, it is independent of the level of the baseline. Figure 6 shows, for 4 neurons of V2, a comparison of the responses to illusion figures with these predictions. The length-response curves are plotted with filled squares, the responses obtained with various sizes of illusion figures with open squares. The prediction (dashed line) is the difference: bar response at corresponding length minus bar response at length equal to the gap width. It can be seen that the actual responses were much greater than the predicted responses in 3 of the 4 cells. In 2 of them the prediction assumed negative values because the length-response curves declined beyond an optimum length. Actual and predicted responses agreed for cell 3GD5; however, this does not mean that the summation model could be accepted here, since this cell showed a strong effect of the intersecting lines (see Fig. 2*A*). We conclude that neither a linear-summation model nor a model with linear summation and threshold can account for the responses to the illusion figure.

Figure 7 shows a similar comparison for 2 negative examples recorded in V2, cells that responded to the illusion figures only if the stimulus invaded the response field and did not show an effect of the intersecting lines. Except for the 2 smallest lengths in cell B, the actual responses fell short of the prediction. Again, there seem to be nonlinear mechanisms that, in this case, impede the response to a stimulus within the region of length summation.

Striate cortex

The results were quite different in area V1. It would be easy to demonstrate this difference using the same dimensions of stimuli as in V2. With the response field centered in the gap of the figure, cells in V1 did not respond at all to those stimuli. However, the response fields were smaller in V1 than in V2 (though they spread over about the same region of visual field), and one could argue that the unresponsiveness was simply due to this difference. We had the impression that there was a more fundamental difference in receptive field structure. In order to show this, we studied cells in V1 with stimuli of smaller dimensions, including figures with gaps so narrow that the response fields were partly stimulated. With gaps smaller than about 40 min arc we cannot be sure about the exact relation of the stimulus to the response field, since the fixational eye movements have about 10 min arc standard deviation (Motter and Poggio, 1984; Snodderly and Kurtz, 1985; we confirmed this for our monkeys by measuring the scatter of the delay of responses of lateral geniculate fibers to repeated movements of bars in various directions). However, if the responses elicited by these stimuli were related to the perception of anomalous contours, we should see a reduction of response when intersecting lines are added.

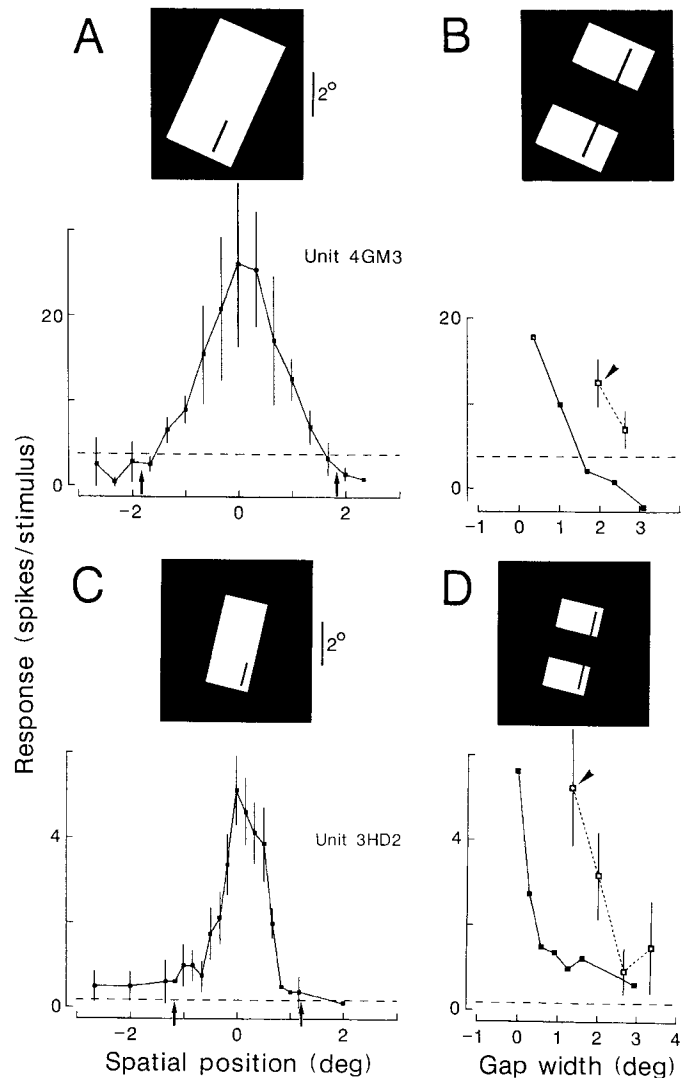


Figure 5. Test of the "length scan prediction" in 2 cells recorded in area V2. *A* and *C*, The receptive fields were scanned by dark bars 8×120 min arc and 6×64 min arc, respectively, and the responses have been plotted as functions of the position on the length axis. *B* and *D*, The responses at symmetrical positions on either side of zero have been added and plotted as functions of the separation between the stimuli at those 2 positions (filled symbols). Open symbols represent the responses actually obtained with illusion figures of corresponding gap widths. The data points corresponding to the figures illustrated in *B* and *D* are marked by arrows. One can see that the actual responses to the illusion figures were generally much greater than the predicted responses.

When the figure was scaled so as to just straddle the response field (gaps 8–80 min arc; mean, 48), 6 of 26 cells tested responded, but only 1 of these showed the reduction effect. One cell that did not respond to the illusion figure was activated by the figure with intersecting lines. Figure 8 shows the distribution of the normalized responses obtained with and without the intersecting lines, plotted as in Figure 3. The figure represents 16 cells; 10 cells that were not activated under these conditions are not included since their responses were not recorded. One can see that most cells are represented on, or below the diagonal, i.e., the intersecting lines had no effect or even improved the responses. The one positive case is marked with a black square. It was recorded in the infragranular layers. According to the position-response curve, its response field was 5 min arc long,

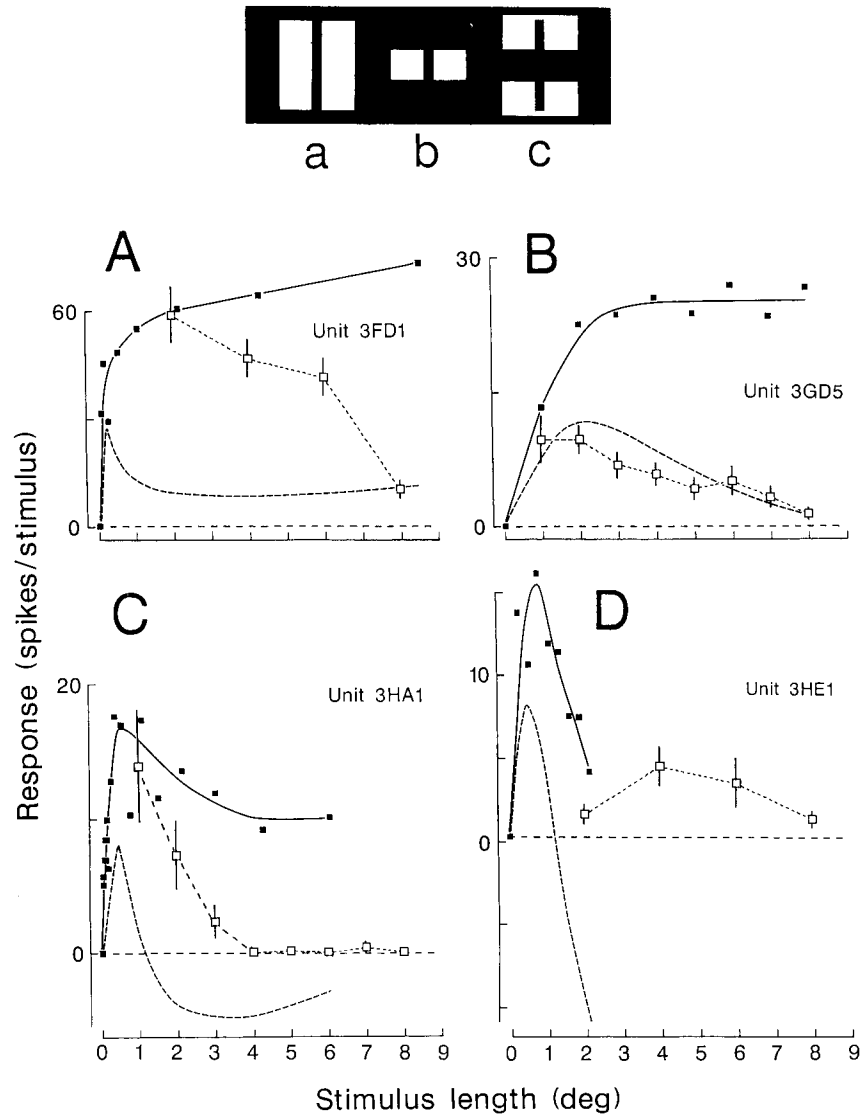


Figure 6. Test of the “length-summation prediction” in 4 cells signaling anomalous contours, recorded in V2. The responses to illusory bar figures *c* were compared with the difference between the responses to bars of the same length (*a*) and the length equal to the gap width (*b*). Various sizes of illusion figures were tested; size was varied by scaling in the length dimension. *Open symbols* with error bars represent the responses to these figures. *Continuous lines* and *filled symbols* are the length-response curves for bars, and the *dashed lines* are the predictions derived from them. One can see that the prediction is acceptable in *B*, but in *A*, *C*, and *D*, the responses to the illusion figure far exceeded the predictions. This argues against a summation-to-threshold model. Narrow dark bars were used for *A–C*; the respective widths were 14, 16, and 6 min arc. The edge of a dark bar was used for *D* (see inset in Fig. 4A).

while its length-response curve leveled off at 33 min arc; the gap of the figure was set to 30 min arc. This cell was also found to signal anomalous contours produced by abutting gratings (von der Heydt and Peterhans, 1989a). For 2 end-stopped cells, plotted with asterisks, we used gaps smaller than the response fields. These cells gave large responses, but we assume that they signaled local features for the reasons explained above for corresponding cells in V2. Both responded well to corners and ends of bars. Their responses to the illusion figures were maximal with gap widths of 15 and 10 min arc, respectively, and dropped to zero at 30–40 min arc.

Most cells in V1 responded, as one would expect, when the stimulus invaded the response field, but they did not show the reduction effect. We verified this by turning down the figure size until the cell just responded and then switching on the intersecting lines; we regularly found that the cells still responded. However, some cells failed to respond to the illusion figure at any size. Nine gave zero or negative responses even though the real ends of the bar were well within the range of length summation or even traversed the response field. Examples of such paradoxical results are shown in Figures 9 and 10.

Figure 9 represents a complex cell recorded in the infragranular layers of V1. A dark bar was the most effective conventional stimulus. The inset on the upper right illustrates how the length of the response field was determined from the position-response curve; 42 min arc was obtained. Ellipses of this length are shown in the inset on the left. The dot displays show the responses to a long dark bar (*a*) and to illusory-bar figures of various sizes (*b–e*). It can be seen that the cell failed to respond with gap widths 80 and 60 min arc (*b, c*), which we normally used in V2, and gave some sporadic responses to small figures with gap widths of 40 and 20 min arc (*d, e*). Since these were mainly 2 volleys of spikes, each elicited during 1 of 24 stimulus cycles, we attribute them to slightly larger than normal deviations of the eyes during fixation. These gaps were so narrow that small flicks could place the response field right on the real portions of the bar.

Figure 10A shows the responses of a simple cell of layer 6 of V1 to a dark bar, illusion figures of 20 and 40 min arc gap widths, and the corresponding figures with intersecting lines. The response field was 32 min arc long, but the cell failed to respond to any of the figures with gaps. Figure 10B represents

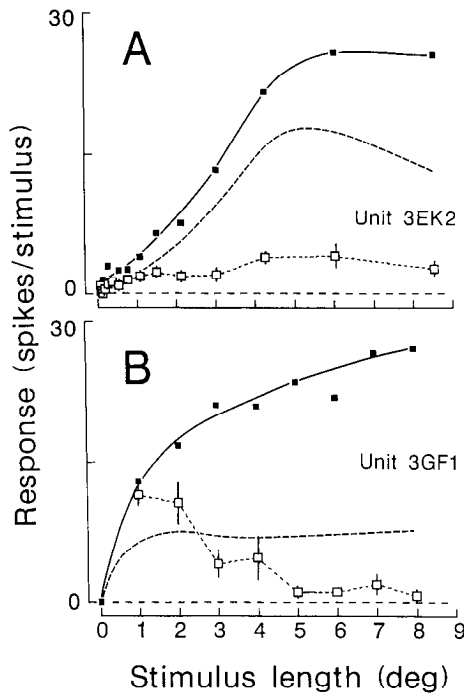


Figure 7. Test of the "length-summation prediction," as in Figure 6, in 2 cells of V2 whose responses did not reflect the anomalous contours. In cell *A*, the actual responses were below the prediction throughout. The same was observed in cell *B* for lengths 3° (gaps 1°) and greater.

a supragranular simple cell whose response field was 80 min arc long. Despite this length, a figure with a gap of 60 min arc evoked no response.

We have seen above that the strength of the anomalous-contour signals in V2 could not be predicted from the cells' length-summation characteristics. This was true also for some of the negative results of V1. In Figure 11 we compare the responses evoked by illusory-bar figures with the predictions from length-response curves (as explained for Fig. 6 above) for 4 cells of V1. Again, continuous lines and black squares are the length-response curves, dashed curves represent the predictions, and open squares indicate the responses actually obtained. One can see that illusory-bar figures generally evoked less response than predicted from length summation. The difference between the results obtained in V1 and V2 is particularly striking if one abuts the data of 2 cells with similar length summation (Fig. 12). Cell *A* is from V1, cell *B* from V2. Cell *A* did not respond when the illusory bar moved over its receptive field, although the gap in the figure was only 1° and the cell exhibited length summation up to 4° at least. The physical portions of the bar covered a range from 1° to 2.7° on the length scale, which, according to the summation curve, accounted for nearly half of the maximum bar response. In the cell of V2 (Fig. 12*B*), a figure stimulating regions that accounted for $\frac{1}{5}$ of spatial summation produced more than half of the maximum response. This cell even responded to a figure with a gap of 4.7° (5.9 spikes/stimulus), in which case the stimulus spared the field of summation entirely.

These results show that gaps in lines and edges are emphasized in V1 rather than filled in.

Results with different anomalous-contour figures

The stimuli used to generate anomalous contours in this study are quite different from those of our previous study (von der

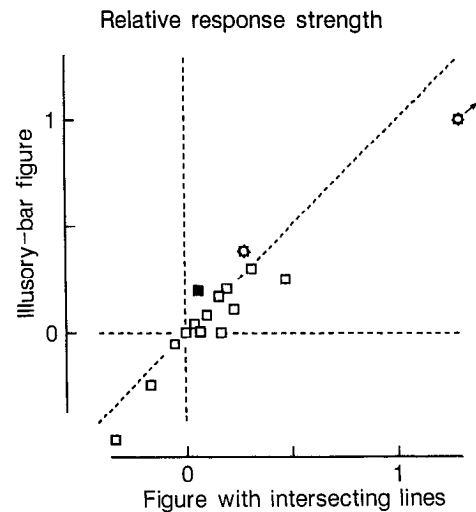


Figure 8. Joint representation of the strengths of responses to the illusory-bar figure and the figure with intersecting lines, as described in the legend of Figure 3 for 16 cells of V1. The *black square* represents a cell that responded to stimulation outside the response field and showed reduction of responses with the intersecting lines. *Asterisks* represent end-stopped cells that presumably signaled local features rather than the anomalous contours.

Heydt and Peterhans, 1989a); solid shapes of light compared with gratings of thin lines; contours that appear as straight continuations of edges or bars compared with contours perpendicular to the inducing lines. It is therefore of interest to see whether one can make any prediction from a test with one type of anomalous contour on the test with the other, or whether the 2 are unrelated. Thirty-eight of the cells tested with the present type of stimulus (Fig. 1) were also tested with abutting gratings, 30 in V2 and the V1-V2 border region, and 8 in V1. Of 15 cells that signaled the line of discontinuity, 9 also signaled the contour of the illusory bar figure, and of the 23 cells that were unresponsive to the line of discontinuity, only 1 responded to the illusory bar figure. In other words, 31 of 38 cells (82%) classified as positive or negative by one test were equally classified by the other. Thus, the 2 tests are related ($p < 0.02$; Geigy 1980, exact probabilities of 2×2 contingency tables).

Representation of orientation and pattern

As we said at the beginning, all cells included in this study responded to edges or bars and were orientation selective. Many of them were also selective for pattern, as shown by a bar/edge preference or a selectivity for the polarity of contrast. If contour information is explicitly encoded at the stage of V2, as we attempt to demonstrate, the activity of a single category of neurons, e.g., those cells that differ only in preferred orientation, or only in receptive field position, etc., should, in principle, indicate orientation, position, and so forth without the context of other signals. If a cell is orientation selective for edges, for example, it should not be necessary to reinterpret its responses as signaling a different orientation when the cell is activated by a more complex pattern.

Figure 13 represents the orientation tuning of 2 cells of area V2 for light or dark bars (continuous curves) and figures producing illusory bars (dotted curves). Figure 13*B* also shows the tuning obtained with abutting line gratings (bottom curve). It can be seen that the curves peak at nearly the same orientation

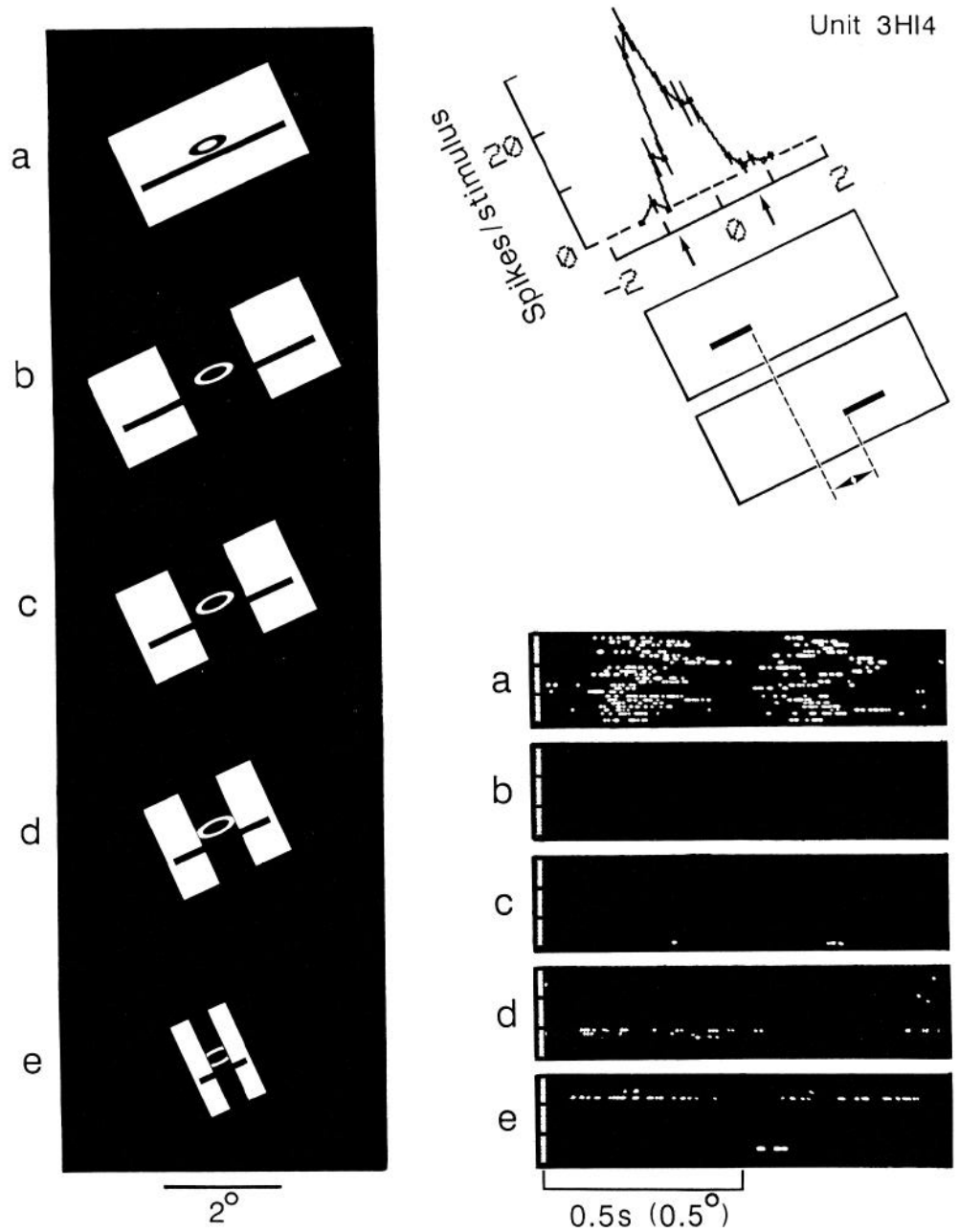


Figure 9. Test for anomalous-contour responses in a complex cell recorded in the deep layers of V1. The *inset at top right* illustrates how the length of the response field was determined. It shows the position-response curve and the stimuli in the limiting positions (*arrows*). The *double-arrow* shows the length of the response field: 42 min arc. Gap widths of 80 (*b*), 60 (*c*), 40 (*d*), and 20 min arc (*e*) were used. The relation between stimuli and response field (*ellipses*) is shown at *left*, and the responses to 24 cycles of movement of each stimulus at *lower right*. The cell responded to the continuous bar, but not to figures that spared the response field (*b, c*). Even figures overlapping the response field evoked only sporadic responses (*d, e*), presumably caused by small deviations of the eyes from the fixation point.

for either cell. This means that the cell categories represented by these examples signal the orientation perceived in the center of each of these figures regardless of the type of contour. Neuron A responded to the illusory bar figure at 2 orthogonal orientations, while neuron B showed only one peak. The observation of 2 peaks may be related to the cross-like appearance of the figure in which either bar of the cross can alternately be perceived as overlaying the other. Indeed, neuron A also responded to edges and wide bars, and thus sensed both orientations, while neuron B had a preference for thin (<5 min arc wide) dark bars, responding much less to wide bars and edges, and therefore signaled only the thin overlaying bar. As other neurons discussed in the preceding paper (von der Heydt and Peterhans, 1989a), neuron B responded to the abutting gratings at 2 orthogonal orientations, one corresponding to the anomalous contour (right-hand peak) and the other to the grating lines.

Some of the signals related to anomalous contours were specific for contrast polarity and pattern. Figure 14 demonstrates this for 2 cells of area V2. The neuron in A was polarity selective, responding to the right edge of a dark rectangle (*a*) but not to the left (*b*). It showed equal selectivity for the edges of the illusory figure (*c, d*). The same result was obtained in another contour neuron selective for edge polarity. Neuron B responded selectively to thin dark bars (*e*), the optimum width being 8 min arc, and barely to edges and light bars (*f-h*). It responded to an illusion figure with a thin dark bar (Fig. 2*B*). This specificity may explain the brightness differences associated with anomalous contours in some figures. In Figure 1, for example, the triangle looks brighter than the background, and in the corresponding negative figure (white sectorized disks on black), the triangle looks darker. The activity of neuron A, in conjunction with that of a sister cell with opposite preference, signal the

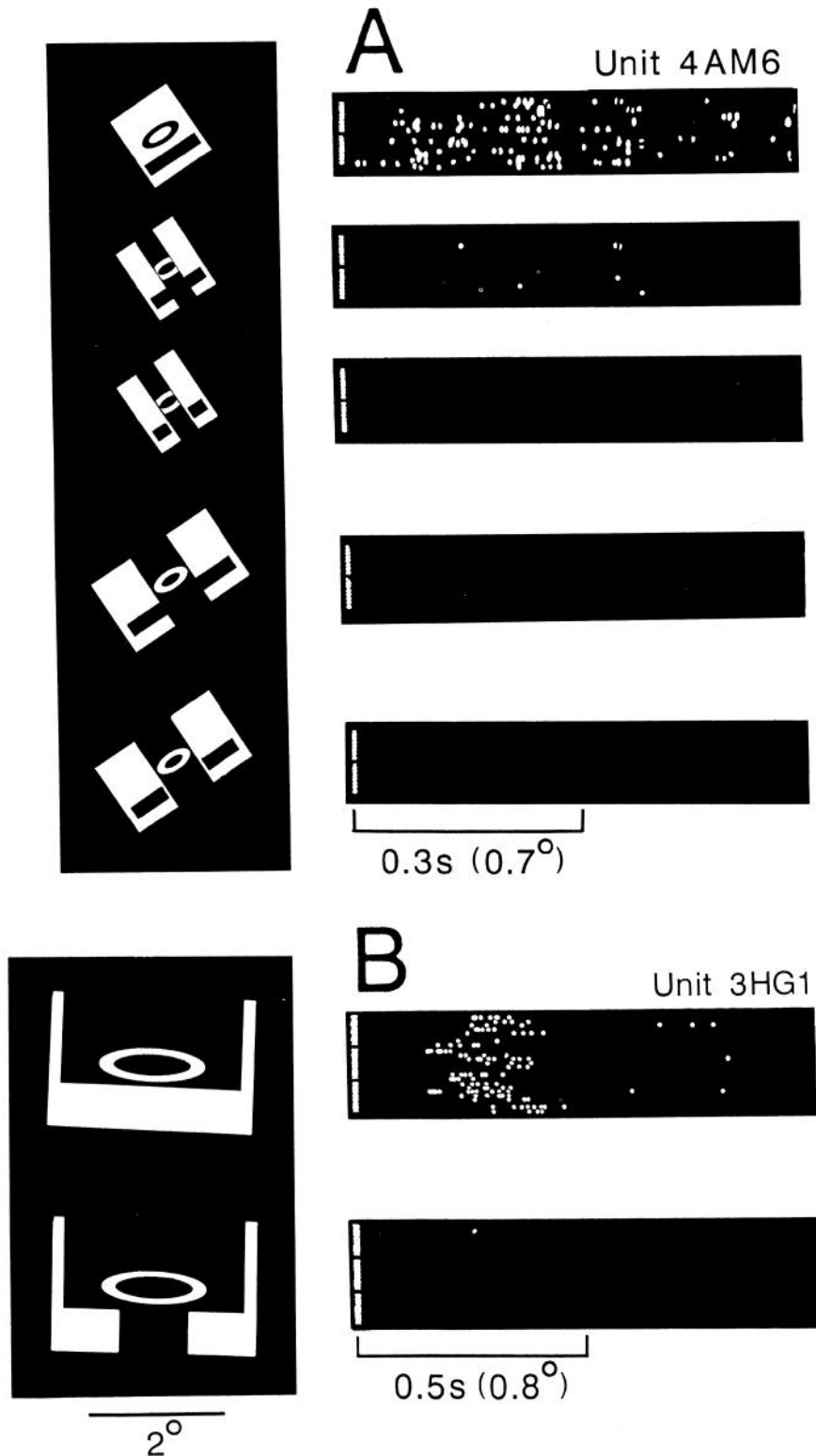


Figure 10. Two examples of simple cells of V1 that failed to respond even to stimuli overlapping the response field. Cell *A* was recorded in the superficial layers, cell *B* in layer 6. The response field of cell *A* was 32 min arc long. It was tested with illusory-bar figures with gaps of 20 and 40 min arc and the corresponding figures with intersecting lines (2 min arc). Each frame represents 16 cycles of movement. Cell *B* preferred edges, had a response field of 80 min arc length, and was tested with a gap of 60 min arc. Each frame represents 24 cycles.

polarity of edge contrast; the response of this cell to edge *b* represents the response of the sister cell to edge *a*. When a real edge is present in the response field, activation of this cell means "darker to the left," and activation of the sister cell means "darker to the right." When the activity is biased by an illusion figure (*c* and *d*), this is also interpreted as a dark-light step in the response field. These edge signals produce the sensation that

the object is darker than the background. With narrower bars, it seems that contrast is not encoded for the edges independently, but for the bar as a whole. This is indicated by the presence of cells selectively responding to either light or dark bars, but not to edges, such as the cell of Figure 14*B*. We assume that the cell would similarly differentiate light and dark illusory bars, although, for a technical limitation, only the latter was tested.

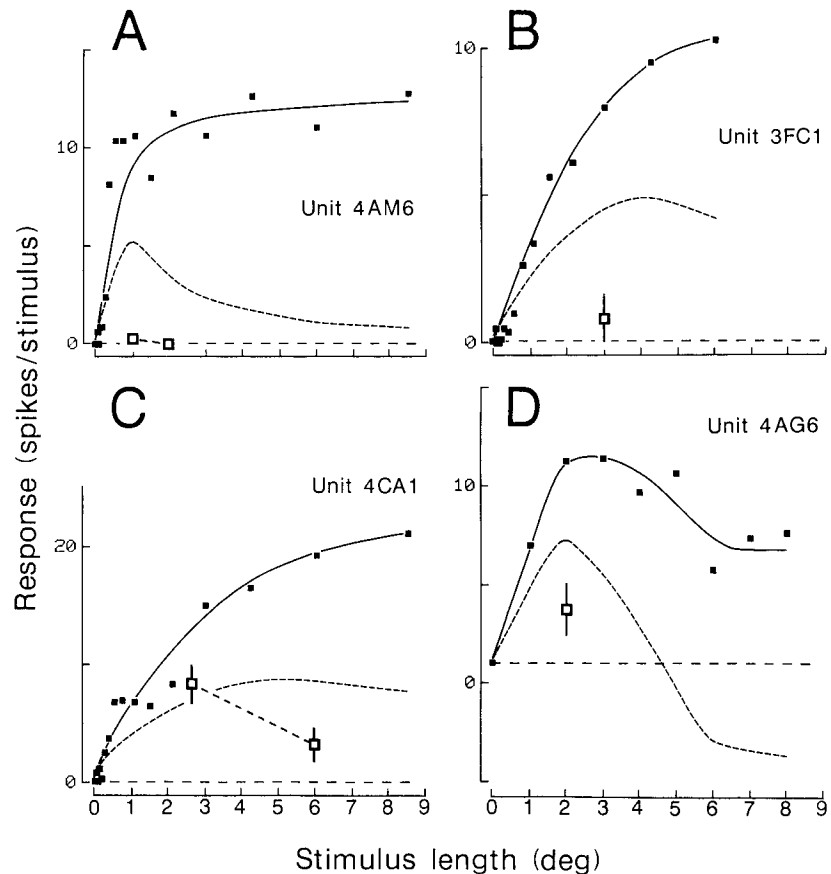


Figure 11. Test of the “length-summation prediction,” as described in Figure 6, in a simple (*A*) and 3 complex cells (*B–D*) of V1. *A* was recorded in layer 6, *B* and *C* in the superficial layers, and *D* in layer 4A. Except for the response of cell *C* to the smaller figure (gap, 50 min arc), the responses to the illusion figures fell short of the prediction. This is again a deviation from the summation-to-threshold model, but in the opposite direction as in the contour cells (Fig. 6).

Responses as in Figures 14, *c*, *d* and 2 may give the impression that edge- or line-detector receptive fields are partially activated by an interrupted edge or bar, but the mechanism is actually quite different, as the above experiments have demonstrated. Thus, the contrast preference of the illusory-contour responses is due to this special mechanism, and not just inherited from an edge-detector input. This will become clearer when we discuss the present results together with those of the preceding paper.

Discussion

It is generally assumed that orientation-selective cortical neurons respond only if a pattern of appropriate orientation is presented within a small region of the visual field, the “response field.” We have shown here that many of these neurons can also be activated by anomalous-contour figures that do not stimulate the response field proper. These responses seem to be related to the subjective contours perceived by a human observer; good responses were obtained with a display that mimics a dark bar overlaying 2 light bars, where subjective contours are salient, and weak or no responses at all when the overlaying bar was intersected by thin lines or when half of the figure was omitted, conditions under which the subjective contours disappear. Position and orientation of such contours were found to be encoded in the responses just as position and orientation of edges or lines. Such responses were obtained in a substantial proportion of cells in area V2 but seem to be rare or absent in V1.

We have further shown that the anomalous-contour responses are not simply due to partial stimulation of the response fields or to activation of subliminal regions, and they cannot be explained by a summation mechanism with threshold. Nonad-

ditivity was demonstrated by testing parts of the figure and the whole, and summation-to-threshold models were ruled out by comparing the actual responses with the predictions from length-summation curves. It might be possible to design a more sophisticated summation model with additional nonlinearities (e.g., saturation) to fit these particular results, but this would still not explain the strong effects of intersecting lines that add only negligible amounts of light.

We were initially worried about the possibility that the results could be confounded by the spontaneous fluctuations of responses, particularly since many cells gave only weak responses to our test stimulus compared with the optimum bar or edge. Assessing nonadditivity, or the effect of intersecting lines, is more delicate than detecting a peak in the orientation tuning, which was the criterion in our previous study. However, we feel confident about the present results because they show again a marked difference between areas V1 and V2, and because double testing of neurons has shown that the results obtained with the present type of anomalous contour correlate strongly with those obtained with the other type, despite the physical differences between these stimuli. Taking the results of the 2 studies together, we find that 55 of 150 cells tested in V2 (37%) signaled anomalous contours with one or the other test compared with only 1 out of 77 cells in V1. Also, 7 of 34 further cells recorded near the border between these areas signaled anomalous contours. The exceptional finding of 1 contour neuron in V1 might indicate that a small fraction of cells in this area also possesses the ability to detect those contours. Given the massive reciprocal connections of areas V1 and V2, these signals might simply reflect the processing in V2. The generally negative result in V1 fits with the earlier report that cells in the cat visual cortex did

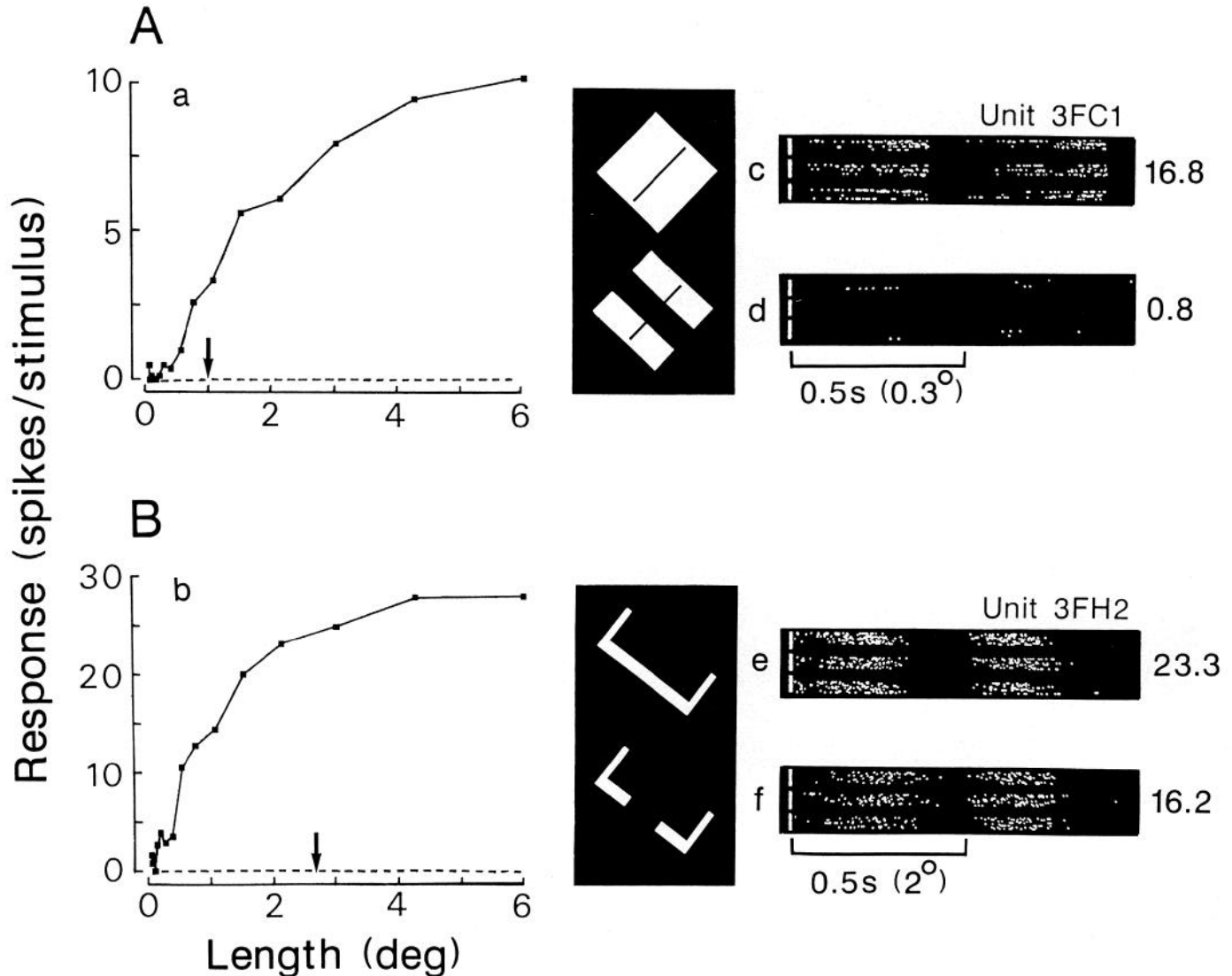


Figure 12. Comparison of the responses to anomalous-contour stimuli of 2 complex cells, one from V1 (*A*) and one from V2 (*B*), with similar length-summation characteristics. Length-response curves were obtained with dark bars (*a*) and edges (*b*). Cell *A* showed summation up to 5° or more, but nevertheless failed to respond to a figure with a gap of 1° (*d*). Cell *B* responded strongly to a figure with a 2.7° gap although most of its summation area was spared (*f*). Arrows in the graphs on the left indicate the lengths spared by the illusion figures. Receptive fields at 2.2° (*A*) and 3° eccentricity (*B*).

not respond to the movement of subjective contours over the receptive field, while they responded to low-contrast edges (Gregory, 1987).

Possible mechanisms of contour-related responses

Let us see now if we can explain our results by a simple forward mechanism. Later, we discuss the possibility of centrifugal influences. Since the 2 types of anomalous contours gave correlated results in the individual neurons, the mechanisms generating the responses to the different stimuli must be similar. Our conclusion that the responses obtained with illusory bar figures have little to do with partial activation of edge-detector receptive fields was confirmed by the observation that 9 out of 10 cells signaling these bars also signaled contours produced only by orthogonal lines, which could not possibly activate such a field. As shown in the preceding paper, the contour neurons in V2 must have a dual input, one from equally oriented edge- or line-

sensitive fields and a second from a group of orthogonally oriented end-stopped fields that we call the "grouping input" (Fig. 15). The grouping input has a peculiar summation property with the effect that excitation is produced only if several input fields at different positions are simultaneously activated. This was obvious when the number of contour-inducing elements was varied (cf. Fig. 12 of the preceding paper). We assume, therefore, that pairs of end-stopped fields are connected in such a way that one signal is gated by the other or the 2 signals are multiplied. This operation is represented by the elements x in Figure 15.¹ Now, since end-stopped neurons often respond to corners as well as to line-ends (Hubel and Wiesel, 1968; Peterhans and von der Heydt, 1987), the grouping input of the contour neuron

¹ An operation with graded output, rather than a logical AND gate is assumed because a gradual reduction of contour responses was observed when intersecting lines were added or when the contour-inducing lines were tilted (Fig. 11 of the preceding paper).

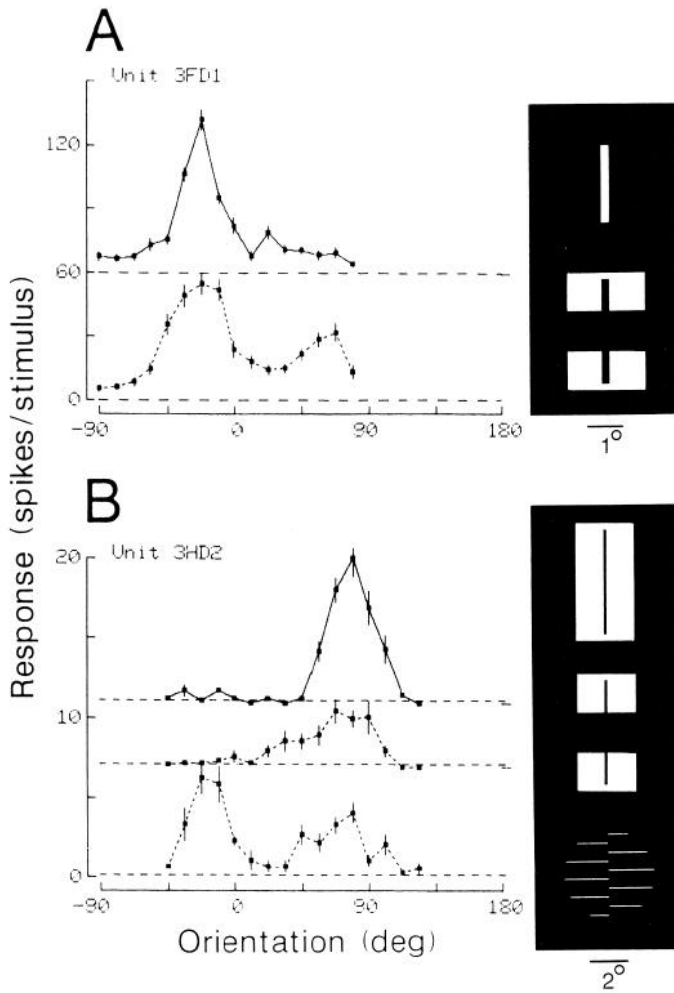


Figure 13. Orientation tuning curves obtained with bars and with anomalous contours, as shown at *right*, in 2 cells recorded in V2. One can see that the best orientation for a real bar was also the optimum for the illusory bar. Cell *A* showed a second, smaller peak of response corresponding to rotation of the figure by 90°; cell *B* showed only one peak of response. Cell *B* also responded to contour produced by abutting gratings (*bottom*). The smaller peak, aligned with the peaks of the upper curves, corresponds to this anomalous contour, the larger peak to the grating lines. The *upper curves* in each graph have been shifted vertically as indicated by the *dashed lines* representing the spontaneous firing levels.

will be excited by the corners on both sides of the gap in the illusory-bar stimulus. This is illustrated in Figure 16*A*.

When half of the figure is omitted, the excitation is reduced to one point on the contour, which is not sufficient to drive the grouping input. This phenomenon was demonstrated in the experiment of Figure 4. It is an instant of the Gestalt rule that “the whole is more than the sum of its parts.” When the “illusory bar” is intersected by lines, the excitation of the end-stopped cells is reduced because the lines fall on their inhibitory end-zones (Fig. 16, *B, D*). This causes the reduction or abolition of responses shown in Figure 2 and corresponds to the “effect of closure” in perception. Note that the receptive field of a contour neuron is composed of much smaller input fields, according to Figure 15. This difference in scale is important. Small lines can have dramatic effects in the small end-stopped fields, while they may barely influence an edge-detector field so large as to bridge the gaps in the anomalous-contour figures.

Our conclusion that features orthogonal to a contour contribute to its cortical representation is counterintuitive: Commonly, one assumes that collinearity is the determinant and that anomalous contours are defined by interpolation between the given pieces of edges or lines (Ullman, 1976; see also Grossberg and Mingolla, 1985; Zucker, 1985). To some extent, the edge-detecting path of our model may serve the extrapolation of edges or lines; the fact that simple and complex cells normally have a positive length of response field means that they extrapolate the stimulus, and this can serve to fill in small gaps (although our recordings from V1 indicate that such filling-in is not a rule; see Figs. 9 and 10). However, the anomalous-contour responses in V2 show that the grouping path that normally they extrapolate the stimulus, and this can serve to fill in small gaps (although our recordings from V1 indicate that such filling-in is not a rule; see Figs. 9 and 10). However, the anomalous-contour responses in V2 show that the grouping path that produced these responses is demonstrated by the effect of the intersecting lines.

We have argued (von der Heydt and Peterhans, 1989b) that the assumption of 2 input paths to the contour mechanism, an “edge detecting path” and a “grouping path,” has its theoretical basis in the fact that various image features are generated at occluding contours and that there are statistical correlations between these features. Various perceptual phenomena can be derived from this idea: the perception of anomalous contours itself, the illusory brightness and depth effects often associated with it, and the effect of oblique intersecting lines on orientation judgements (the Zöllner and related illusions). The biasing effect of oblique lines was demonstrated on the neuronal level in the preceding paper. Examples for the origin of the brightness illusion are shown in Figure 14 of the present paper. It results from an imbalance between units of opposite edge preference produced by unilateral corners. Unilateral line-ends must have a similar effect that causes the Ehrenstein illusion. These correlates need to be demonstrated in more detail and in larger samples, and the correlate of the depth effect still has to be discovered. Thus, the model of Figure 15 is not just a mechanism conceived to explain the present results; it reflects a general principle for the detection of occluding contours.

Grossberg and Mingolla (1985) have interpreted some of our results (von der Heydt et al., 1984), in terms of a cooperative neural network model of more general scope. In particular, they had independently postulated the excitation produced by orthogonal orientations and the gatelike interaction of distant parts of a figure. In their model, line-ends induce perpendicular “illusory line segments” that are weak on their own but can cooperatively interact if they are lined up. The cooperative connections are thought to extend in directions parallel to the orientations in order to enable inward completion of contours that occurs, for example, in the perception of a dashed line. This process also completes the “illusory line segments” at the ends of lines to a perceptual contour. The mechanism that we have suggested is different, but parallels may be drawn to some extent. The “illusory line segments” correspond to the signals of the end-stopped cells that form the second input to the contour neurons in our model, and the boundary completion scheme of figure 11 of Grossberg and Mingolla (1985) may be compared with the multiplicative connection and summation of the end-stopped cell signals in our Figure 15. Thus, the spatial interaction *parallel* to the “illusory line segments” in their model corresponds to the *perpendicular* connectivity of end-stopped receptive fields in ours.

Although we recognize Grossberg and Mingolla’s (1985) model as a unique attempt to explain a large body of knowledge about human vision by a relatively simple principle, we do not

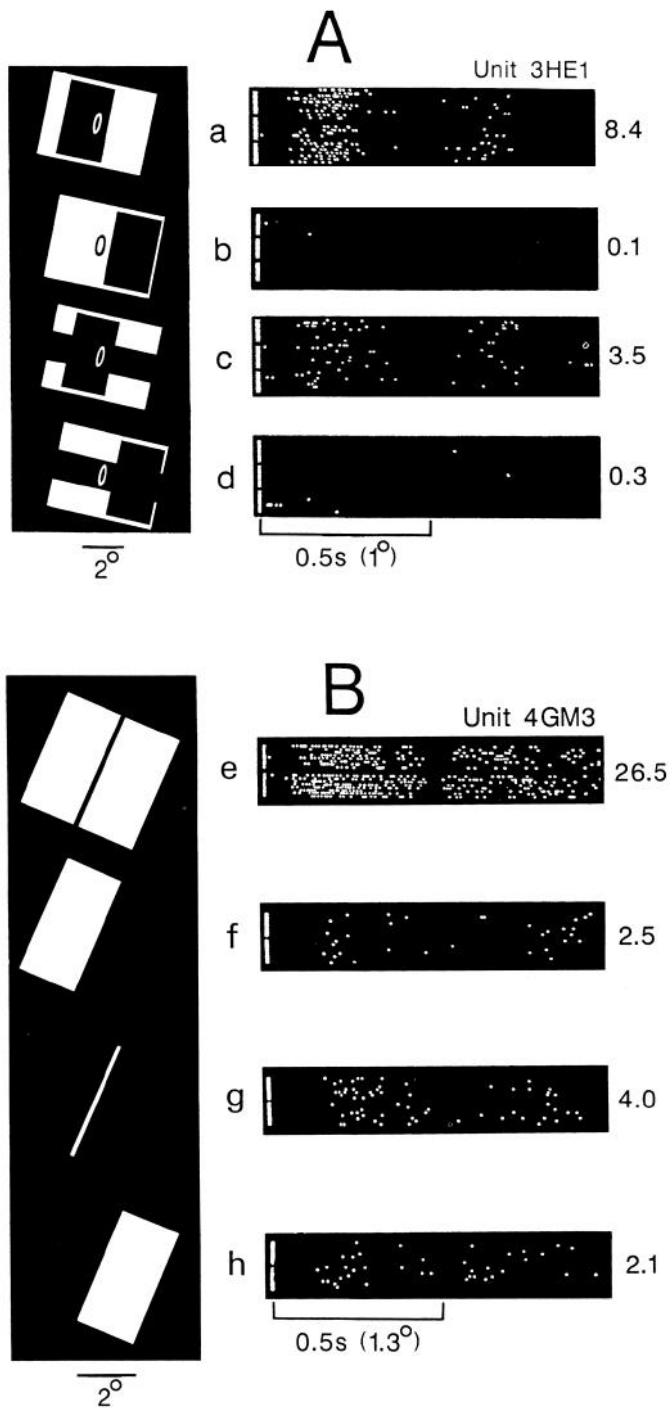


Figure 14. Pattern selectivity of contour cells. *A*, This cell was selective for edge polarity. It responded when darkness was on the left side (and mostly during right-left movement) but not to edges with darkness on the right. It also signaled the edge of an illusory bar that *appears* to be darker than the background, when the apparent darkness was to the left. The gap size was 80 min arc (see also Fig. 4*A* for responses of the same neuron). *B*, Responses of the same cell as in Figure 2*B* to edges and light and dark bars. The cell responded selectively to narrow dark bars. The differential activation of cells with opposite contrast preference is thought to underlie the illusory brightness effect in the Kanizsa triangle and similar figures.

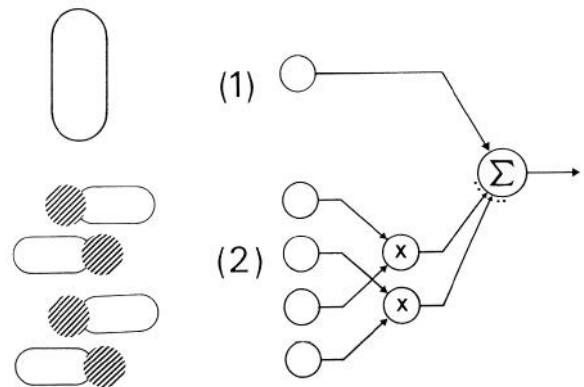


Figure 15. Principle of a hypothetical cortical mechanism for the perception of contour. We assume that 2 groups of signals are summed in a contour neuron (*C*), one from edge- or bar-detector units (*I*) and a second originating from units that are sensitive to corners and line-ends (*2*). The input fields of (*I*) and (*2*) are centered on the same patch of retina. The "end-stopped receptive fields" (*2*) are scattered along the axis of (*I*) and oriented about perpendicular to it. Only 4 have been drawn, but they are thought to cover the patch of visual field densely. Distant pairs of these fields are connected with multiplying or gating units (*x*), which has the effect that signals sum at *C* only if 2 or more of these fields are excited. We call (*I*) the "edge-detecting input" and (*2*) the "grouping input." (After Peterhans et al., 1986.)

want to commit ourselves to all its assumptions. Whether they are compatible with the known physiology of the visual cortex in general, and our experimental data in particular, is hard to say. The crucial assumption is, of course, that of cooperative feedback in the network. We shall come back to this point later. Another important feature is the interaction between the "boundary contour system," as sketched above, with a "feature contour system," which determines the perception of brightness and color. We have seen in Figure 14 that some contour neurons of V2 are selective for the polarity of contrast. To us, this seems to indicate that brightness information is carried along with contour information, including orientation. Finally, we cannot identify in Grossberg and Mingolla's (1985) model the functional group of end-stopped receptive fields. End inhibition in form of spatial center-surround antagonism between elements of like orientation is present at the stage of "short-range competition," the input layer of the cooperative mechanism. All elements at this stage share this property, signal orthogonal line segments at the ends of lines, and, by virtue of cooperative feedback, represent anomalous contours. In the cortex, only part of the orientation-selective cells are end-stopped (hypercomplex). These highlight the corners and line-ends in anomalous-contour figures (Peterhans and von der Heydt, 1987), but, in general, they do not signal anomalous contours. Except for the contour neurons in V2, we have never observed that orientation-selective neurons in monkey V1 or V2 were activated by ends of lines orthogonal to their preferred orientation.

We cannot definitely rule out processes of attention, or cognition (Gregory, 1972), since we did not attempt to vary these factors in our experiment. However, the responses to the anomalous-contour stimuli were stereotyped and could be reproduced over and over again, often for hours. They were quite similar in this respect to the responses obtained with conventional stimuli in V2 or even V1. If a cognitive process were involved, it would probably not be so reproducible. Attention is not likely to be a major factor in these experiments because the animals

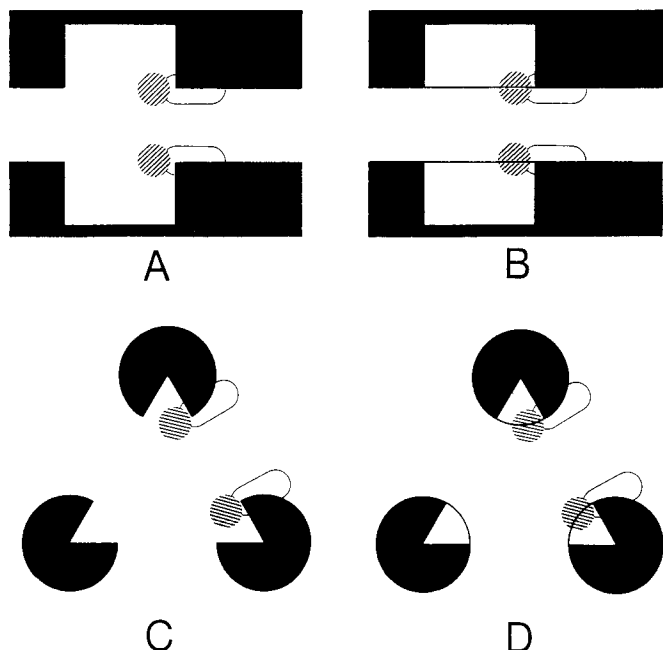


Figure 16. Origin of illusory contours and the effect of figure closure. Corners on opposite sides of the gap excite a pair of end-stopped fields (A, C), which is sufficient to drive the grouping input. The closing lines fall on the inhibitory end-zones and thus reduce this activation (B, D).

are trained to pay attention to the fixation target and probably succeed to ignore the additional visual stimuli as much as possible.

Another point is that central influences would take some time to develop after the onset of a stimulus. However, in the preceding paper we have shown that anomalous contours can be signaled with short latency (von der Heydt and Peterhans, 1989a, Fig. 19). The observation that orientation selectivity was there right from the beginning also argues against the possibility that the neural process determining anomalous contours is iterative; in a cooperative network one would see the final orientation signaled only after several (at least one) cycle of iteration. In such a network, analog signals have to be circled with some accuracy, which takes time if spike frequency coding is assumed (see Marr, 1982, p. 107). One could trade in number of cells for time by coding signals in parallel activity; but cortical neurons may not be abundant since, besides orientation, several other dimensions have to be represented (see Ballard et al., 1983). Further experiments are necessary to work out the time dependence of the contour-related neuronal responses.

The cognitive explanation of illusory contours (Gregory, 1972; Rock and Anson, 1979) is widely accepted. It conceives the contours as the result of a problem-solving process, the decision between perceptual hypotheses. This theory has difficulties with some observations that our physiological concept can easily explain. In the Ehrenstein figure, the hypothesis of an occluding disk-shaped object is equally acceptable whether the lines are radial or oblique, but the perceived contour is much weaker with oblique lines, and Figure 15 explains why. When, in the image of a 3-dimensional scene, several lines and edges terminate at a straight or smoothly curved virtual line, this line is likely to be the contour of an occluding object, and the more linear structures terminate, the more likely it is. In our scheme, the summation in the grouping path reflects this knowledge, and

explains the gradual increase of neuronal responses. Also, the perception increases gradually (see Fuld and O'Donnell, 1984, for quantitative data). This is at odds with the cognitive theory; how can a decision be gradual? The observation that anomalous contours can produce tilt aftereffects just as edge-type contours (Smith and Over, 1975) is more easily explained in our physiological concept: Orientation of either type of contour is signaled by the same neurons. Finally, the demonstration by Spillmann et al. (1984) that the illusory darkness (or brightness) in the Ehrenstein pattern can be canceled by patches of light (or darkness) is direct psychophysical evidence for our model. Effects of line-ends and light-dark edges can only cancel if the corresponding signals sum algebraically, as in the summation unit in Figure 15. Can a cognitive figure be canceled by a patch of light?

Conclusion

The discussion of response mechanisms should not conceal the primary goal of the present studies—determining what the cortical neuron responses might represent. Our experiments were guided by the idea that the contours that we perceive are not stimulus features but a creation of the brain. Perception of contour is not just a matter of detection, because nothing of this kind exists in the light distribution given to the eyes. Contours are inferences. A large body of knowledge exists about the perception of contours, under which conditions they appear, where they are located, and what their qualities are. We have tried to use this knowledge for interpreting neural signals, and this attempt might also help to understand the phenomena of contour perception.

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