

74 Visual Segmentation and Illusory Contours

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THERE IS AN IMPORTANT transformation that takes place in visual perception between the analog representation of the visual image in the retina and surfaces and objects as they appear to us. The retinal image represents numerous different brightness levels and colors at a very large number of different points in space, with no explicit representation of which points belong together. But the image we perceive consists of a much smaller number of surfaces and objects that are segregated from the background and from each other. There are probably many stages of this transformation, but one stage of this process is known to be of great importance: visual segmentation. Segmentation is a process of parsing the different surfaces in an image, as well as grouping together the parts of the same surface that are separated from each other in the image by another, occluding surface. Segmentation therefore involves resolving the depth relationships between surfaces and objects in a scene.

Understanding segmentation will lead to insight about one of the major theoretical problems in visual neuroscience, namely, how neural signals about small, localized pieces of the visual image are combined into a complete representation of the spatially extended visual image. This is a particularly important example of a general problem in neuroscience: how to go from the local to the global level of object representation in the brain. In this chapter, we review some of the large body of work on visual segmentation in human subjects and animals. The aim is to present a coherent body of experimental results that all relate to the question How is fragmentary visual information completed and made into wholes? There is another significant body of work, on the theory of segmentation computations in perception, that is beyond the scope of this chapter. That would make another interesting separate chapter of visual neuroscience.

Illusory contours

As with many brain computations, we can understand segmentation better by observing its action when it deals with an exceptionally difficult task. Usually segmentation is done so efficiently by the brain that we (as observers) are unaware that it is happening. But for certain special visual images, the segmentation process becomes evident. This is the reason for the fascination with these special images, the so-called illusory contours (ICs). An example of such a visual image is

Figure 74.1, an image referred to as a *Kanizsa triangle*, named after the Italian Gestalt psychologist Gaetano Kanizsa, who made this image famous (Kanizsa, 1979). In this figure, the perception of a bright white triangle is very strong, but if one scrutinizes the boundaries of the triangle, it becomes evident that there is no difference in the amount of light coming to the eye from the regions inside and outside the perceived triangle. Yet we see the inside as a bright surface segmented from its background by sharp contours along the boundary of the triangle. In this sense, the boundary between the inside and outside of the triangle is an IC. This image is a classical example in favor of the basic concept of the Gestalt psychologists, also echoed in the work of Donald Hebb, that the brain is “searching” for meaningful patterns. In this case, the brain manufactures a perceptual triangle from fragmentary information because a meaningful pattern, an occluding triangle, is consistent with the available image information even though other perceptions are possible. It is reasonable to believe that the segmentation computations the visual system performs on these exceptional Kanizsa images are the same as for more typical images.

One of the main points of scientific investigation of ICs is the nature and location of the brain area that performs the segmentation of the illusory figure from its background. Some psychologists have favored an explanation in terms of perceptual problem solving and think of ICs as *cognitive contours* (e.g., Gregory, 1987). Such cognitive approaches do not usually specify or even speculate about the brain areas involved in the perception. However, we could speculate that such a cognitive explanation would involve both visual cortical areas in the posterior cerebral cortex, as well as frontal and temporal cortex. In opposition to the top-down cognitive approach, more bottom-up, stimulus-driven approaches have been proposed (e.g., Grossberg, 1997; Heitger and von der Heydt, 1993). The bottom-up explanation would seem to imply the involvement in IC perception of early visual areas in which visual signals are still arranged retinotopically. There are psychophysical as well as neurophysiological and brain imaging studies of the nature of IC processing and also of localization of IC-evoked signals. The results of these different studies provide a fairly compelling case for the concept that IC perception is the result of the combined and cooperative action of early and later, or more retinotopic and more abstract, visual cortical areas. In this chapter, we

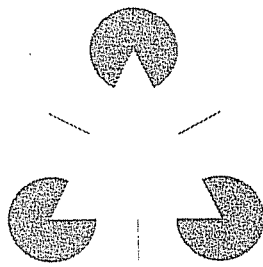


FIGURE 74.1. Kanizsa triangle. The occluding triangle that appears in front of the three circles and the three line segments has the same physical brightness as the surroundings. But it appears somewhat brighter, and appears to be a solid surface in front, because of perceptual processes.

begin by discussing psychophysical studies we have done on these problems, followed by a consideration of neurophysiological and brain imaging results on IC perception and segmentation.

Psychophysics of ICs

We have developed a psychophysical technique which was designed to provide an objective measure of the perceptual strength of ICs. This technique has yielded many new and interesting results that may enable us to forge a link between the perception and the neural mechanisms of perception related to segmentation. Figure 74.2 illustrates the technique: a shape discrimination task with ICs. The shapes are formed by Kanizsa-style Pacmen that are rotated around their centers by an angle α (see the figure legend for details). (*Pacman* is a term that refers to the shape of an agent in a video game from the early 1980s. The shape of Pacman was exactly the same as the cut-off circles used by Kanizsa in the IC figures he originated much earlier.) Two categories of shapes are formed: *thin* when $\alpha > 0$ and *fat* when $\alpha < 0$. The subject in the experiment must classify the shape. The pattern is flashed for about 100 msec, and then a mask follows presentation. With a series of control experiments, we showed that performance on this task is facilitated significantly when the subject sees the ICs compared to her or his performance when it is based on the local inducers' orientation. One control experiment was done to measure discrimination performance when all the inducers face outward. Then performance on the task was quite poor. Another control experiment proved that it was contour completion in the blank spaces between the pacmen inducers that was crucial for task performance (rather than the symmetrical rotation of the inducers, for instance). This second control experiment involved the placement of lines arranged along the boundaries of a virtual square that overlapped the thin or fat illusory figures. Such masking that is remote from the inducers does degrade performance by a factor of 2 or more. Thus, a high level of performance on the shape

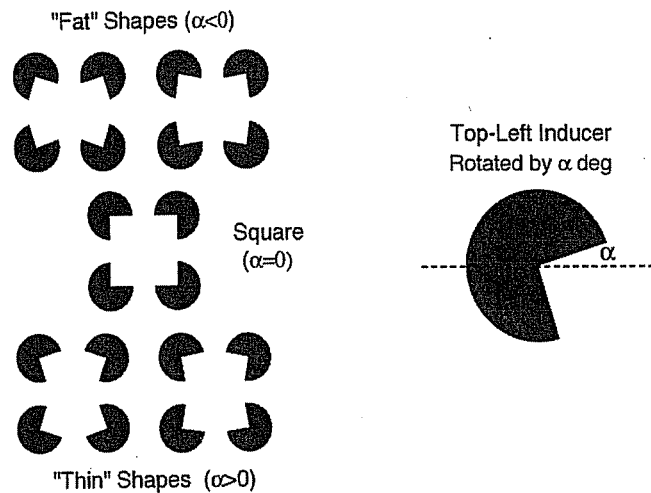


FIGURE 74.2. The thin-fat task used for psychophysics of ICs. *A*, A family of Kanizsa-like figures. The rotation parameter α specifies the angle of rotation of the upper-left inducer around its center, as shown in *B*. Adjacent inducers are rotated in opposite directions to achieve a consistent shape deformation of the illusory surface. (From Ringach and Shapley, 1996.)

discrimination task does, we believe, require perception of the illusory figures. We have used the task performance to answer quantitatively several important questions about illusory contours.

SPATIAL SCALE Ringach and Shapley (1996) found that ICs can span 15 degrees of visual angle, and thus must be formed by integration of neural signals over large distances in visual cortex. They also investigated the issue of spatial scale invariance. Scale-invariant properties of ICs were suggested by prior studies. Shipley and Kellman (1992) presented subjects with Kanizsa squares which varied in their absolute size and the radii of the inducing pacmen. They found that ratings of IC clarity were approximately scale invariant. In other words, the rating of a figure depended mainly on the ratio between the radius of the inducer and the side of the square. This ratio, termed the *support ratio*, is the crucial spatial parameter for ICs. In Ringach and Shapley's experiments on spatial scale, they collected shape discrimination data, as described above, with ICs at five different scales but always with the same support ratio. Figure 74.3 shows the variation in IC strength as a function of scale, and it is seen to be a relatively flat function. This is direct evidence for the spatial scale invariance of IC perception.

DYNAMICS Ringach and Shapley found that ICs can be formed by inducing elements that flash for a period of 100 msec, but that neural integration must proceed for longer than 250 msec for the contours to be completed. This is the conclusion of backward masking experiments in which

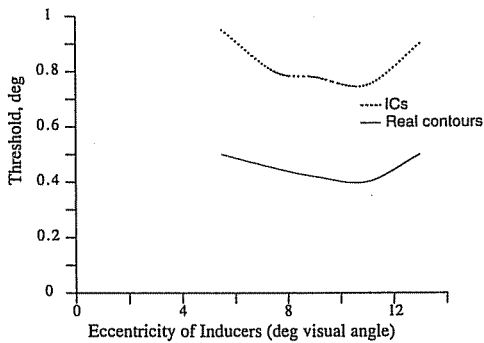


FIGURE 74.3. Scale invariance of IC perception. Thresholds for seeing ICs and real contours are plotted versus separation between the inducers. The real contours were drawn in the image connecting the corners of the inducers. Thresholds are expressed in terms of the rotation angle α that enables the observer to reach a criterion number of correct responses in the thin-fat task. (Figure derived from the data in Ringach and Shapley, 1996.)

the authors blocked the perception of a curved IC by the later presentation of a Kanizsa square. Control experiments with real contours show that shape discrimination is much faster with real contours than with ICs. That more time is needed to create the ICs than is required to perceive shapes defined by luminance contours suggests that recurrent neural networks that require some time to compute the shapes may be involved in IC perception. Receptive field models like the ones proposed by Heitger and von der Heydt (1993) or Grossberg (1997) would produce ICs without any cost in time, and this seems to be disconfirmed by the behavioral data.

UPPER AND LOWER VISUAL FIELDS A prominent anatomical property of retinotopic visual areas such as V1/V2 is that the representation of the visual field is split into disjoint portions of the cortical sheet. There is the well-known anatomical break between the left and right hemispheres, each of which represents the contralateral visual fields in early visual areas, as discussed below. In addition, there is a wide separation between the upper and lower hemifield representations in extrastriate visual cortex such as V2 or V3. Introspectively, we are not aware of these discontinuities in the cortical retinotopic representation. Surfaces that cross the horizontal or vertical meridians appear unitary and whole. Nevertheless, under careful experimental conditions, it is possible to uncover behavioral effects that may be the result of the anatomical discontinuities of the cortex. Rubin et al. (1996) found such a behavioral effect: human observers exhibit a greater tendency to perceive ICs when the inducing stimuli fall on their lower visual field. There were two experiments that led to this conclusion, both illustrated in Figure 74.4. The stimulus used in the first experiment was a stereogram similar to that depicted in Figure 74.4A. When subjects fixated the upper cross in that figure, they perceived

a bright illusory horizontal stripe, bounded by ICs, linking the two filled rectangles. In contrast, when they fixated the lower cross, the illusory stripe “faded away” and the two filled rectangles were perceived to be disjoint. The stimulus is symmetric with respect to reflection about its horizontal midline, and therefore the only difference is that the (identical) stimulation falls on the upper versus lower visual hemifields. This is the first experimental result that indicates that ICs are perceived more easily in the lower visual field.

Rubin et al.’s second experiment utilized the thin-fat task to measure IC strength in the upper and lower visual fields, as depicted in Figure 74.4B with the data from a single subject. The left panels in Figure 74.4B show the results of an individual observer on the IC task, while the right panels show the results for a complete (or luminance) contour task. The upper and lower graphs show the subject’s psychometric functions as a measure of performance when the stimulus fell on the upper and lower hemifields, respectively. The lower hemifield shows a marked advantage for the performance of the IC task, as can be seen by examining the psychometric functions on the left side of Figure 74.4B. The psychometric function for the lower visual field is much steeper, indicating better performance. Also shown in this figure in the right-hand panels are the psychometric functions for filled-in Kanizsa figures, for which the support ratio was 1.0—that is, these were real contours entirely defined by luminance difference. Defining threshold performance as the amount of rotation of the inducing elements needed for the subject to reach 82% correct discrimination, the thresholds for the IC figures were 2 degrees and 7.8 degrees for the lower and upper hemifields, respectively. For figures that were completely defined by luminance contours, the thresholds were not different in the different visual fields: thresholds for the lower and upper hemifields were, respectively, 1.1 and 0.9 degrees. Thus, a performance-based measure also showed that the lower visual field segmented the ICs more easily than the upper visual field.

VERTICAL MERIDIAN Perceptual completion can link widely separated contour fragments and interpolate ICs between them, but can it cross the “seams” in visual cortex, the vertical meridian representation that demarcates the boundary between the visual field representations in the left and right cerebral cortical hemispheres, and the horizontal meridian representation that separates upper and lower field representations? As illustrated in Figure 74.5, Pillow and Rubin (2002) answered this question using a variant of the thin-fat shape discrimination task, but with the variation that only one arm of the angle in an inducer was varied in a single presentation, either the arm that faced horizontally or the one that faced vertically. Thus, with inducers arranged symmetrically around the fovea, they could test whether hor-

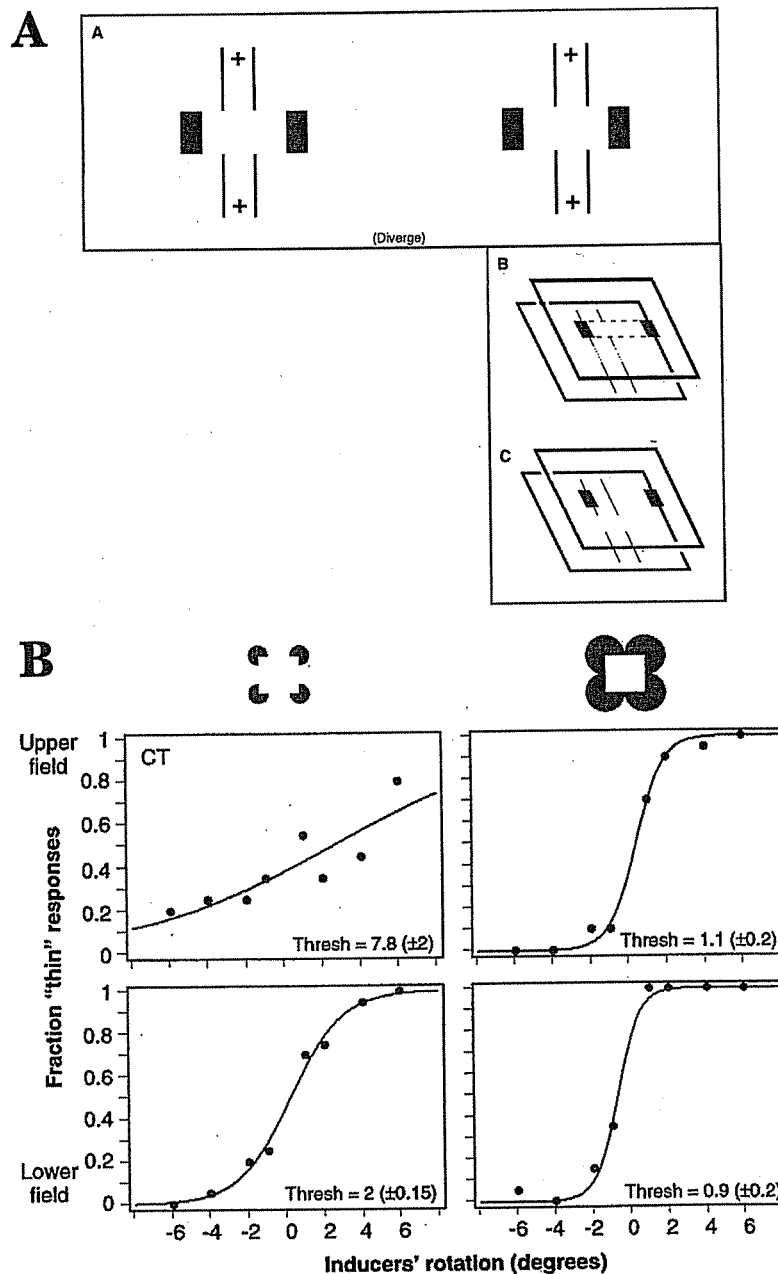


FIGURE 74.4. Upper/lower field asymmetry in IC perception. *A*, Stereogram that can be placed in the upper or lower visual field, depending on the placement of fixation. If the reader free-fuses the stereogram, she or he should observe a qualitative difference in the percept, as described in the text. *B*, Psychometric functions for the thin/fat task for ICs (*left panels*) and filled-in luminance contours (*right panels*). The inducer rotation angle α is the coordinate, is

labeled on the horizontal axis as "Inducer rotation." The fraction of thin responses is plotted on the vertical axis. The upper panels are for the upper visual field; the lower panels are for the lower visual field. Steeper psychometric functions are indicative of better discrimination performance. The shallowest psychometric function is for IC perception in the upper visual field. (From Rubin et al., 1996.)

horizontal contours that crossed the vertical meridian could be perceived as well as contours that were contained within a single hemifield. They found that completion is much poorer when ICs cross the vertical meridian than when they reside entirely within the left or right visual hemifield and cross the horizontal meridian. This deficit reflects limitations in cross-hemispheric integration. The authors also showed that the

sensitivity to the interhemispheric divide is unique to perceptual completion: a comparable task which did not require completion showed no across-meridian impairment. Pillow and Rubin proposed that these findings support the existence of specialized completion mechanisms in early visual cortical areas (V1/V2), since those areas are likely to be more sensitive to the interhemispheric divide.

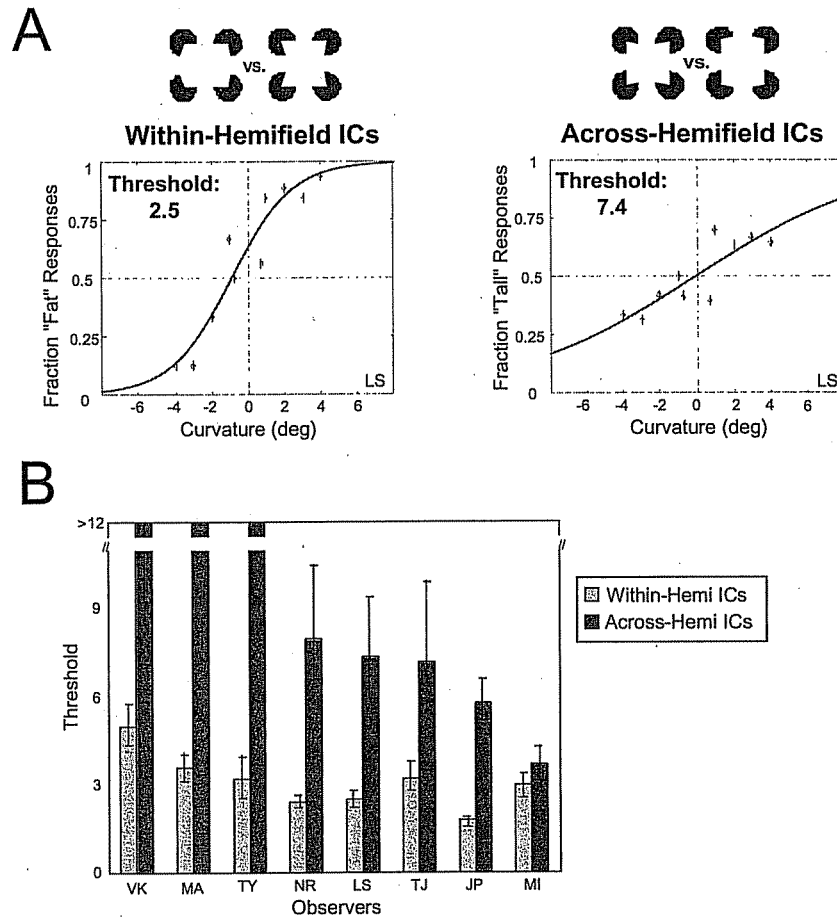


FIGURE 74.5. Meridional asymmetry in IC formation. *A*, Psychometric functions for the modified thin-fat task, as described in the text. Plotting conventions are as in Figure 74.4*B*. The steeper psychometric function for the within-hemifield IC (*left panel*)

indicates that performance is better for ICs that do not cross the vertical meridian. *B*, Summary of thresholds for within- and across-hemifield contour completion for all subjects tested. (From Pillow and Rubin, 2002.)

PERCEPTUAL LEARNING OF ICs Perceptual learning also has been used to investigate the cortical mechanisms of IC perception. From a study of human perceptual learning and IC perception, Rubin et al. (1997) concluded that the abrupt, insight-like perceptual learning observed in that study demanded that high-level visual areas, in which templates of remembered visual objects are stored, must interact with lower-level visual areas that have an analog representation of the visual image. Such multilevel interactions were needed to explain the stimulus size dependence of IC perceptual learning and at the same time its abrupt, insight-like onset. These results may help to reconcile psychophysical and neurophysiological results, which suggest that early retinotopic visual areas must be involved in IC perception, with brain imaging results that found IC-related activity in higher, nonretinotopic cortical regions. This issue is brought up again in the “Conclusions.”

Neurophysiology of ICs

The first neurophysiology work we discuss tends to support a bottom-up, stimulus-driven explanation of IC perception. From electrophysiological single-cell recordings in awake monkeys, Peterhans and von der Heydt and their colleagues found that Kanizsa-type images and other IC images could excite spike activity in neurons in early visual cortex (see Chapter 76). Peterhans and von der Heydt (1989) recorded from single neurons in area V2 of the macaque visual cortex. Such a neuron responds with excitation to a luminance contour that crosses its receptive field. When an IC (as perceived by us) crosses its receptive field, the cell produces a slightly delayed excitatory response resembling the same cell’s response to a real contour. As a control to ensure that the response is not merely a weak response to the remote features of the IC stimulus, the investigators made a small image manipulation (closing the inducing boundary), and this eliminated the neuron’s response. Peterhans and von der Heydt also performed several quan-

tative studies on these IC-responsive V2 neurons, in particular measuring the orientation tuning for ICs and real contours on the same population of V2 neurons; they found that real contours and ICs produced similar orientation tuning in IC-responsive neurons in V2. Thus, these neurons seem to be a candidate neural substrate for IC perception. There also have been reports of IC responses in neurons in V1. This is a controversial point since von der Heydt and Peterhans and their colleagues maintained that they observed very few V1 neurons that produced IC responses. In part the discrepancy may occur perhaps because of the use of different stimuli and in part because of different views of what constitutes an IC. For our present purposes, it is enough to conclude that IC responses can be observed in retinotopic areas in the monkey's brain, areas that are traditionally thought of as stimulus driven.

The connection of the monkey V2 neurons with IC perception in humans needs to be established more firmly. We do not know the nature or quality of IC perception in monkeys because there are insufficient animal data using rigorous experiments to test for IC perception. Once we know that monkeys can exhibit behavior that proves that they see ICs in Kanizsa-type images, further experiments will be necessary to find out whether or not the V2 neurons have the same sort of parameter dependence on size, contrast, and retinal location as the behavior. One important question is, how do the V2 neurons respond to an IC that crosses the horizontal meridian? Humans respond as well to such ICs as they do to ICs that do not cross the horizontal meridian. The reader can observe this by fixating the middle of the Kanizsa triangle in Figure 74.1 and observing the robust lateral ICs that traverse the horizontal meridian in her or his visual field. But in V2 there is a marked separation between neurons that represent the visual field just above and just below the meridian (see Horton and Hoyt, 1991). So one might expect some deleterious effect on IC responses for meridian-crossing ICs in V2 neurons. If that dropoff in IC sensitivity in V2 neurons were observed, it might cast doubt on the role of V2 alone in IC perception. Moreover, as we will discuss below, the human brain imaging data point to other brain areas as the major processing sites for ICs in humans. The monkey results could be interpreted to indicate that similar IC-related activity is going on in human V2, but the functional magnetic resonance imaging (fMRI) and other techniques used on humans are too insensitive to measure it. A second possibility is that the V2 activity seen in monkeys is related to IC perception but that it is not the central mechanism involved in the percept. Another possibility is that human and monkey perception and neural mechanisms are fundamentally different at this midlevel stage of visual processing.

Human responses to ICs have been measured with fMRI techniques. Most fMRI studies have involved the measure-

ment of the activation of Kanizsa squares or diamonds compared with the same pacman-shaped inducers rotated outward or all in the same direction. An earlier study by Hirsch and colleagues (1995) found that there was activation of the occipital cortex lateral to V1 by Kanizsa-type figures, but they could not pinpoint the cortical location because the IC experiments were not combined with retinotopic mapping. Therefore, these studies established that signals related to segmentation were present in occipital cortex, but further work is needed to be more precise about localization.

The extensive research of Mendola and colleagues (1999) at Massachusetts General Hospital established that IC-related signals were observed in retinotopic area V3 and also in LO, the lateral occipital area previously discovered by Malach and colleagues (Malach et al., 1995). Figure 74.6 is an fMRI image from the Mendola paper indicating the large region of cortical activation evoked by the Kanizsa diamonds used as stimuli in that study. The early retinotopic areas V1 and V2 did not produce statistically significant activation, as seen in the figure. Mendola and her colleagues also used different inducers for ICs, such as aligned line endings, and found a similar pattern of brain activation in V3 and LO. These results are important in implicating extrastriate cortex in the process of visual segmentation in humans. But it is important to note the apparent conflict between these results and the findings of Peterhans and von der Heydt (1989) that implicated V2 in IC processing in monkeys. The brain imaging results on humans suggest that higher-level visual areas produce the major response to ICs.

Figure-ground and border ownership

While ICs are often chosen for studying visual segmentation, there are other visual phenomena that can also lead to an understanding of segmentation. The assignment of an image region as figure or ground is one such phenomenon. As Edgar Rubin, the famous perceptual psychologist, pointed out, such assignment is automatic and inescapable (Rubin, 1921). But ambiguous figures exist in which figure and ground assignments flip back and forth, and perception changes when that happens. Rubin's familiar face/vase figure is the most widely reproduced example, but there are other examples from E. Rubin that illustrate the consequences of figure-ground assignments even more. One of these is the Maltese cross figure in Figure 74.7. This example is described in Koffka's (1935) book but not depicted there. The diamond-shaped arms of the cross can appear to be grouped in fours, with a vertical and a horizontal pair grouped together as figures in front (resembling a propeller in shape) and then two diagonal pairs grouped together as figures in front (the vertical-horizontal pairs are then in back). The brightness contrasts in the figure are arranged

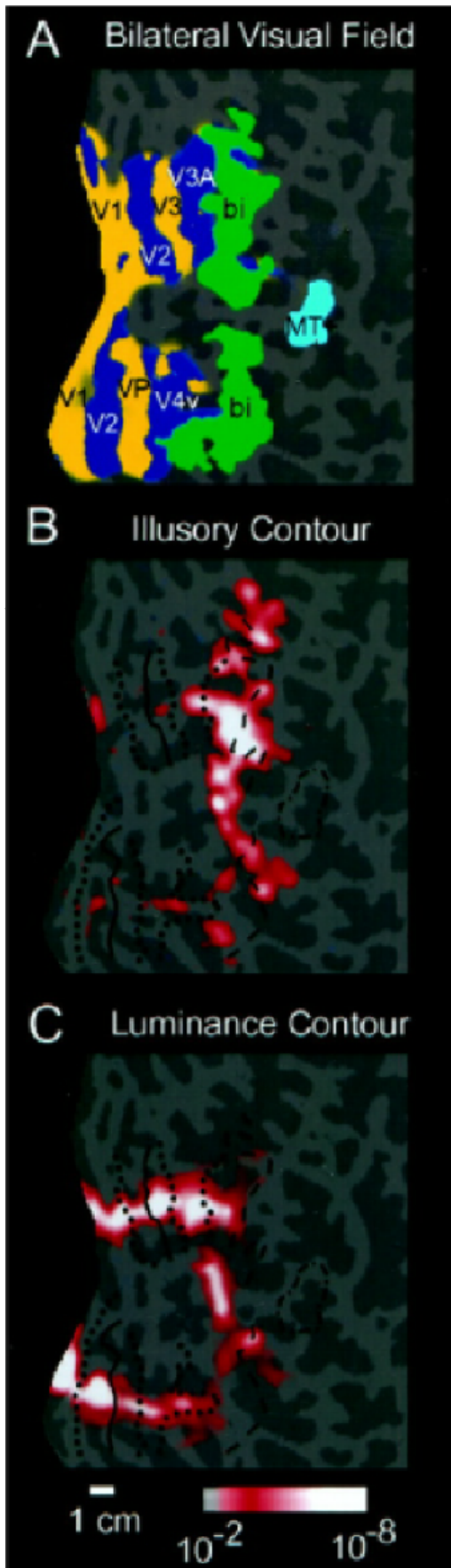


FIGURE 74.6. Mapping of IC responses in human cortex with fMRI. *A*, Map in human visual cortex of retinotopic visual areas and the interhemispheric region (labelled *bi* and colored green) using phase mapping. *B*, The region of differentially high activity when Kanizsa ICs are compared with activation produced by the unorganized pacman inducers. The main activation is in V3A and in the interhemispheric region. *C*, Activation produced by a square defined by luminance contours. (From Mendola et al., 1999, with permission.) (See color plate 48).

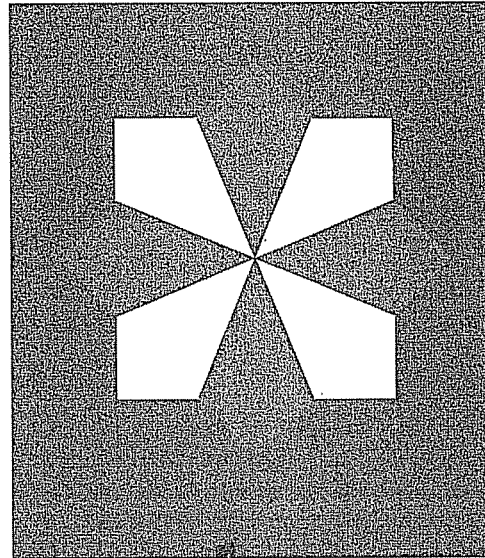


FIGURE 74.7. E. Rubin's Maltse cross figure. There are two sets of vanes, white and mid-gray. They group together to produce propeller figures that alternate front and back. When the propeller of a given color is seen in back, it tends to complete, into a gray diamond or a white square, respectively. Some observers report that the perceived value of the mid-gray changes, becoming darker when the gray regions form a propeller in front and lighter when they form a diamond in back. (Drawn from a description in Koffka, 1935.)

such that the vertical-horizontal propeller shape looks darker in front than it does when it is perceived in back, looking like a light gray diamond behind the white tilted propeller. This is because of the enhanced effect of brightness contrast across borders that define a figure and on the regions to which such borders are attached, as E. Rubin noted (cited in Koffka, 1935). Similar effects can be seen in color. This is only one of many illustrations of the deep consequences of figure-ground assignment. For instance, another consequence of the importance of figure-ground is that people remember the shapes of figures, not grounds. Thus, understanding the neural basis for this phenomenology is likely to be an important clue to the function of the visual system.

Figure-ground assignment is a special case of a more general problem in vision, the assignment of border ownership. Assignment of a region as figure or ground is all one

has to do if there is only one figure surrounded by the background. But if there are many figures, and if one is in front of another so that it partly occludes the shape of the second figure in the visual image, then the visual system must decide on the basis of image information which surface is in front along the boundary between the two figures in the image. Briefly, the brain has to decide which figural region owns the border between them; that is the front surface. Assignment of border ownership is a problem that must be solved in almost every visual image.

There have been only a few investigations of neural mechanisms for border ownership and figure-ground assignments. One study is by Zhou and colleagues (2000) on single cells in V1 and V2 cortex of macaque monkeys. By keeping local edge contrast the same but varying the global stimulus so that different regions own the boundary between them perceptually, Zhou et al. tested sensitivity to border ownership in single cortical neurons. The experimental design and results in an archetypal border-ownership cell are shown in Chapter 76 in this book from the work of Zhou et al. (2000). A substantial fraction of border-ownership cells like that cell are encountered in monkey V2 cortex. Baylis and Driver (2001) reported recently that many neurons in monkey inferotemporal (IT) cortex respond differentially to figure or ground, and thus these also must reflect signals about border

ownership. Since IT cortex is supposedly involved in object recognition, it is very reasonable that neurons in this area should be affected by border ownership that is necessary for accurate object recognition in the real world.

Studies in human cortex of figure-ground reversals using fMRI, by Kleinschmidt and his colleagues (1998) at the Wellcome Imaging Center in London, revealed activation over a number of areas in occipital, temporal, parietal, and even frontal cortex. The involvement of temporal, parietal, and frontal cortex seems to imply that activation of top-down influences from high-level cortical areas could be necessary for figure-ground reversal of border ownership. However, as in the case of ICs, it is also possible that there also may be signals associated with figure-ground assignment in "early" retinotopic areas like V1 or V2 that are undetectable with fMRI.

Amodal completion

An important part of segmentation in human visual perception is the phenomenon of amodal completion, that is, completion and grouping together of the parts of a partially occluded object that are visible. This completion process is crucial for normal object perception in the real world. Evidence that amodal completion affects the firing rates of

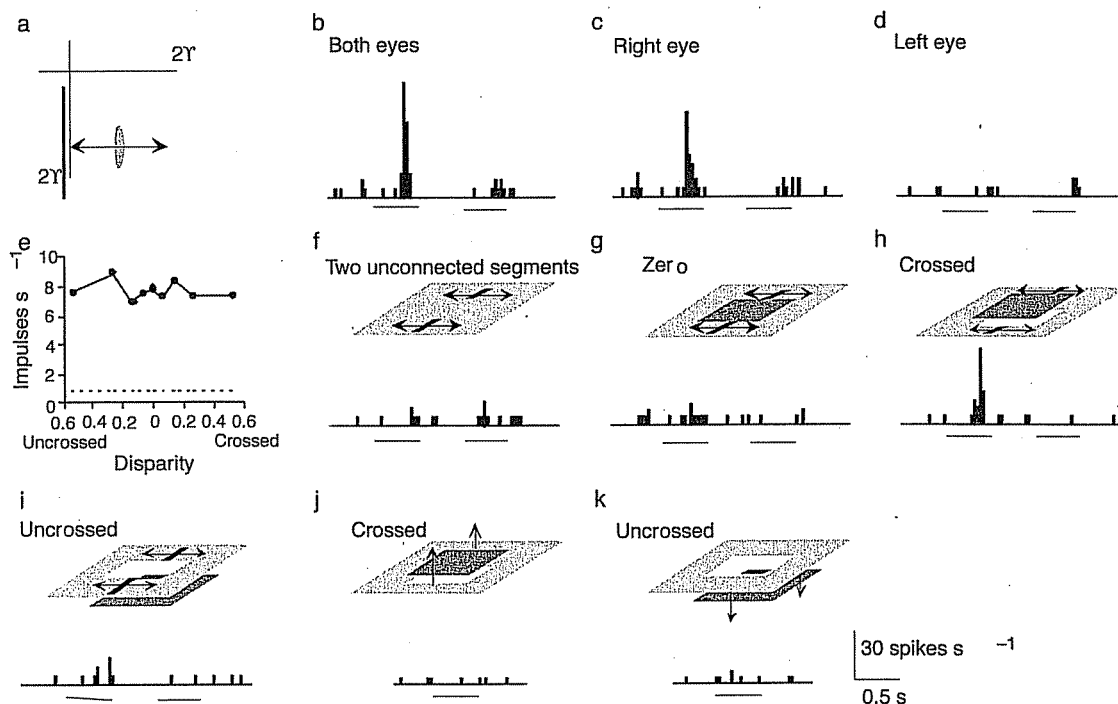


FIGURE 74.8. Sugita-amodal completion V1. Responses from a neuron in an awake, behaving monkey. The neuron responds to a long contour in its receptive field, as in *a*. It responds to both eyes (*b*) and to the right eye alone (*c*) but not to the left eye alone (*d*). The interesting manipulation is in *f* to *h*. In *f* the neuron does not

respond to two unconnected segments. In *g* it does not respond to the same two segments when they are perceived as being in front of a gray region. But there is a response when the retinal disparity is such that the gray region is in front, occluding the two line segments (*h*). (From Sugita, 1999, with permission.)

V1 neurons in macaque V1 was obtained by Y. Sugita by manipulating apparent occlusion using stereopsis, as shown in Figure 74.8. Only a small fraction of V1 neurons were affected by amodal completion, but still it is a significant result.

Amodal completion in human perception was studied by Ringach and Shapley (1996) using the thin-fat task. This was done by enclosing each pacman inducer with an annulus of the same gray scale as the inducer and investigating how accurately and with what speed the observers could perform the task. The accuracy of amodal completion was almost the same as for ICs. The speed of the processes leading to amodal versus IC completion was measured with a backward masking paradigm. The results of these experiments indicated that amodal completion was significantly slower than IC formation, up to 50 msec slower. However, the only masks that were used in this experiment were local pinwheel masks that overlapped spatially with the pacman, or modified pacman, inducers. This suggests that the difference in timing between amodal and IC completion may be caused by the neural computations that are used to define the junctions at the corners of the inducers. In other work not discussed here, psychophysical experiments on ICs and occlusion of the inducer corners indicated the great importance of neural signals about local junctions for global segmentation (Rubin, 2001).

Conclusions

Some of the psychophysical results reviewed here indicate that the process of segmentation requires recurrent networks for completion in early visual cortex. These are the results on dynamics, visual field dependencies, and the size specificity of perceptual learning of ICs. Such results tend to rule out models based simply on collection of signals by large receptive fields in higher visual areas. However, there are other results, such as size scale invariance and the abruptness of perceptual learning, that point to the necessary involvement of higher-level, more abstract representations only in higher-level visual areas. This duality is also reflected in the pattern of neurophysiological and brain imaging results.

The full spectrum of results about ICs and segmentation that we have reviewed here indicates that such perception is not simply the result of a single unitary process in the brain. A reasonable deduction from this pattern of results is that multiple visual areas collaborate on producing the IC percept and visual segmentation generally. Multistage processing and cooperation in vision have been suggested before in general terms, for instance, by Ullmann (1998). The picture that emerges from all the studies of segmentation we have reviewed is of a visual cortical network with intense feedback between higher-level visual areas and

lower-level areas that are exciting the higher-level areas. This cortical network acting as a feedback loop is hunting for structure in the visual image. Related ideas have been proposed more than once before, but now the weight of neurophysiological, brain imaging, and psychophysical evidence points more and more strongly to the visual cortex (that is, primary and extrastriate cortex taken altogether) as an array of feedback loops that cooperate in the segmentation of the visual image.

REFERENCES

- Baylis, G. C., and J. Driver, 2001. Shape-coding in IT cells generalizes over contrast and mirror reversal, but not figure-ground reversal, *Nat. Neurosci.*, 4:937–942.
- Gregory, R. L., 1987. “Illusory Contours and Occluding Surfaces,” in *The Perception of Illusory Contours* (S. Petry and G. Meyer, eds.), New York: Springer-Verlag. pp. 81–89.
- Grossberg, S., 1997. Cortical dynamics of three-dimensional figure-ground perception of two-dimensional pictures, *Psychol. Rev.*, 104:618–658.
- Heitger, F., and R. von der Heydt, 1993. A computational model of neural contour processing: figure-ground segregations and illusory contours, in *Proceedings of the International Conference on Computer Vision*, pp. 32–40.
- Hirsch, J., R. De La Paz, N. Relkin, J. Victor, K. Kim, T. Li, P. Borden, N. Rubin, and R. Shapley, 1995. Illusory contours activate specific regions in human visual cortex: evidence from functional magnetic resonance imaging, *Proc. Natl. Acad. Sci. USA*, 92:6469–6473.
- Horton, J. C., and W. F. Hoyt, 1991. Quadrantic visual field defects. A hallmark of lesions in extrastriate (V2/V3) cortex, *Brain*, 114:1703–1718.
- Kanizsa, G., 1979. *Organization in Vision*, New York: Praeger.
- Kleinschmidt, A., C. Buchel, S. Zeki, and R. S. Frackowiak, 1998. Human brain activity during spontaneously reversing perception of ambiguous figures, *Proc. R. Soc. Lond. B Biol. Sci.*, 265:2427–2433.
- Koffka, K., 1935. *Principles of Gestalt Psychology*, San Diego, CA: Harcourt, Brace.
- Malach, R., J. B. Reppas, R. R. Benson, K. K. Kwong, H. Jiang, W. A. Kennedy, P. J. Ledden, T. J. Brady, B. R. Rosen, and R. B. Tootell, 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex, *Proc. Natl. Acad. Sci. USA*, 92:8135–8139.
- Mendola, J. D., A. M. Dale, B. Fischl, A. K. Liu, and R. B. Tootell, 1999. The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging, *J. Neurosci.*, 19:8560–8572.
- 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.
- Pillow, J., and N. Rubin, 2002. Perceptual completion across the vertical meridian and the role of early visual cortex, *Neuron*, 33:805–813.
- Ringach, D., and R. Shapley, 1996. Spatial and temporal properties of illusory contours and amodal boundary completion, *Vis. Res.*, 36:3037–3050.
- Rubin, E., 1921. *Visuell wahrgenommene Figuren*, Copenhagen: Gyldendal.

- Rubin, N., 2001. The role of junctions in surface completion and contour matching, *Perception*, 30:339–366.
- Rubin, N., K. Nakayama, and R. Shapley, 1996. Enhanced perception of illusory contours in the lower vs. the upper visual hemifields, *Science*, 271:651–653.
- Rubin, N., K. Nakayama, and R. Shapley, 1997. Abrupt learning and retinal size specificity in illusory contour perception, *Curr. Biol.*, 7:461–467.
- Shipley, T., and P. Kellman, 1992. Strength of visual interpolation depends on the ratio of physically specified to total edge length, *Percept. Psychophys.*, 48:259–270.
- Sugita, Y., 1999. Grouping of image fragments in primary visual cortex, *Nature*, 401:269–272.
- Ullmann, S., 1998. *High Level Vision*, Cambridge, MA: MIT Press.
- Zhou, H., H. S. Friedman, and R. von der Heydt, 2000. Coding of border ownership in monkey visual cortex, *J. Neurosci.*, 20:6594–6611.