70 Contour Integration and the Lateral Connections of V1 Neurons

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THERE IS AN OFTEN repeated claim that the only man-made object that can be seen from space is the Great Wall of China (Fig. 70.1): a structure that is in some sections over 2500 years old, and that snakes over some 6000 km of countryside. In reality, at the altitude of orbital flights, astronauts report seeing a variety of man-made structures, including roads and large seaway projects such as the Suez and Panama Canals. What characterizes many of these structures is the length and smooth continuity of the contours they create across the surface of the earth.

The notion that continuity is important to visual perception was a central idea of the Gestalt psychologists, who, in the first half of the twentieth century, described a set of perceptual grouping principles that included the *law of good continuation*. In formulating their laws, the Gestalt psychologists had rebelled against the belief that perception could be described as the consequence of simple accretion of visual elements.

Over the past 10 years, cognitive neuroscience has renewed its interest in the representation of contours and continuity. Researchers in visual anatomy, neurophysiology, computer science, and visual psychophysics have combined their approaches to develop models of how contours are perceived and integrated by the visual system. The reasons for this interest are several. Perhaps of primary importance is the fact that up to recently, much of the work on vision has concentrated on the properties of single neurons. Neuroscience data have provided considerable insight into the properties of the individual neurons that occur along the visual pathway. This work suggests that in the early stages of visual processing, the image of our visual environment is transformed into the responses of large arrays of neurons, each selective to properties such as orientation, position, spatial frequency, and direction of motion. Indeed, it has been argued that these basic properties of the visual system may produce a solution that is close to optimal for describing our natural environment (e.g., Field, 1987; see Chapter 108, for review). However, the question remains of how this information, encoded by different neurons, is integrated into the perception of whole objects and scenes. One common theme is that the visual system does so by building a hierar-

chy of ever more complex receptive fields through series of feedforward connections.

In this chapter, we review recent work that takes a different approach. This work suggests that, as early as primary visual cortex, neurons cannot be treated as simple feedforward devices that merely receive input from the retina. Their response properties depend on a complex relationship between the neighboring neurons and their input. In particular, this recent work demonstrates that neurons in primary visual cortex make use of long-range lateral connections that allow integration of information from far beyond the classical receptive field, and the evidence suggests that these connections are involved in associating neurons that respond along the length of a contour.

The classical description of a cortical neuron in primary visual cortex is that of a neuron, with feedforward inputs from the lateral geniculate nucleus, whose pattern of connections produces the receptive field profiles described in the 1960s by Hubel and Weisel (see Hubel, 1988, for review). This classical receptive field of a visual neuron is defined as the area of the visual field that has the capacity to modify the resting potential of the neuron. However, while this basic feedforward linear model of the simple-cell receptive field has been invoked to explain a wide variety of perceptual phenomena ·and is at the heart of a wide range of modeling studies—it is essentially wrong. Some of the earliest studies that measured receptive field properties of cortical neurons recognized that stimuli presented outside the classical receptive field can modify the activity of the neuron, even if those regions by themselves cannot effect a response (e.g., Maffei and Fiorentini, 1976).

The neurons in primary visual cortex show a variety of interesting nonlinearities, with many occurring within the classical receptive field. However, the nonlinearities that are of interest to us here are the responses to regions outside the classical receptive field. Stimulation of these areas typically does not produce a response but can modulate the activity of the neuron. This modulation in activity has commonly been described as inhibitory, and a variety of theories have been proposed (e.g., Allman et al., 1985). One popular account has argued that this inhibition can serve to
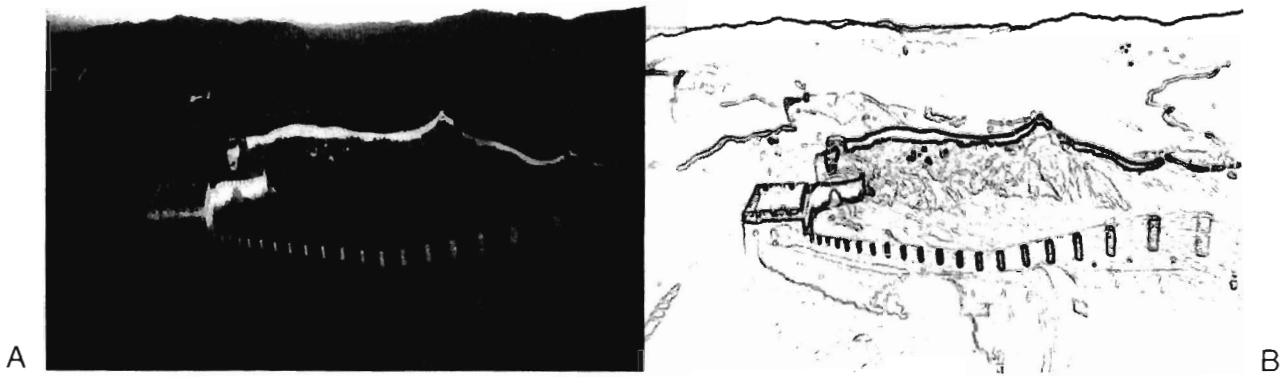
FIGURE 70.1. The Great Wall of China is one of a small number of man-made structures visible from space. The length and continuity of the contour etched on the surface of the earth by the wall allow the structure to be visible at considerable distances. The figure in *B* is an edge map of the picture of the Great Wall (*A*) using a simple (Sobel) edge detector. In the classical view, a neuron in primary visual cortex responds to only a limited region of the visual field and responds to a restricted range of stimulus orientation. To see the contour formed by the wall as a single entity, some process must integrate the different pieces of the contour. (*Christopher Liu/ChinaStock, All Rights Reserved.)

normalize the neuron's response and make more efficient use of the neuron's limited dynamic range (Heeger, 1992; Schwartz and Simoncelli, 2001).

In this chapter, we concentrate on a new theory to account for some of these nonlinear effects. This theory proposes that the nonclassical surrounds of receptive fields are intimately involved in a process called *contour integration*. We do not mean to imply that contour integration is their only role; however, the evidence suggests that it is one role. Indeed, the evidence suggests that some of the effects that have given rise to the notion of nonclassical surrounds are generated by the active grouping or *association* of cells in neighboring regions of the visual field. In accord with the term *receptive field*, we have used the term *association field* to describe the region of associated activity (Field et al., 1993), while others have used the term *integration field* (e.g., Chavane et al., 2000) or *contextual field* (e.g., Phillips and Singer, 1997; see also Chapter 113).

In the following pages, we address four questions and explore some of the research that is providing answers. The questions are as follows: (1) What is contour integration, and why is it important? (2) What do the anatomy and physiology suggest about the underlying mechanism? (3) What does the behavior of individuals –humans and nonhuman primates —suggest about the underlying mechanism? (4) What insights are provided by computational models of the process?

We should note that when putting this review together, we discovered over 500 papers published in the past 10 years that bear directly on these issues of integration. Recently, a number of excellent reviews and discussions have been published on the topic or on associated topics. We recommend Fitzpatrick (2000), Gilbert (1998), and Callaway (1998) for discussions of anatomy and physiology; Polat (1999) and Hess and Field (1999) for reviews of psychophysics; and Li (1998) and Yen and Finkel (1998) for their comprehensive discussions of the computational issues. In the limited space of this chapter, therefore, we will concentrate on a few issues which we feel have not received the primary attention of the above authors.

What is contour integration?

Consider the image shown in Figure 70.1*A*. Because reflection and illumination vary across the different surfaces, occlusions between surfaces commonly produce a luminance discontinuity (i.e., an edge), as shown in the edge map in Figure 70.1*B*. However, edges in scenes do not occur only at occlusions. They may also arise from textures within surfaces, as well as from shading discontinuities.

In the 1980s, a number of modeling studies were published that proposed computational strategies that would help to identify which of the edges in a scene made up the principal boundaries of an object. Under the assumption that boundary edges were likely to extend over large regions of the visual field, the computations were designed to extract only those edges that were continuous over an extended area. The algorithms that were developed were based on the assumption that the problem could be at least partially solved by integrating over neighboring regions that had similar orientations. However, although some of these integration models included, or were derived from, known physiology (e.g., Grossberg and Mingolla, 1985; Parent and Zucker, 1989), the evidence that an integration algorithm of this kind was actually performed by the visual system was not widely accepted.

Two lines of research have recently helped to support the plausibility of a scheme such as the one described above. The first line comes from a series of anatomical and physiological studies that used both cat and primate and suggest that there exist long-range connections between neurons in

primary visual cortex that link neurons with similar orientations. The second line consists of two types of psychophysical study that have provided evidence for the sorts of associations implied by the physiological and anatomical results (Field et al., 1993; Polat and Sagi, 1993, 1994). The results of these studies converge on an account that suggests that neurons in primary visual cortex integrate information from outside the classical receptive field in a way that promotes the integration of contours. Below we review some of these studies.

Physiology and anatomy of lateral connections

As noted above, a variety of early studies showed that stimuli outside of the classical receptive field of a neuron in visual cortex can modulate that neuron's activity. The sources of modulation potentially originate from feedforward connections, feedback connections from neurons farther along the visual pathway, lateral projections from neighboring neurons, or a combination of all three. Although we concentrate here on lateral connections, the modulation activity is almost certainly dependent on a more complex circuit involving all three. What has been remarkable over the past few years, however, has been the close ties found between lateral connections and visual behavior of humans and macaques when completing appropriate psychophysical tasks.

Early studies exploring the horizontal connections in visual cortex discovered that pyramidal neurons have connections that extend laterally for 2 to 5 mm parallel to the surface and have terminations that are patchy and selective (Gilbert and Wiesel, 1979; Rockland and Lund, 1982). Studies on the extent and specificity of lateral projections have now been completed on the tree shrew (e.g., Bosking et al., 1997; Rockland and Lund, 1982), primate (e.g., Malach et al., 1993; Sincich and Blasdel, 2001), ferret (e.g., Ruthazer and Stryker, 1996), and cat (e.g., Gilbert and Wiesel, 1989), with largely good agreement between species but also some important differences.

Figure 70.2A provides an example of one of the impressive techniques that reveals the specificity of projections using a combination of optical imaging and anatomical data. These results from Bosking et al. (1997) show an overlay of the orientation columns revealed by optical imaging, with the lateral projections of pyramidal neurons near the injection site synapsing onto the surrounding regions. The lateral projections are revealed through extracellular injections of biocytin which label a small number of neurons near the injection site, along with their projections. The orientation tuning of a particular neuron is estimated by its location within an orientation column.

As the figure shows, the orientation column of the injection (shown by the dark areas) has the same orientation as those of the columns where the long range projections project (i.e., they synapse onto neurons that are also in the dark regions). The short-range projections do not show such specificity. Bosking et al. also found that in tree shrew the extent of the long-range projections was significantly greater along the axis corresponding to the orientation of the central neuron.
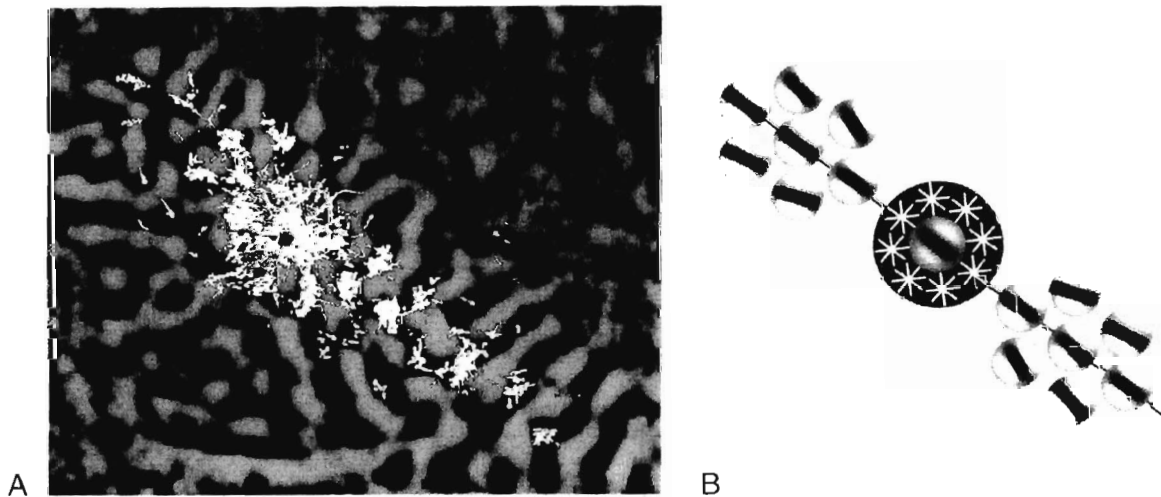

FIGURE 70.2. A, Results modified from Bosking et al. (1997) demonstrating the orientation-specific projections of a set of V1 neurons in the tree shrew. Optical imaging is used to reveal the orientation columns, while injections of biocytin are used to map the projections of a set of neurons taking up the biocytin (shown in white). As can be seen, the location of the orientation column of the injection is the same in most cases as the orientation column of the projection. B, An experimentally and theoretically derived association field (Field et al., 1993) summarizing our beliefs regarding the underlying projections. Short-range connections are theorized to be largely inhibitory and independent of orientation, while long-range connections are theorized to be orientation specific and largely excitatory.

contour-integration effects are due to dynamic changes to the classical receptive field. Do these effects simply reflect the expansion of the receptive field? This explanation may account for the effects of the contrast threshold, but there are three reasons why, for the contour integration task, it may not be an adequate explanation. First, the threshold effects are strongly dependent on the phase or polarity of flanks (Williams and Hess, 1998), while contour integration has little phase dependence (Field et al., 2000). Second, contour integration occurs between elements that differ by more than 30 degrees (Field et al., 1993) when the alignment is appropriate (Fig. 70.3A), but there is no evidence that the expansion of the receptive field's length would allow such integration. Third, there appears to be little evidence that perceived contrast is enhanced by flanking stimuli. We will return to this issue in the next section, but the reader can view Figure 70.3A and ask whether the elements in the path appear to be higher in contrast. Hess et al. (1998) found that large variations in contrast had no effect on the ability to detect the presence of the contour. Xing and Heeger (2001) also found no changes in perceived contrast when grating patches were surrounded by patches of similar contrast. Changes were noted only when the flanking patches were significantly higher in contrast.

Other psychophysical techniques have demonstrated intriguing results. Chavane et al. (2000) have demonstrated that the speed of an oriented element appears higher when it moves in a direction collinear to its axis than when it moves in a direction orthogonal to its axis. They argue that long-range connections may be responsible. Kapadia et al. (2000) have demonstrated that elements placed along the ends of a central element can induce a perceived change in the orientation of the central element toward the orientation of the central element. However, when the flanking elements are placed along the opposite axis (adjacent to the central element), the central element can be shifted away from the orientation of the flanking elements. They also demonstrated that the spatial distribution of this effect showed good agreement with the neurophysiology of cortical facilitation produced by the flanking lines. Mareschal et al. (2001) have also demonstrated that with a collinear arrangement, flanking grating patches can significantly increase the orientation discrimination thresholds of the central patch. Furthermore, the threshold increase is significantly higher in the collinear arrangement than when the orientation of the elements is perpendicular to the positions of the three patches.

Kovacs and Julesz (1993) demonstrated that when measuring the visibility of a path of elements as a function of the density of the surrounding elements, the path is significantly more visible if the contour forms a closed figure. Pettet et al. (1998) argue that this effect may be related to the directional smoothness of the contours (i.e., a circular

figure has all the elements changing orientation in a consistent direction). In either case, both results demonstrate that sensitivity depends on elements farther away than the immediate neighbors. The simple model, based on excitatory effects between neighbors, will not produce this effect. Of course, there is no reason to assume that these psychophysical effects necessarily occur in V1, and these psychophysical results may be an indication of the direction of attention toward features that undergo predictable change. Nonetheless, the results suggest that thresholds for perceiving contours depend on complex relationships.

We conclude this section on the psychophysical phenomena with a fascinating study by Kovacs et al. (1996). As noted earlier, Hess and Field (1995) demonstrated that it was possible to integrate contour fragments that had relatively large binocular disparities between them; Kovacs et al. went much further and presented to observers binocular image pairs that would be expected to produce rivalry. Consider the presentation of two completely different natural scenes to each eye. Under such conditions, one would expect one eye or the other to dominate much of the time. Kovacs et al. presented such images to observers and then broke up each pair so that each eye received patches from both images, such that the left eye received the complement of the right (e.g., the right eye gets 1,2,1,2,2,1 with the left eye receiving 2,1,2,1,1,2). As one can readily see by observing their demonstrations, Kovacs et al. found that observers commonly see complete images (1,1,1,1,1,1 or 2,2,2,2,2). The contours and other visual information were successfully integrated between the two eyes into a single perceptual whole. This result implies that the process involved in integrating contours is not eye specific.

Computational modeling

In some cases, computational models are simple reflections of the data found experimentally. They can be considered *existence proofs* demonstrating that it is at least possible to perform the desired task with the proposed architecture. They cannot demonstrate that the visual system necessarily uses the architecture of the model, but they can demonstrate that such a model would work if that architecture did underlie the task. However, at times, these models are most useful when they fail, and that may well be the case in the following studies we discuss.

To integrate contours, a variety of algorithms have been proposed that use the technique of integrating similar orientations along collinear directions. Part of the argument for using a collinearity algorithm appears to be that the nature of the task demands it. However, these early studies also went to some lengths to explain how such an algorithm might fit with the known physiology and anatomy (e.g., Grossberg and Mingolla, 1985; Parent and Zucker, 1989;

Shashua and Ullman, 1988). In the past 5 years, as our understanding of the underlying physiology has increased, so has the sophistication of computational models (e.g., Geisler and Super, 2000; Li, 1998, 2000; Yen and Finkel, 1998). These models have demonstrated that the architecture revealed by the physiology and anatomy can be used to provide an efficient means of extracting contours in natural scenes, and it can be used to account for a significant amount of the psychophysical data.

Our work on contour sensitivity (Field et al., 1993) was partly motivated by the belief that the properties of natural edges would be more efficiently coded by a linking process rather than by a high-level neuron tuned to the particular contour in question. The difficulty with the high-level neuron model is that the number of possible contours in the natural world, or even in our experiments, is much too large to have a neuron for every contour.

Geisler et al. (2001) and Sigman et al. (2001) have taken the ecological approach further and asked whether the contour integration model is an efficient means of coding natural scene contours. They measured the co-occurrence statistics of edge elements in natural scenes and found that the relative orientations of neighboring contour segments match well with those predicted physiologically, and with psychophysically defined association fields. Geisler et al.'s results are particularly interesting because of the requirements needed to measure these co-occurrence statistics. As they argue, these statistics are multidimensional in nature. Given an edge at a particular location with a particular orientation, the region around that location is a three-dimensional probability map of x-position by y-position by orientation. Only by mapping out this full probability map does one see the full set of statistical dependencies. And it is in these conditional probabilities that one finds the orientation dependencies that map onto the association field properties. The probability map is much higher in dimension if we include the additional dependencies across scale, chromaticity, motion, and disparity. Indeed, our own work (Hayes and Field, in prep.) suggests that both perceptual integration over scale and the structure of natural edges through scale follow similar rules.

A potential difficulty for all recent models (e.g., Geisler and Super, 2000; Li, 1998; Yen and Finkel, 1998), as well as for earlier models (e.g., Grossberg and Mingolla, 1985), is that they generally assume that recurrent activity increases the responses of the neurons along the contour. This assumption is supported by some neurophysiological results which show an increase in response rate with flanking collinear lines (Kapadia et al., 1995; Nelson and Frost, 1985). The difficulty is in understanding how the visual system untangles the relationship between neural activity and contrast. Responses increase with contrast, and they also increase with collinear arrangements. How does the visual

system decipher differences in contrast variation from differences in context (i.e., collinearity)?

Using human psychophysical techniques, Hess et al. (1998) found that contrast changes have little effect on the visibility of a contour. Consider the image shown in Figure 70.3. The contrast of the path elements is perceived to be the same as that of the background. Such results suggest that neurons must somehow carry the code for contrast separately from the code for the continuity of the contour. There are various possibilities for how this might be achieved. One possibility is that neurons that code contrast are different from those that code the contour. Under this hypothesis, we would need to assume that both neurons coding for contrast and neurons coding for continuity are present in V1.

A second approach proposes that continuity is represented by a temporal code, presumably tied to the synchronous activity of neighboring neurons. This approach to *binding* has received considerable recent attention and has some experimental support (Singer and Gray, 1995; see also Chapter 113). The difficulty with this model is that it requires a mechanism to detect the synchrony. Hess et al. (1998) suggest a rather different and more basic version of a temporal code. They suggest that contrast information is represented by the initial response generated by the feedforward activity, with the later response determined by the lateral connections and the context of the surrounding regions. The contrast signal could then be extracted from the collinearity signal by simply tracking the timing of the response. This hypothesis was derived from the neurophysiological work of Zipser et al. (1996). Using textures as stimuli, they found results consistent with this theory. However, Kapadia et al. (1999) provide data that are supportive in some ways but also make the story more complex. As noted in the previous section, Kapadia et al. found that collinear facilitation for neurons in V1 occurs only at low contrasts or at high contrasts in complex backgrounds. They also noted that this facilitation occurs after the initial transient response of the neuron during the *sustained* component of the response. This aspect of the response fits the model proposed by Hess et al. (1998). However, at high contrasts, the neurons do not show this sustained response, but only the sharp transient response. What sort of model predicts this high-contrast behavior? It may involve some degree of contrast normalization (e.g., Heeger, 1992), but at present we are not aware of any model that predicts both the timing of responses and the lack of facilitation at high contrasts.

There is also the question of whether lateral feedback has the appropriate timing to account for the neurophysiological findings. Along these lines, Van Rullen et al. (2001) provide an interesting alternative to the above models. They argue that models that iterate toward a solution using recurrent lateral feedback are too slow to explain reaction-time data and neurophysiological responses measured during

visual recognition. They suggest that the contours might be represented not by the magnitude of the neural response, but by the relative speed at which responses pass through the visual system. They argue that lateral connections may serve to facilitate the initial response allowing the collinear context to push the most "meaningful" information most quickly through the visual system.

However, all of the models fail to predict the smoothness constraint described by Pettet et al. (1998), whose results demonstrate that a contour which changes in a consistent direction is more visible than a contour which has multiple changes in direction. Such results suggest that sensitivity is a function of more than immediate neighborhood interactions. Contours changing orientation in a consistent angular direction provide for greater sensitivity. But whether this sensitivity is related to the lateral connections in V1, or to higher-level interactions or higher-level feedback, remains to be seen.

Some remaining questions

There remain a number of interesting and fruitful directions for research in this area, as well as a number of problems.

Psychophysical research, computational modeling, and measurements on natural scenes all support a particular mapping, such as that shown in Figure 70.2B. They suggest that off-axis projections will project to off-axis orientations along the lines of smooth curves. Our own eyeball estimates of the published anatomical data of Bosking et al. (1997) seem to suggest that the off-axis projections project to orientation columns that are slightly shifted from those along the primary axis. To our knowledge, though, no quantitative study has been conducted to support or dismiss this hypothesis.

Another question of interest is how contours are integrated across the midline. In V1, communication across the midline must pass across the corpus collosum, a pathway that is significantly longer and possibly less efficient. However, there appear to be no large differences between the integration across the midline or within a hemifield. Presumably, if integration occurs across the midline, this would show up as a delay in processing or a reduction in sensitivity. In our own unpublished work on this problem, no significant delay was found. Indeed, if no differences were found between contour integration across hemifields versus within hemifields, it would argue that much of the contour integration task (or at least the limiting factors in the task) must be performed by areas beyond V1.

There also remain questions regarding the relation between contour integration effects and the wide range of studies on illusory contours. A large number of studies that have investigated the perception of illusory contours, and have explored the conditions which produce the appearance of an illusory surface partially bounded by illusory edges (e.g., see Lesher, 1995, for a review). The perception of the illusion depends on the *relatability* of the supporting contours (Kellman and Shipley, 1991), meaning that the supporting contours must fall along first-order curves, as shown in Figure 70.4A. However, the illusion also depends on the end junctions of the supporting contours (e.g., Rubin, 2001). Figure 70.4B shows an example where the illusion is blocked by converting the L-junctions inducing corners into T-junctions. Kapadia et al. (1995) have demonstrated that T-junctions can also reduce the sensitivity in a contour integration task when the elements are made of T-elements rather than simple line elements. Kapadia et al. also demonstrated that with single neurons, the effects produced by flanking collinear lines are also reduced with such flanking lines.

Although there are clearly some important relationships between illusory contours and contour integration, the illusion is certainly not a necessary component of the integration process. As readers may see for themselves, the perception of the contour in Figure 70.3A does not result in an illusion of luminance or the perception of structure between the elements. We should also note that while lateral connections presumed to underlie the contour integration task are found with V1 neurons, neural responses corresponding to illusory contours are not found earlier than V2 (Peterhans and von der Heydt, 1989; von der Heydt et al., 1984). Zhou et al. (2000) have also found that over half of the neurons in V2 and V4 also show selectivity to border ownership. Given the same local contour information (the same information within the classical receptive field), the majority of neurons were found to respond differentially to larger object properties. For example, a neuron responding to a vertical edge may produce a larger response, depending on whether the contour is part of an object to the left or to the right of the contour. In contrast to V2, only 18% of the neurons in the top layer of V1 show this differential response. Zhou et al. (2000) also noted that the differential response to border ownership occurred within 25 msec of
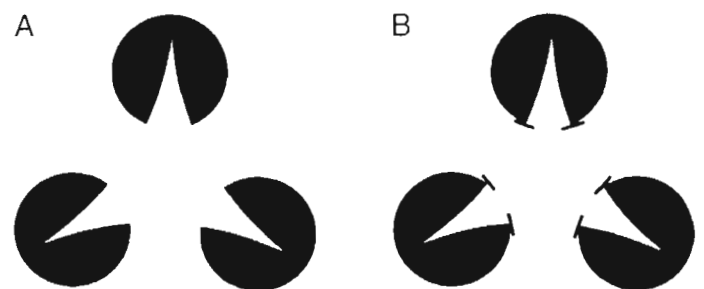

Figure 70.4. A shows a modified Kaniza figure that typically results in the perception of an illusory contour. B demonstrates the importance of the supporting endpoints in this illusion. The T-junction will typically reduce the strength of the illusory triangle.

response onset, arguing that the solution is generated within the visual cortex.

These results imply that lateral connections in V1 are important to the integration of contours, but they are not directly involved in the more complex "object" relationships portrayed by illusory figures and by object identity.

Summary

The anatomical, neurophysiological, psychophysical, and computational research of the past decade provides a compelling argument that neurons in area V1 integrate information from beyond the classical receptive field in a manner that assists in the integration of contours. Integrated contours represent a critical component of natural scenes important to early vision. They are important in defining the boundaries and extents of the objects in our world.

The lateral connections between neighboring neurons are certain to play a number of roles besides contour integration. As argued by a number of investigators, these connections are likely to play a role in contrast normalization, stereo, motion, and texture segregation, among others. Furthermore, the facilitation with single neurons is contrast dependent, and this may imply that the facilitation at collinear positions is a secondary effect to the inhibition found in much of the nonclassical surround. It is also likely that few of these computational problems are "solved" in V1. V1 neurons receive a large amount of input from higher visual areas, which undoubtedly plays a significant role. Indeed, there is ample evidence that both task outcome and the activity of these neurons can be modulated by attention (e.g., Ito and Gilbert, 1999) suggesting that our final model of V1 will be considerably more complex.

Overall, the studies reviewed here call into question the notion that V1 codes the visual world by breaking it down into an array of independent features. Although V1 neurons are differentially selective to a variety of visual features, their lateral connections, and the related perceptual phenomena, suggest that V1 should be considered as a complex web of interactions. Each neuron's response depends in a complex way on its neighbors, on its inputs, and on feedback from higher levels. With the current surge of studies exploring these interactions, a clearer picture of their role is expected to develop over the next few years. At this time, however, the evidence suggests that the Gestalt psychologists of the early twentieth century had a profound insight with their law of good continuation. The integration of contours represents one task well served by the complex interactions found in early vision.

REFERENCES

Allman, J., F. Miezin, and E. McGuinness, 1985. Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons, *Annu. Rev. Neurosci.*, 8:407–430.

Bosking, W. H., Y. Zhang, B. Schofield, and D. Fitzpatrick, 1997. Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex, *J. Neurosci.*, 17:2112–2127.

Callaway, E. M., 1998. Local circuits in primary visual cortex of the macaque monkey, *Annu. Rev. Neurosci.*, 21:47–74.

Chavane, F., C. Monier, V. Bringuier, P. Baudot, L. Borg-Graham, J. Lorenceau, and Y. Fregnac, 2000. The visual cortical association field: a Gestalt concept or a psychological entity? *J. Physiol. (Paris)*, 94:333–342.

Dakin, S. C., and R. F. Hess, 1998. Spatial-frequency tuning of visual contour integration, *J. Opt. Soc. Am. A*, 15:1486–1499.

Dakin, S. C., and R. F. Hess, 1999. Contour integration and scale combination processes in visual edge detection, *Spatial Vis.*, 12:309–327.

Das, A., and C. D. Gilbert, 1999. Topography of contextual modulations mediated by short-range interactions in primary visual cortex, *Nature*, 399:655–661.

Field, D. J., 1987. Relations between the statistics of natural images and the response properties of cortical cells, *J. Opt. Soc. Am. A*, 4:2379–2394.

Field, D. J., A. Hayes, and R. F. Hess, 1993. Contour integration by the human visual system: evidence for a local "association field," *Vis. Res.*, 33:173–193.

Field, D. J., A. Hayes, and R. F. Hess, 2000. The roles of polarity and symmetry in contour integration, *Spatial Vis.*, 13:51–66.

Fitzpatrick, D., 2000. Seeing beyond the receptive field in primary visual cortex, *Curr. Opin. Neurobiol.*, 10:438–443.

Geisler, W. S., J. S. Perry, B. J. Super, and D. P. Gallogly, 2001. Edge co-occurrence in natural images predicts contour grouping performance, *Vis. Res.*, 41:711–724.

Geisler, W. S., and B. J. Super, 2000. Perceptual organization of two-dimensional patterns, *Psych. Rev.*, 107(4):677–708.

Gilbert, C. D., 1998. Adult cortical dynamics, *Physiol. Rev.*, 78:467–485.

Gilbert, C. D., and T. N. Wiesel, 1979. Morphology and intracortical projections of functionally characterised neurones in the cat visual cortex, *Nature*, 280:120–125.

Gilbert, C. D., and T. N. Wiesel, 1989. Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex, *J. Neurosci.*, 9:2432–2442.

Grossberg, S., and E. Mingolla, 1985. Neural dynamics of perceptual grouping: textures, boundaries, and emergent segmentations, *Percept. Psychophys.*, 38:141–171.

Hayes, A., 2000. Apparent position governs contour-element binding by the visual system, *Proc. R. Soc. Ser. B*, 267:1341–1345.

Heeger, D. J., 1992. Normalization of cell responses in cat striate cortex, *Vis. Neurosci.*, 9:181–197.

Hess, R. F., and S. C. Dakin, 1997. Absence of contour linking in peripheral vision, *Nature*, 390:602–604.

Hess, R. F., S. C. Dakin, and D. J. Field, 1998. The role of "contrast enhancement" in the detection and appearance of visual contours, *Vis. Res.*, 38:783–787.

Hess, R. F., and D. J. Field, 1995. Contour integration across depth, *Vis. Res.*, 35:1699–1711.

Hess, R., and D. Field, 1999. Integration of contours: new insights, *Trends Cogn. Sci.*, 12:480–486.

..., R. L., A. Hayes, and F. A. A. Kingdom, 1997. Integrating contours within and through depth, *Vis. Res.*, 37:691–696.

Hubel, D. H., 1988. *Eye, Brain, and Vision*, New York: Scientific American Library.

Ito, M., and C. D. Gilbert, 1999. Attention modulates contextual influences in the primary visual cortex of alert monkeys, *Neuron*, 22:593–604.

Kapadia, M. K., M. Ito, C. D. Gilbert, and G. Westheimer, 1995. Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys, *Neuron*, 15:843–856.

Kapadia, M. K., G. Westheimer, and C. D. Gilbert, 1999. Dynamics of spatial summation in primary visual cortex of alert monkeys, *Proc. Natl. Acad. Sci. USA*, 96:12073–12078.

Kapadia, M. K., G. Westheimer, and C. D. Gilbert, 2000. Spatial distribution of contextual interactions in primary visual cortex and in visual perception, *J. Neurophysiol.*, 84:2048–2062.

Kellman, P. J., and T. F. Shipley, 1991. A theory of visual interpolation in object perception, *Cogn. Psychol.*, 23:141–221.

Kisvarday, Z. F., and U. T. Eysel, 1992. Cellular organization of reciprocal patchy networks in layer III of cat visual cortex (area 17), *Neuroscience*, 46:275–286.

Kovacs, I., and B. Julesz, 1993. A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation, *Proc. Natl. Acad. Sci. USA*, 90:7495–7497.

Kovacs, I., T. V. Papathomas, M. Yang, and A. Feher, 1996. When the brain changes its mind: interocular grouping during binocular rivalry, *Proc. Natl. Acad. Sci. USA*, 93:15508–15511.

Lee, S. H., and R. Blake, 2001. Neural synergy in visual grouping: when good continuation meets common fate, *Vis. Res.*, 41:2057–2064.

Lesher, G. W., 1995. Illusory contours: toward a neurally based perceptual theory, *Psychonom. Bull. Rev.*, 2:279–321.

Li, Z., 1998. A neural model of contour integration in the primary visual cortex, *Neural Comput.*, 10:903–940.

Li, Z., 2000. Pre-attentive segmentation in the primary visual cortex, *Spatial Vis.*, 13:25–50.

Maffei, L., and A. Fiorentini, 1976. The unresponsive regions of visual cortical receptive fields, *Vis. Res.*, 16:1131–1139.

Malach, R., Y. Amir, M. Harel, and A. Grinvald, 1993. Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocyting injections in primate striate cortex, *Proc. Natl. Acad. Sci. USA*, 90:10469–10473.

Mareschal, I., M. P. Sceniak, and R. M. Shapley, 2001. Contextual influences on orientation discrimination: binding local and global cues, *Vis. Res.*, 41:1915–1930.

Mullen, K. T., W. H. Beaudot, and W. H. McIlhagga, 2000. Contour integration in color vision: a common process for the blue-yellow, red-green and luminance mechanisms? *Vis. Res.*, 40:639–655.

Nelson, J. I., and B. J. Frost, 1985. Intracortical facilitation among co-oriented, co-axially aligned simple cells in cat striate cortex, *Exp. Brain Res.*, 61:54–61.

Nugent, A. K., R. Keswani, R. L. Woods, and E. Peli, 2001. Contour integration in the peripheral field of normal and low vision observers, *Invest. Ophtalmol. Vis. Sci.*, 42(4):5612.

Parent, P., and S. Zucker, 1989. Trace inference, curvature consistency and curve detection, *IEEE Tran. Pattern Anal. Machine Intell.*, 11:823–839.

Peterhans, E., and R. von der Heydt, 1989. Mechanisms of contour perception in monkey visual cortex II: contours bridging gaps, *J. Neurosci.*, 9:1749–1763.

Pettet, M. W., S. P. McKee, and N. M. Grzywacz, 1998. Constraints on long range interactions mediating contour detection, *Vis. Res.*, 38:865–879.

Phillips, W. A., and W. Singer, 1997. In search of common foundations for cortical computation, *Behav. Brain Sci.*, 20:657–722.

**Polat, U., 1999. Functional architecture of long-range perceptual interactions. *Spatial Vis.*, 12:143–162.

Polat, U., K. Mizobe, M. W. Pettet, T. Kasamatsu, and A. M. Norcia. 1998. Collinear stimuli regulate visual responses depending on cell's contrast threshold, *Nature*, 391:580–584.

Polat, U., and D. Sagi, 1993. Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments, *Vis. Res.*, 33:993–999.

Polat, U., and D. Sagi, 1994. The architecture of perceptual spatial interactions. *Vis. Res.*, 34:73–78.

Rockland, K. S., and J. S. Lund, 1982. Widespread periodic intrinsic connections in the tree shrew visual cortex, *Science*, 215:1532–1534.

Rubin, N., 2001. The role of junctions in surface completion and contour matching, *Perception*, 30:339–366.

Ruthazer, E. S., and M. P. Stryker, 1996. The role of activity in the development of long-range horizontal connections in area 17 of the ferret, *J. Neurosci.*, 16:7253–7269.

Schwartz, O., and, E. P. Simoncelli, 2001. Natural signal statistics and sensory gain control, *Nat. Neurosci.*, 4(8):819–825.

Shashua, A., and S. Ullman. 1988. Structural saliency: the detection of globally salient structures using 2 locally connected network. In *Proc. Int. Conf. Comput. Vis. (ICCV) Tampa, FL*, 482–488.

Sigman, M., G. A. Guillermo, C. D. Gilbert, and M. O. Magneasco, 2001. On a common circle: natural scenes and Gestalt rules, *Proc. Natl. Acad. Sci. USA*, 98:1935–1940.

Sincich, L. C., and G. G. Blasdel, 2001. Oriented axon projections in primary visual cortex of the monkey, *J. Neurosci.*, 21:4416–4426.

Singer, W., and C. M. Gray, 1995. Visual feature integration and the temporal correlation hypothesis, *Ann. Rev. Neurosci.*, 18:555–586.

Van Rullen, R., A. Delorme, and S. J. Thorpe. 2001. Feed-forward contour integration in primary visual cortex based on asynchronous spike propagation, *Neurocomputing*, 38:1003–1009.

von der Heydt, R., E. Peterhans, and G. Baumgartner, 1984. Illusory contours and cortical neuron responses, *Science*, 224:1260–1262.

Walker, G. A., I. Ohzawa, and R. D. Freeman, 1999. Asymmetric suppression outside the classical receptive field of the visual cortex, *J. Neurosci.*, 19:10536–10553.

Williams, C. B., and R. F. Hess, 1998. Relationship between facilitation at threshold and suprathreshold contour integration, *J. Opt. Soc. Am. Ser. A*, 15:2046–2051.

Xing, J., and D. J. Heeger, 2001. Measurement and modeling of centre-surround suppression and enhancement, *Vis. Res.*, 41:571–583.

Yen, S. C., and L. H. Finkel, 1998. Extraction of perceptually salient contours by striate cortical networks, *Vis. Res.*, 38:719–741.

Yoshioka, T., G. G. Blasdel, J. B. Levitt, and J. S. Lund, 1996. Relation between patterns of intrinsic lateral connectivity, ocular

dominance, and cytochrome oxidase–reactive regions in macaque monkey striate cortex, *Cereb. Cortex*, 6:297 310.

Zhou, H., H. S. Friedman, and R. von der Heydt, 2000. Coding of border ownership in monkey visual cortex, *J. Neurosci.*, 20:6594 6611.

Zipser, K., V. A. F. Lamme, and P. H. Schiller, 1996. Contextual modulation in primary visual cortex, *J. Neurophysiol.*, 16:7376-7389.