

# Perceptual Completion across the Vertical Meridian and the Role of Early Visual Cortex

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## Summary

Perceptual completion can link widely separated contour fragments and interpolate illusory contours (ICs) between them. The mechanisms underlying such long-range linking are not well understood. Here we report that completion is much poorer when ICs cross the vertical meridian than when they reside entirely within the left or right visual hemifield. This deficit reflects limitations in cross-hemispheric integration. We also show 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. We propose 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.

## Introduction

Illusory contours (ICs) are surface boundaries which are perceived in the absence of any luminance gradient (Kanizsa, 1955, 1976, 1987; see also Figures 1A and 1B). ICs have been used extensively to study perceptual completion—the reconstruction of occluded or missing edges in images of 3D scenes. Human observers can use ICs to make very accurate judgments about the shapes of the surfaces bound by those ICs (Gold et al., 2000; Kellman et al., 1998; Ringach and Shapley, 1996). Good performance is maintained even when the luminance-defined fragments of the contour are separated by very large gaps, of 10° visual angle or more (Ringach and Shapley, 1996; Rubin et al., 1997; see also below). The ability of the visual system to link such widely separated contour fragments is well motivated ecologically since real-world scenes often contain very large occluding surfaces. At the same time, explaining how long-range completion is performed by the brain presents significant challenges.

Physiological studies have so far not provided a clear-cut answer as to how contour completion is achieved in the brain. There is evidence that V1 and V2 neurons in the macaque monkey respond to ICs, i.e., to stimuli which contain no luminance gradients within their “classical receptive field” (Bakin et al., 2000; Grosz et al., 1993; Lee and Nguyen, 2001; Peterhans and von der Heydt, 1989; Sugita, 1999; von der Heydt et al., 1984; see also Seghier et al., 2000). However, a recent fMRI study reported that the human lateral occipital complex

(LOC) shows strong BOLD responses to Kanizsa-type illusory contours, with very little or no activation detected in earlier cortical areas (Mendola et al., 1999). LOC is anterior to V4 and has been shown to pool information from large portions of the visual field and to respond preferentially to familiar objects and object fragments (Grill-Spector et al., 1998; Malach et al., 1995; Tootell et al., 1998). The much stronger responses to ICs in LOC have cast doubt on the role that early cortex plays in perceptual completion, raising the possibility that the early responses observed in electrophysiological studies might be due to feedback from higher areas. The idea that completion is achieved in LOC may seem particularly appealing for very long ICs, given the large receptive fields of cells in LOC (Grill-Spector and Malach, 2001). However, large receptive field cells are not the only mechanism by which long-range completion could be achieved. Visual information can be integrated over large retinal distances in early cortex as well, via a cascade of activity percolating through a chain of lateral connections (Gilbert et al., 1996; Gilbert and Wiesel, 1985; cf. Field et al., 1993; Geiger et al., 1998; Sha’ashua and Ullman, 1988; Ullman, 1976 for models of such mechanisms). Thus, while physiological studies have not provided conclusive evidence that perceptual completion relies on computations done in early cortex, the architecture of early cortex in and of itself does not preclude this possibility, even for long-range linking.

Behavioral studies can play a key role in exploring the functional significance of neural activity observed in physiology and imaging experiments. In particular, finding that a well-performed sensory skill breaks down under very specific conditions can be revealing about the mechanisms underlying that skill (Blake, 1995). This is the approach we take here. While studying the formation of ICs using a shape discrimination task, anecdotal observations suggested that IC completion was relatively weak for ICs traversing the vertical meridian. We conjectured that this impairment might be related to the interhemispheric divide, and that this could in turn shed light on the mechanisms underlying contour completion. Here, we present evidence that IC completion is indeed impaired when information about the contour must be integrated from both hemispheres. We also show that a visual task which requires integration of visual information from similar spatial locations, but which does not involve perceptual completion, does not show sensitivity to the hemispheric divide. Thus, perceptual completion suffers uniquely from the need to integrate information from the two hemispheres. We discuss the implications of these findings, and propose that they provide evidence for the involvement of early cortex in perceptual completion.

## Results

The quality of IC perception was assessed with a task which required observers to discriminate the shapes of slightly deformed Kanizsa-type illusory squares (Ka-

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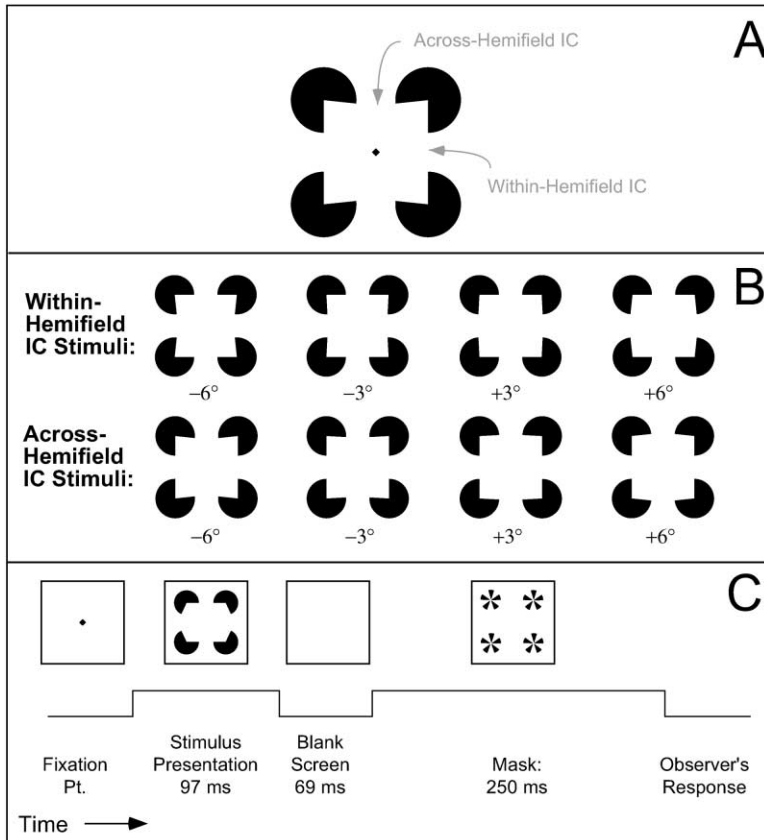


Figure 1. Stimuli and Experimental Paradigm (A) Example illusory square stimulus, with deformed top and bottom (across-hemifield) ICs. The central dot is the fixation point, and gray arrows indicate the two relevant types of ICs, whose curvature was varied independently.

(B) A set of stimuli used to evaluate the perception of within-hemifield ICs (top row) and across-hemifield ICs (bottom row). Stimuli are labeled by the deviation of inducer openings from 90°. Angle of the inducer openings grows monotonically from left to right, giving rise to IC curvature that varies from very concave (at left) to very convex (at right).

(C) Experimental paradigm. Each trial consisted of a single IC stimulus, which observers then had to classify on the basis of the direction of curvature of its ICs. Both types of stimuli (within- and across-hemifield) were randomly interleaved during an experimental block. The briefly presented stimulus was followed by a mask to limit processing time.

nizsa, 1976; Ringach and Shapley, 1996). Previous studies have shown that good performance in this task depends on the ability to perceive ICs (Gold et al., 2000; Ringach and Shapley, 1996; Rubin et al., 1997). It was also shown that the dependence of performance in this task on the visual field location of the ICs can shed light on the underlying brain organization (Rubin et al., 1996). The original task was modified to allow for independent assessments of within-hemifield and across-hemifield perceptual completion. The angular openings of the inducers were varied so that two of the ICs of the Kanizsa figures were curved. The difficulty of the task was controlled by varying how much the angular openings deviated from 90°, which induced differing degrees of curvature in the illusory edges. The curvature of the top/bottom (across-hemifield) and side (within-hemifield) ICs was varied independently. Observers were asked to determine the direction of curvature (convex or concave). Figure 1 illustrates the experimental paradigm used.

The results show a marked advantage for discrimination of within-hemifield ICs compared to across-hemifield ICs. Figure 2A shows the results of an individual observer (LS) for the two types of stimuli. (LS was naive to the purpose of the experiment.) The graph shows the fraction of times the observer judged the IC to be convex as a function of the amount of curvature in the ICs (determined by the deviation of the inducer openings from 90°; negative values denote concave IC curvature). Defining threshold as the amount of curvature an observer needed to perform at the 82% correct level, LS had thresholds of 2.5° for within-hemifield ICs versus 7.4°

for across-hemifield ICs. Figure 2B shows the results for all the observers who participated in the experiment (see Experimental Procedures). All eight observers performed better on within-hemifield than on across-hemifield ICs. Seven observers had a highly significant difference in thresholds ( $p < .005$ ), comparable to or greater than that shown by LS, while for one subject (MI) the difference was not statistically significant.

A second experiment examined whether the difficulty integrating visual information across the vertical meridian is specific to perceptual completion. The task required integration of information from spatial locations similar to those in the first experiment, but the stimuli did not give rise to perceptual completion. Observers were asked to determine the relative displacement of two parallel, nearly colinear line segments. The lines were widely separated and were shifted so as not to be precisely colinear; we term this the distal misalignment (DM) discrimination task. As in the IC experiment, there were two conditions: within-hemifield and across-hemifield (see Experimental Procedures and illustrations in Figure 3). Given that the spatial (and temporal) distribution of information in this task was nearly identical to that in the first, one might expect a similar difference in performance between within- and across-hemifield stimuli. However, the DM line segments do not give rise to perceptually completed contours or surfaces. Therefore, if the difficulty integrating across-hemifield information is unique to perceptual completion, the DM task should not show performance asymmetry. (There is evidence that line segments that lie along a smooth arc are perceptually linked, albeit more weakly, even

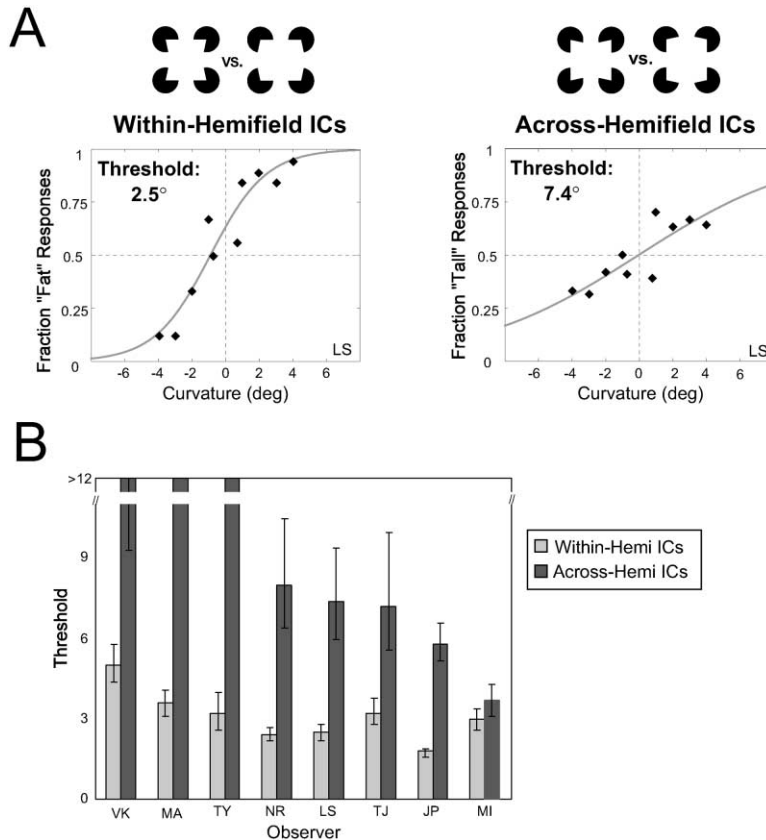


Figure 2. Results of Main IC Experiment  
(A) Comparison of performance on within-hemifield and across-hemifield ICs for observer LS. Each graph shows the fraction of “convex” responses as a function of the deviation from 90° of the angular inducers. The gray line is a fitted psychometric function, used to calculate discrimination threshold (see Experimental Procedures). Threshold of 2.5° on within-hemifield IC stimuli (left) indicates much better performance than on across-hemifield ICs (right, threshold = 7.4°). (B) Comparison of thresholds across observers. All observers show better performance on within-hemifield ICs, seven of the eight with a significance level of  $p < .005$ . Error bars show  $\pm 1$  SD confidence intervals for threshold, based on bootstrap resampling of the data (N = 2000).

when they do not depict occlusion; cf. Murray et al., 2001. For this reason, we used misaligned line segments rather than simply replacing the “pacmen” edges with line segments. See Discussion.)

The results showed no consistent asymmetry between the within-hemifield and across-hemifield conditions for the DM task. Figure 3A shows the results when data from all six observers are averaged: the psychometric functions for the two conditions are statistically indistinguishable. Individually, three observers showed no significant difference between conditions, two performed better on the across-hemifield condition, and one performed better on the within-hemifield condition. Note that although performance is rather poor in this task (i.e., thresholds are high), we need not be concerned that the similar performance in the two conditions is due to a “floor effect.” The psychometric functions span a range of performance up to 80% correct, ensuring that the two conditions are performed similarly even at rather high performance levels. (Similar thresholds were also obtained when the masks were removed, leading to substantially higher levels of performance; data not shown.) Thus, not all tasks that require integration over wide gaps are impaired when information is distributed on opposite sides of the vertical meridian. Perceptual completion seems to show unique sensitivity to across-hemifield integration.

Finally, we conducted a series of control experiments to confirm that the poor performance in the across-hemifield completion IC task indeed resulted from greater difficulty performing completion across the vertical meridian. Three alternative explanations for the per-

formance asymmetry were considered. One is that observers might have a bias to attend to the sides of the figure more than to the top and bottom. The sides of the figure contained within-hemifield ICs and the top and bottom contained across-hemifield ICs. Because the two types of stimuli were presented randomly within the same experimental session, an observer who attended preferentially to the side ICs would be expected to better discriminate curvature in within-hemifield ICs than in across-hemifield ICs. To test this possible explanation, we repeated the experiment using a blocked design. Each block of trials contained only within-hemifield or only across-hemifield stimuli. Thus, observers knew which part of the image contained the task-relevant information, and could allocate attention optimally in each case. Five observers participated in this experiment. Figure 4 shows their averaged performance for the within-hemifield (left) and across-hemifield (right) experimental blocks. The thresholds obtained were 2.4° and 5.1°, respectively. Under these conditions of reduced uncertainty, performance increased for both types of stimuli, but the superior performance for within-hemifield ICs persisted, indicating that better performance on within-hemifield ICs cannot be accounted for by an attentional bias. The results of this control experiment also suggest that the stronger “behavioral receptive fields” found along the within-hemifield ICs by Gold et al. (2000) reflected a difficulty in across-hemifield integration, and not an attentional bias.

A second alternative explanation for the performance asymmetry is that it was related to the underlying shapes used in the discrimination task, not to the completion

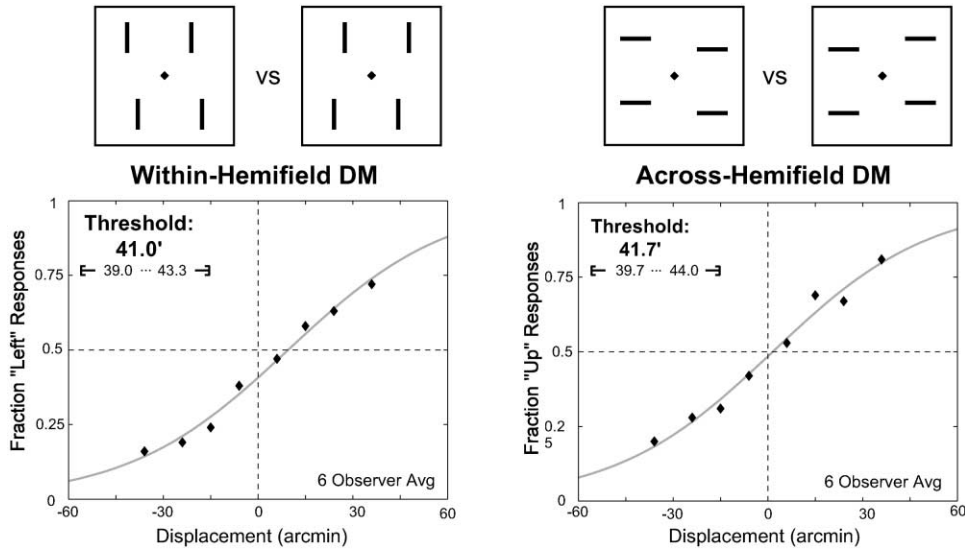


Figure 3. Results of the Distal Misalignment Discrimination Task

Icons above each graph show the types of stimuli used. Observers had to determine the direction of relative displacement in pairs of nearly colinear line segments. (Each stimulus contained two line pairs with identical displacements, so observers could base their judgments on either pair.) When the line segments were vertical (left graph), each pair of lines was contained within a single hemifield. When the segments were horizontal, the task required across-hemifield comparison (right graph). Graphs show the average performance of six observers (J.L., J.P., M.I., N.R., T.J., V.K.) on these two conditions. Thresholds were computed as the amount of displacement needed for 82% correct discrimination (in degrees visual angle). Confidence intervals ( $\pm 1$  SD) are shown below each threshold estimate, and were computed using bootstrap resampling of the data. The thresholds obtained (41' and 41.7') were not significantly different, indicating that the DM task shows no deficit when information is integrated across the vertical meridian.

process. In other words, even when the shapes are fully bounded by luminance edges, the curvature of the top and bottom edges may be more difficult to discriminate than the curvature of the sides. Figure 5 shows that this is not the case. Observers discriminated equally well using the top/bottom contours as using the side contours when the contours are defined by luminance edges. This means that performance in the completion

task was not determined by a differential sensitivity to the underlying shapes used for testing within- and across-hemifield completion. We also addressed the question of what happens for intermediate cases, where the proportion of the shape outlined by real versus illusory contours takes on intermediate values. We explored this question by varying the size of the angular inducers while leaving the size of the illusory surface

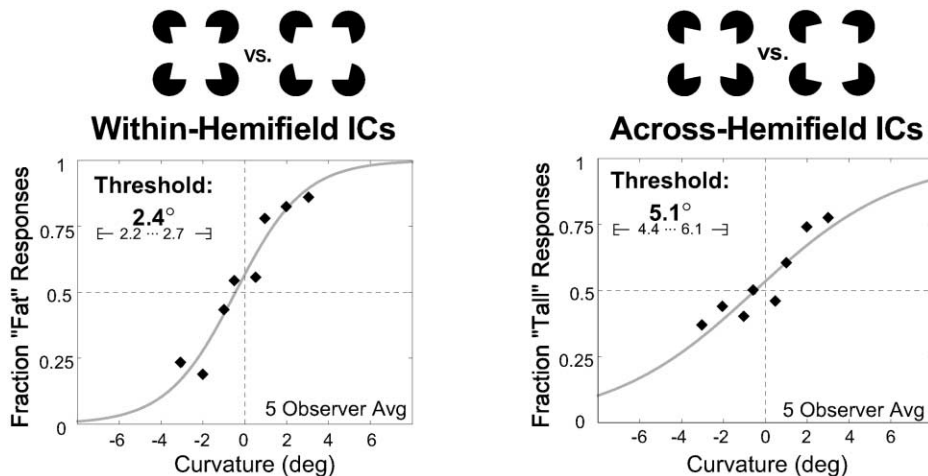


Figure 4. Results for Blocked-Trials Control Experiment

Separate experimental blocks were used for within-hemifield stimuli (left) and across-hemifield stimuli (right). Graphs show psychometric functions for the averaged performance of five observers (VK, TY, TJ, JP, MI). Threshold values indicate that better performance on within-hemifield IC stimuli persists ( $p < .001$ ) when spatial attention is allocated to optimize performance for each type of stimuli. Numbers below each threshold indicate confidence intervals of  $\pm 1$  SD, based on bootstrap resampling of the data. Individually, four of the five observers showed better performance on within-hemifield than across-hemifield ICs, while one observer (MI) showed no difference in performance.

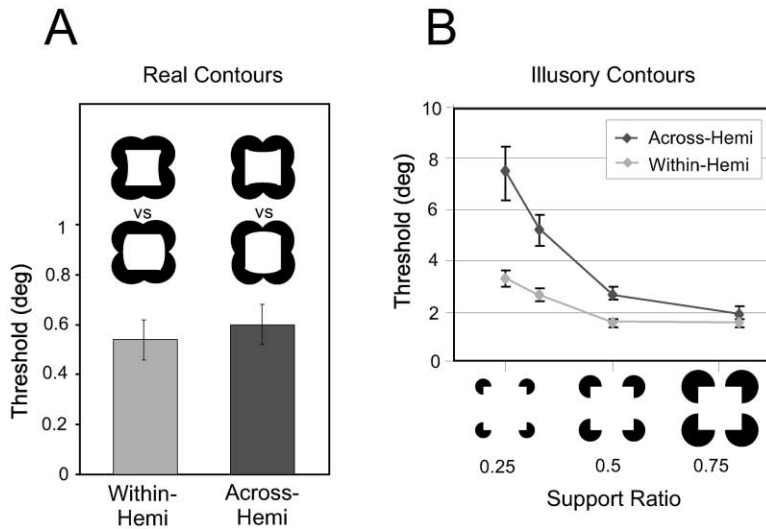


Figure 5. Results for Real Contour Control Experiments

(A) Averaged performance of six observers (HG, JL, JP, MH, TY, VK) discriminating thin/fat or tall/short shapes bounded by real contours. Icons above bars show schematics of the stimuli used (see Experimental Procedures). The difference in performance between the two types of stimuli is not statistically significant.

(B) Averaged performance of four observers (HG, JP, MH, VK) on within- and across-hemifield discrimination as a function of support ratio (the fraction of the perimeter defined by real contours). Consistent with the results in (A), the difference in performance between within- and across-hemifield stimuli vanishes as the length of the “illusory” (i.e., completed) part of the contour decreases. Error bars show  $\pm 1$  SD based on bootstrap resampling of the data.

fixed. Figure 5B shows that as the fraction of the perimeter defined by illusory contours becomes smaller, the difference in performance between within- and across-hemifield performance goes smoothly to zero. This is consistent with our interpretation that performance asymmetry between these two conditions is a hallmark of perceptual completion processing.

A third possible explanation for the observed performance asymmetry is that vertical ICs might be processed better than horizontal ICs, independent of their location in the visual field. (The within-hemifield ICs presented were vertical, while across-hemifield ICs were horizontal.) To test this hypothesis, we conducted a control experiment where the entire IC shape was contained within a single quadrant, located so that the horizontal and vertical IC edges were at an equal distance from the fixation point. Figure 6 shows the average per-

formance of a group of four observers. For these eccentric stimuli, overall performance was worse than before, but there was no consistent difference in performance for vertical versus horizontal IC stimuli. Thus, horizontal ICs are not intrinsically more difficult to perceive than vertical ICs, and the differences in discrimination performance on within- and across-hemifield ICs cannot be attributed to their different orientations.

### Discussion

We assessed the quality of perceptual completion across different portions of the visual field with an illusory contour (IC) shape discrimination task. We found a marked deficiency in processing illusory contours that cross the vertical meridian (across-hemifield ICs), compared to ICs of the same eccentricity confined to one

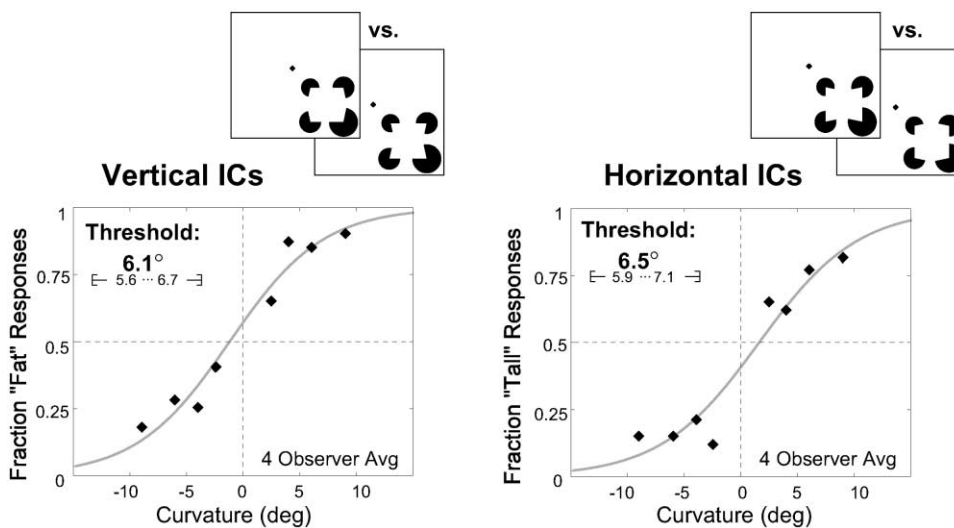


Figure 6. Results for Peripheral IC Shape Control Experiment

Graphs show psychometric functions for the averaged data of four observers (VK, TJ, NR, JP). The icons (above each graph) show sample stimuli, with IC figures peripheral to the fixation point and scaling of the inducers to compensate for cortical magnification. Threshold estimates of  $6.1^\circ$  for vertical ICs and  $6.5^\circ$  for horizontal ICs are not statistically different, indicating that the performance asymmetry in the original experiment did not result from a difference in processing horizontal versus vertical ICs.

hemifield (within-hemifield ICs). This difference was found only for perceptually completed contours, and not for luminance-defined contours. Two other control experiments showed that the superior performance on within-hemifield ICs was not a result of attentional bias, nor was it due to an inherent advantage for vertical over horizontal ICs. We conclude that the difficulty integrating visual information across the vertical meridian was a consequence of the interhemispheric divide in the representation of the visual field. Furthermore, sensitivity to the interhemispheric divide was unique to perceptual completion. This was demonstrated using a task which did not involve perceptual completion, the distal misalignment (DM) task. Like the IC task, the DM task required integration of visual information from widely separated locations in the image, and yet it showed no difference in performance between within-hemifield and across-hemifield conditions.

The differential sensitivity to the interhemispheric divide of the IC and DM tasks suggests that these tasks involve different cortical mechanisms. This is consistent with the fact that the tasks also differ greatly in ecological relevance. Perceptual completion is an important component of visual segmentation. The ability to link together image fragments which belong to the same surface is of central importance in vision, given the frequent occurrence of occlusion in real-world scenes. It is therefore reasonable to expect that the brain developed expert mechanisms to perform perceptual completion accurately and efficiently. (That perceptual completion is poorer across the interhemispheric divide does not refute the existence of such mechanisms, but rather illustrates their limited flexibility—a common characteristic of highly specialized brain processes; cf. Ellis and Young, 1988; Fodor, 1983).

In contrast, the DM task has little ecological relevance. Two misaligned contour segments are not likely to belong to the same surface, and therefore there is no reason to link them. Generally, contour segments will tend to be linked if they are “relatable”—roughly speaking, if they can be connected with a smooth contour without inflection points. (Kellman and Shipley, 1991. Relatable contours fragments may lead to some perceptual completion even when they do not depict occlusion; cf. Murray et al., 2001.) The inducing edges of the ICs are indeed relatable, while the misaligned segments in the DM task are not. In the absence of perceptual linking, it is likely that observers had to resort to ad hoc strategies to judge the direction of misalignment of the two widely separated line segments. Inspection of the level of performance in the two tasks supports this conjecture. While it is not straightforward to compare the performance in the IC and DM tasks due to the different stimulus manipulation in each, some rough comparisons can be made. To achieve threshold performance (82% correct) in the DM task, the contour segments had to be displaced by 41 arcmin visual angle (on average). In the within-hemifield condition in the IC task, the angular opening of the luminance-defined inducers had to be set at 2.7° to achieve threshold performance. This corresponds to a displacement of only 5.1 arcmin of visual angle of the corner of the luminance-defined edge. Thus, the within-hemifield IC task required a significantly smaller physical change in the stimulus to achieve the

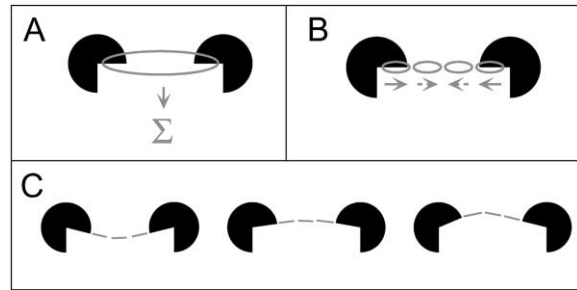


Figure 7. Two Types of Models to Implement IC Completion in the Brain

(A) The receptive field approach: ICs are detected by a single unit sensitive to the presence of the inducing elements of a particular contour in visual space.

(B) The cascade approach: ICs are generated via a cascade of activity passed between neighboring, small receptive-field units.

(C) Cascade models can provide flexibility and precision in representing ICs of many possible shapes, sizes, and orientations.

same level of performance, supporting the notion that it is performed with greater efficiency.

To see how our findings may shed light on the cortical mechanisms underlying perceptual completion, we first make a distinction between two possible models of linking. One option is that each IC is detected by a single unit which responds whenever two (or more) line segments that induce this IC fall within the unit’s receptive field (Grossberg, 1997; Heitger et al., 1992). This is schematized in Figure 7A. Since the brain is able to link widely separated contour fragments, many of these hypothetical units would need to pool information from large portions of the visual field. The natural cortical loci to posit for such units would therefore be higher level visual areas such as LOC or IT, where cells have large spatial receptive fields. We term this the “receptive field” approach.

An alternative model for linking involves populations of small receptive-field units that tile the entire visual space and can interact laterally, in analogy to the architecture of early visual cortex (V1/V2). In such a network, long-range linking may be achieved by propagating information across chains of neighboring units. This “cascade” approach, schematized in Figure 7B, has been used in several models of segmentation (Field et al., 1993; Geiger et al., 1998; Sha’ashua and Ullman, 1988; Ullman, 1976; Williams and Jacobs, 1997; Yen and Finckel, 1998).

We propose that our results are more consistent with IC completion relying on cascade-like mechanisms in early cortex than on receptive-field IC detectors in higher cortex. Within each hemisphere, information can be propagated through the dense network of lateral connections known to exist in early cortex (Gilbert et al., 1996; Gilbert and Wiesel, 1985). Propagation of information between the two hemispheres, on the other hand, would need to make use of callosal connections. The callosal connections in early cortex are limited to connections between cells with receptive fields near the vertical meridian (Clarke and Miklossy, 1990; Innocenti, 1986; Kennedy et al., 1986; Newsome and Allman, 1980). Those connections could be used to link cascade pro-

cesses across the two hemispheres, but it is likely that this would cause cross-hemispheric integration to be less efficient than within-hemisphere integration. There is evidence that callosal transfer can indeed slow propagation of information in early cortex. In a recent study, Wilson et al. (2001) measured the rate at which waves of monocular stimulus dominance swept across cortex during binocular rivalry. They found that propagation rates were constant throughout cortex, except when the wave crossed the vertical meridian. They concluded that propagation through the corpus callosum entailed a “time penalty” averaging 173 ms, presumably reflecting callosal transit as well as some time to “rekindle a [rivalry] wave in the opposite hemisphere.” Given the brief presentation of our stimulus (97 ms), it is therefore consistent that cascade mechanisms implemented in early cortex should fail to complete the across-hemifield ICs. (Interestingly, Wilson et al. also found that propagation speed doubled when waves traveled along continuous contours, which is also consistent with an implementation of linking mechanisms in early cortex. See also Field et al., 1993.)

In contrast, the deficit we observed in across-hemifield completion is not naturally explained by receptive-field type mechanisms for IC completion implemented in higher cortex. Although high-level visual areas, such as IT in the monkey and LOC in the human, also rely on the corpus callosum to integrate information from the two hemispheres, it is likely that the efficiency of callosal transfer in those areas is high. Interhemispheric integration is crucial for high-level visual cortex, which specializes in tasks such as object recognition. Since visual information about objects often spans both hemifields, inefficient interhemispheric integration would lead to noticeable costs in performance. Such performance costs are not observed behaviorally: observers are able to recognize objects that span the vertical meridian even when they are presented as briefly as 100 ms (Biederman et al., 1974; Potter, 1975). Physiologically, the dense callosal connections reaching all parts of high-level visual cortex (Gross et al., 1977; Innocenti, 1986) offer a natural substrate to implement this efficient integration. Estimates from visual evoked potential (VEP) studies in humans put the temporal delay for interhemispheric transfer in area LOC at only 15–20 ms (Saron et al., 2002; see also Ringo et al., 1994 for a slightly higher estimate of 25 ms in IT). If the linking of contour fragments necessary for perceptual completion were performed by cells in high-level visual areas, it would therefore be hard to explain the poor performance on across-hemifield ICs. Of course, these arguments cannot rule out the possibility that linking is nevertheless achieved by high-level cells, and that the deficit we observed arises for other reasons—e.g., because the brain simply devotes fewer such units for detecting across-hemifield ICs. But, in the absence of any obvious a priori reason for such a strategy (completion across the vertical meridian is as ecologically relevant as within a hemifield), such an account seems less plausible.

Implementing perceptual completion in early cortex might seem like a doubtful strategy if it leads to problems in across-hemifield linking. There are nevertheless several reasons why it might be advantageous to achieve contour completion in early visual cortex. A reliable link-

ing process should be able to complete smooth contours of a very large number of different lengths and curvatures. The abundance of small receptive field V1/V2 cells sensitive to different locations and orientations offers a natural substrate within which to implement this requirement via a cascade mechanism. This is illustrated in Figure 7C for three sample curves. In contrast, with the receptive-field approach, one would have to posit that the brain prewired units to detect and represent each of the completed contours in Figure 7C—and, by extension, all other possible contours. This would lead to a “combinatorial explosion” in the number of high-level units required (Mumford, 1994). Another advantage of implementing completion in early cortex is that those areas have immediate access to high spatial resolution information about the image, and details at those resolutions can often determine whether illusory or occluded contours are perceived (Gillam, 1987; Lee et al., 1998; Minguzzi, 1987; Rubin, 2001). Similarly, binocular disparity information, in particular the presence of unpaired points in the image, can provide important occlusion cues (Anderson, 1994; Nakayama and Shimojo, 1990), and therefore it would be advantageous to perform segmentation computations in areas where eye-of-origin information is readily available. Given those advantages, the difficulty in integrating cross-hemifield stimuli may be a reasonable cost. (Note, moreover, that the deficit in perceiving across-hemifield ICs is limited to briefly presented stimuli, and does not extend to steadily viewed IC figures; the reader can see this by fixating the center of one of the IC surfaces in Figure 1B.)

Finally, while we interpret our results as evidence that early visual cortex (V1, V2, or both) plays a functional role in contour completion, we do not propose that completion relies exclusively on computations in early cortex. Feedback from higher visual cortical areas may be quite important for completion—for example, in directing early cortex to launch cascade processes in only restricted parts of the image in cluttered scenes. This may explain the observations of fMRI activation of area LOC in response to illusory contour stimuli (Mendola et al., 1999), as well as more recent VEP findings of LOC activation in response to IC stimuli (Murray et al., 2002). Behavioral studies showing the effects of attention and learning on perceptual completion also point to the involvement of higher level areas (Peterson, 1994; Rock, 1987; Rubin et al., 1997; Wallach and Slaughter, 1988). There are also indications that within early cortex itself, V1 may be receiving feedback from V2 in processing ICs (Lee and Nguyen, 2001). Taken together, the evidence suggests that perceptual completion, a central component in scene segmentation, involves a large, multilevel network comprising both early and high-level visual cortex.

#### Experimental Procedures

Stimuli were generated on a Silicon Graphics computer and presented at a refresh rate of 72 Hz. Viewing distance was 60 cm and stimuli had a Weber contrast of 57%. Stimuli were presented for 97 ms, followed by a blank screen for 69 ms, and then a mask for 250 ms (see Figure 1C). Prior to participating in the experiments, observers were tested to establish that they could perform shape discrimination based on such briefly presented ICs at an adequate

level. Eleven out of fifteen observers were asked to participate in the experiments reported here based on this screening procedure. In all experiments, there was a fixation point at the center of the screen and observers were instructed to look at it at all times. Observers indicated their responses by pressing buttons on a computer mouse.

The IC inducers had a radius of 1.8° visual angle. They were presented 10.5° away from the fixation point (distance from fixation to inducers' centers), at the four corners of a square. This gave rise to ICs that subtended 11.1° visual angle. The *support ratio*, defined as the fraction of the IC square's perimeter bounded by luminance edges, was 0.25 (except where noted, see below). Pilot experiments showed that this support ratio gave rise to nonsaturating performance with small degrees of curvature in the ICs at the presentation intervals used. The difficulty of the task was controlled by varying  $x$ , the deviation of the mouths of the angular inducers from 90°. The deviation  $x$  was the independent variable and was varied using the method of constant stimuli. This allowed for averaging the performance of different observers to obtain a single psychometric function. Each stimulus contained curvature only in its within-hemifield or its across-hemifield ICs. Stimuli were sorted according to whether they contained within-hemifield or across-hemifield curved ICs. For the main experiment, each observer performed at least 36 trials for each stimulus (datum point in the psychometric functions); in the three IC control experiments, observers performed 20, 24, and 12 trials for each stimulus, respectively. Responses were fit (least squares) with a psychometric function  $0.5 * [1 + \tanh(.745(x - \beta) / \alpha)]$ , where  $\alpha$  is threshold performance (82% correct) and  $\beta$  is bias. Confidence intervals ( $\pm 1$  SD) for threshold were calculated using a parametric bootstrap method with  $N = 2000$  samples for each psychometric function.

The main experiment was conducted using a "mixed block" design; this meant that observers did not know whether the curvature would be in the within-hemifield or the across-hemifield ICs. Three different sets of stimuli were used, to ensure generality across a wide range of ICs, and to control for their arbitrary association with button presses (see Figure S1 in Supplemental Data at <http://www.neuron.org/cgi/content/full/33/5/805/DC1>). Each set contained a mixture of within-hemifield and across-hemifield curved IC stimuli. All sets gave rise to a similar asymmetry in the processing of across versus within-hemifield ICs; the data shown were therefore averaged for each observer across stimulus sets. Each trial contained one stimulus drawn randomly from the stimulus set, which observers had to classify by discriminating the direction of curvature of its ICs. This design served to prevent strategies based on discriminating the absolute angle of the inducer openings (acute versus obtuse) instead of the curvature of the ICs, and to discourage eye movements away from the fixation point.

The three IC control experiments used stimuli like those shown in Figure 1 (set A in Figure S1 on *Neuron* website), but with several variations. In the first control experiment, each block contained only within-hemifield or only across-hemifield IC stimuli. In the second control experiment, the radius of the pacman inducers was varied while keeping the distance between their centers fixed. This gave rise to shapes in which the support ratio took values of 0.25 (original experiment), 0.33, 0.5, and 0.8. A shape completely bounded by real contours (support ratio = 1) was generated using circular arcs to define the curved sides of the shape. (For these stimuli, the independent variable  $x$  was defined as the deviation from 90° of each corner of the stimulus.) The third control experiment used IC stimuli located in the periphery in either the lower left or lower right quadrant, at an eccentricity of 7° (center of the IC square) and reduced in size by a factor of 3. The support ratio in these trials was 0.5, but the radius of each inducer was scaled by a function of its eccentricity:  $1 + E/E2$ , where  $E$  is the eccentricity of the inducer and  $E2 = 0.6$  is an estimate of eccentricity at which acuity decreases by a factor of two. This scaling compensated for the decrease in cortical magnification with eccentricity and gave the inducers equal perceived acuity. The icons in Figure 6 show a schematic of these stimuli.

For the DM experiment, stimuli had the same contrast and duration as in the IC shape discrimination experiment. The mask consisted of eight randomly shifted line segments in each of the four corners of the stimulus. The line segments in the stimulus and mask subtended 1.1 by 0.07° visual angle. Stimulus line segments were

located 10.8° from the fixation point on average, but the entire stimulus was shifted randomly on each trial (orthogonal to the line orientation) uniformly over the range  $\pm 3^\circ$ . This random shifting ensured that the position of line segments relative to the fixation point could not be used as a cue. The gap between a pair of DM line segments was 9.8°. The independent variable in these experiments was the distance one member of a DM line pair was shifted relative to the other. Stimuli were presented in mixed blocks (within- and across-hemifield stimuli randomly interleaved) and uniform blocks (one kind of stimulus for an entire block). Mixed and uniform blocks gave rise to similar results. Data presented here were averaged over both kinds of blocks. The method of constant stimuli was used, with shift values of 6.6, 7, 26.5, and 40 arcmin of visual angle. Each observer performed 28 trials per stimulus (datum point in the psychometric function). Thresholds and confidence intervals were estimated using the methods described for the IC experiments.

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