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Illusory Contour Perception and Amodal Boundary Completion: Evidence of a Dissociation Following Callosotomy

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Abstract

■ A fundamental problem in form perception is how the visual system can link together spatially separated contour fragments to form the percept of a unitary shape. Illusory contours and amodal completion are two phenomena that demonstrate this linking process. In the present study we investigate these phenomena in the divided hemispheres of two callosotomy ("split-brain") patients. The data suggest that dissociable neural mechanisms are responsible for the generation of illusory contours and amodal completion. Although both cerebral hemispheres appear to be equally capable of perceiving illusory contours, amodal completion is more readily utilized by the right hemisphere. These results suggest that illusory contours may be attributable to low-level visual processes common to both hemispheres, whereas amodal completion reflects a higher-level, lateralized process. ■

INTRODUCTION

To perceive objects in the environment as unified wholes, the visual system must often extrapolate from incomplete contour or boundary information. Under certain conditions extrapolated contours are perceived in areas of homogeneous retinal stimulation. Because such contours are not present in the physical stimulus, they are referred to as "illusory" or "subjective." Illusory contours are often perceived when the contours or edges of elements in the visual array are consistent with the presence of a superimposed surface or object. An example is the "Kanisza rectangle" shown in Figure 1a, which appears to most observers as a white rectangle superimposed on four black circles. There is an apparent brightness discontinuity between the inside and outside of the rectangle so that the inside appears brighter than the outside. This apparent brightness transition forms the illusory contour (see Kanisza, 1976; 1979).

However, visual grouping processes can act to generate perceived shapes from incomplete boundary information without producing such illusory contours. For example, in Figure 1b most observers perceive a white rectangle mostly occluded by a surface with four holes in it so that only the corners are visible. In contrast with Figure 1a, no illusory contours are seen. In such cases, the grouping process responsible for the perception of the rectangle has been termed "amodal completion" (Michotte, Thines, & Crabbe, 1964).[1]

The relationship between amodal completion and the formation of illusory contours has been controversial. It has been suggested that a common mechanism may be responsible for both of these phenomena (e.g., Kellman & Loukides, 1987; Kellman & Shipley, 1991; Ringach & Shapley, 1996) or that amodal completion may be a prerequisite for the generation of illusory contours (Minguzzi, 1987). However, the fact that amodal completion and the perception of illusory contours can dissociate under certain conditions has caused some investigators to argue that these linking processes are mediated by different neural mechanisms (e.g., Sambin, 1987).

Our initial aim in this study was to investigate the perception of illusory contours by the divided hemispheres of two right-handed callosotomy patients, J.W. and V.P. Evidence from functional neuroimaging studies, investigations of clinical populations with unilateral brain damage, and psychophysical investigations with normal observers has suggested that the mechanism or mechanisms responsible for illusory-contour perception may be preferentially lateralized to the right cerebral

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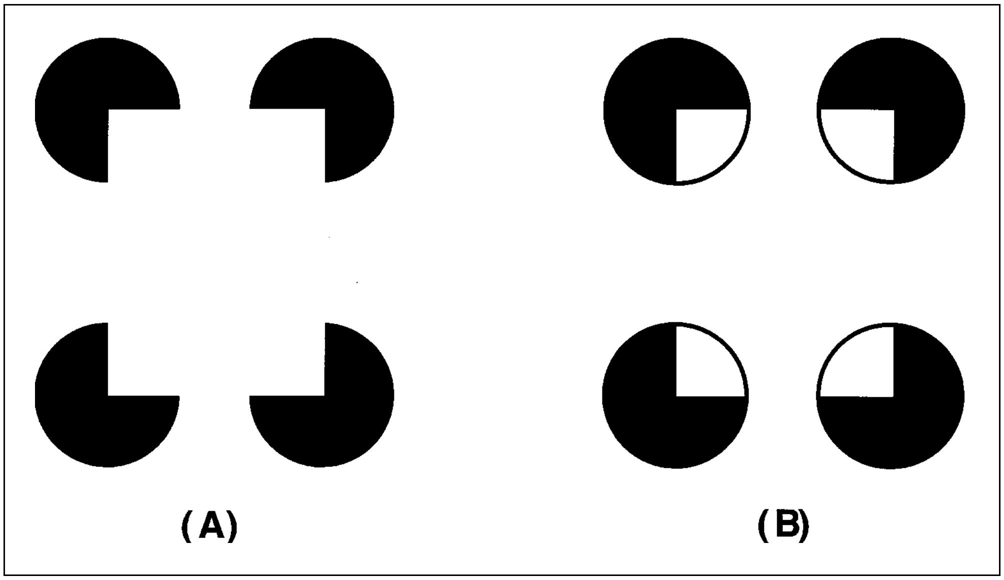
Figure 1. (a) A Kanisza rectangle. This configuration is typically perceived as a white rectangle superimposed on four black circles. (b) An amodally completed rectangle. This configuration is typically perceived as a white rectangle viewed through four apertures in an occluding surface. Note that although the shape of the rectangle is still readily visible, no illusory contours are perceived.



hemisphere (Atchley & Atchley, 1998; Hirsch et al., 1995; Wasserstein, Zapulla, Rosen, Gerstman, & Rock, 1987). If this is the case, the left hemisphere of a split-brain patient ought to be significantly impaired at the perception of illusory contours relative to the right hemisphere. We therefore designed an experiment to directly investigate the perception of illusory contours by each of the isolated hemispheres of two such patients.

A second goal of our investigation was to compare amodal boundary completion to illusory contour perception in each hemisphere. We reasoned that if amodal completion and illusory-contour perception depend on the same mechanisms, any relative hemispheric advantage for one of these effects should also be found for the other. If, however, amodal completion depends on different mechanisms than illusory-contour perception, these processes might exhibit different patterns of lateralization.

We investigated illusory-contour perception and amodal boundary completion using a lateralized version of the shape-discrimination task introduced by Ringach and Shapley (1996). In this task the observer is asked to judge whether a deformed illusory rectangle appears to have convex or concave vertical sides (i.e., appears "fat" or "thin;" see Figure 2a and b). The deformed illusory rectangles are created by rotating the "pacman" inducers by a small amount so that the sides of the rectangle appear to bend, creating the appearance of a thin or fat rectangle. Subjects' ability to discriminate thin from fat illusory rectangles is compared to performance in a "local orientation" control task in which the inducers all face in the same direction and the subjects judge whether they are tilted "up" or "down" (see Figure 2c). Ringach and Shapley have shown that neurologically normal observers can detect smaller pacman rotations in the shape-discrimination task than in the control task. The magnitude of this difference provides an index of the strength of the binding processes that produce the perceived shape. In neurological normals, similar improvements in performance are obtained in conditions in which illusory contours are perceived and when the pacmen are modified (see Figure 2d) so that perceiving the illusory rectangle depends upon amodal completion (Ringach & Shapley, 1996).

In our lateralized version of this task, illusory-contour (IC), amodal-completion (AC), or local-orientation (LO) control stimuli were briefly flashed to the left or right of a fixation point, so that their processing would be confined to the hemisphere contralateral to the side of fixation to which they were presented. Two callosotomy patients, J.W. and V.P., were asked to judge whether the Kanisza rectangle appeared thin or fat (IC and AC tasks) or whether the pacmen tilted up or down (LO control task).

RESULTS AND DISCUSSION

Separate analyses were conducted for the comparison between the IC and LO tasks and between the IC and AC tasks. Psychometric functions showing percentage correct as a function of angular displacement of the pacman inducers for both patients are displayed in Figures 3 (IC versus LO tasks) and 4 (IC versus AC tasks).

Patient J.W.

Illusory Contours vs. Local Orientation

Inspection of Figure 3 indicates that J.W.'s discrimination performance was better for the IC task than the LO task in both hemifields. This suggests that both hemispheres are capable of perceiving illusory contours. It is also apparent from Figure 3 that J.W.'s performance at both tasks was better in the left visual field (LVF) than the right visual field (RVF).

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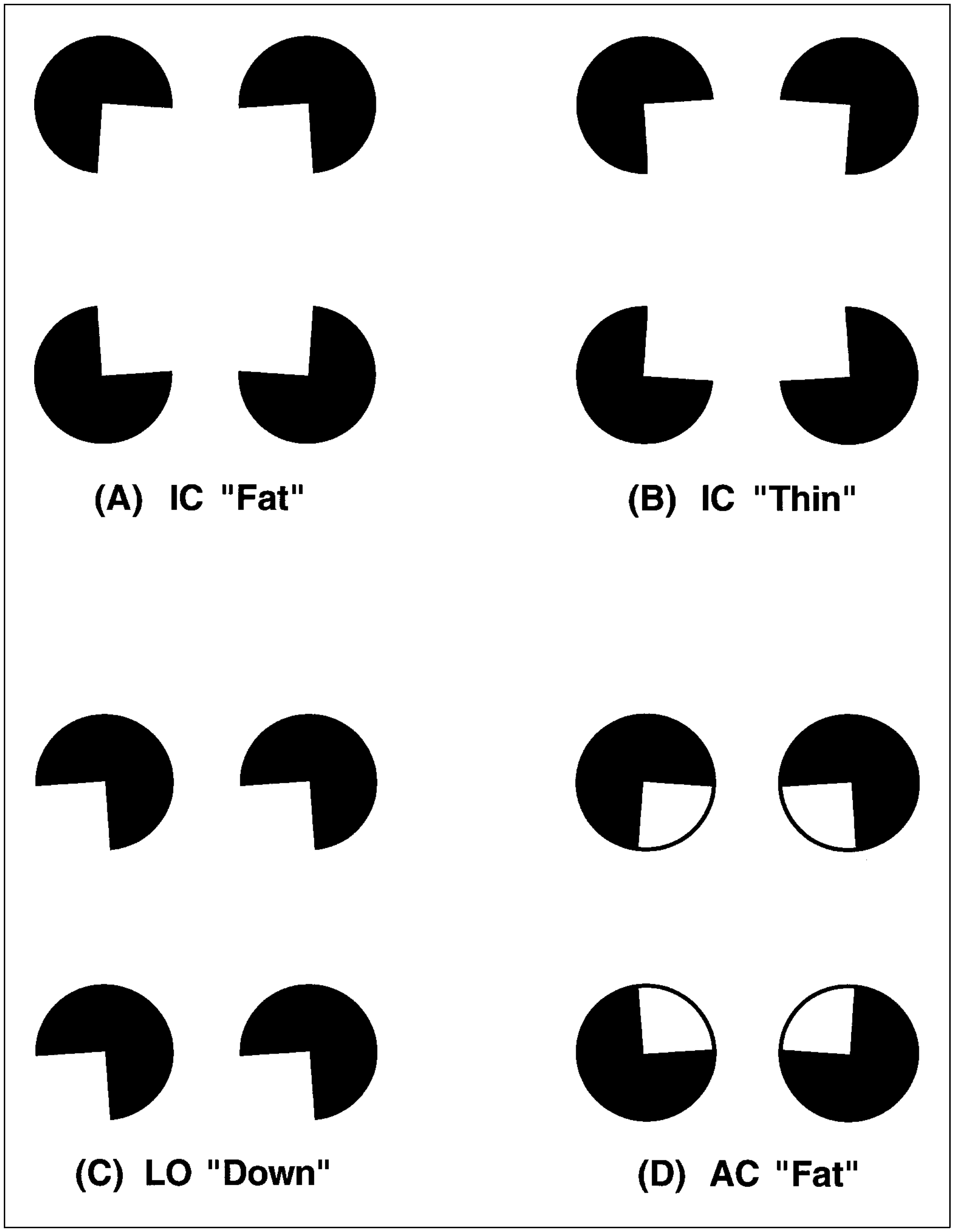

Figure 2. Examples of the stimuli used in these experiments. (a) A "fat" Kanisza rectangle used in the IC task. The inducers in this figure are each rotated by 4° so that the vertical sides of the rectangle appear to be convex. (b) A "thin" Kanisza rectangle used in the IC task. The inducers in this figure are each rotated by 4° so that the vertical sides of the rectangle appear to be concave. (c) An example of a stimulus from the LO task. The pacmen in this figure are each rotated downward by 4°. (d) A "fat" stimulus from the AC task. The inducers in this figure are each rotated by 4° so that the vertical sides of the rectangle appear to be concave.

Multidimensional-χ^2 analyses (Winer, Brown, & Michels, 1991) were conducted to determine the effects of task (IC versus LO), hemifield (LVF versus RVF), angle (1, 2, 3, or 4°) and stimulus condition (thin/up versus fat/down) on response choice (thin/up versus fat/down). In this analysis, discrimination accuracy is indexed by the interaction between stimulus condition and response. The effects of other factors, or combinations of factors, on accuracy are indexed by higher-order interactions involving both condition and response. The interaction between stimulus condition and response choice was significant ($\chi^2(1) = 212.25, p < 0.01$), indicating that that J.W.'s overall performance was significantly better than chance (overall proportion correct was 0.703). A significant interaction between task, condition, and response reflects J.W.'s superior performance in the IC task over the LO task ($\chi^2(1) = 28.94$, $p < 0.01$; proportion correct = 0.778 for the IC task, 0.628 for the LO task). Finally, an interaction between hemifield, condition, and response reflects his overall superior performance when stimuli were presented in the LVF ($\chi^2(1) = 17.19, p < 0.01$; proportion correct = 0.761 for the LVF, 0.645 for the RVF). The four-way interaction between task, hemifield, condition, and response was not significant ($\chi^2(1) = 1.01$, *n.s.*). This indicates that the difference in discrimination accuracy between the IC and LO tasks was not significantly different for LVF and RVF stimuli. No interactions involving angle reached significance.

Overall, the results of this analysis suggest that al-

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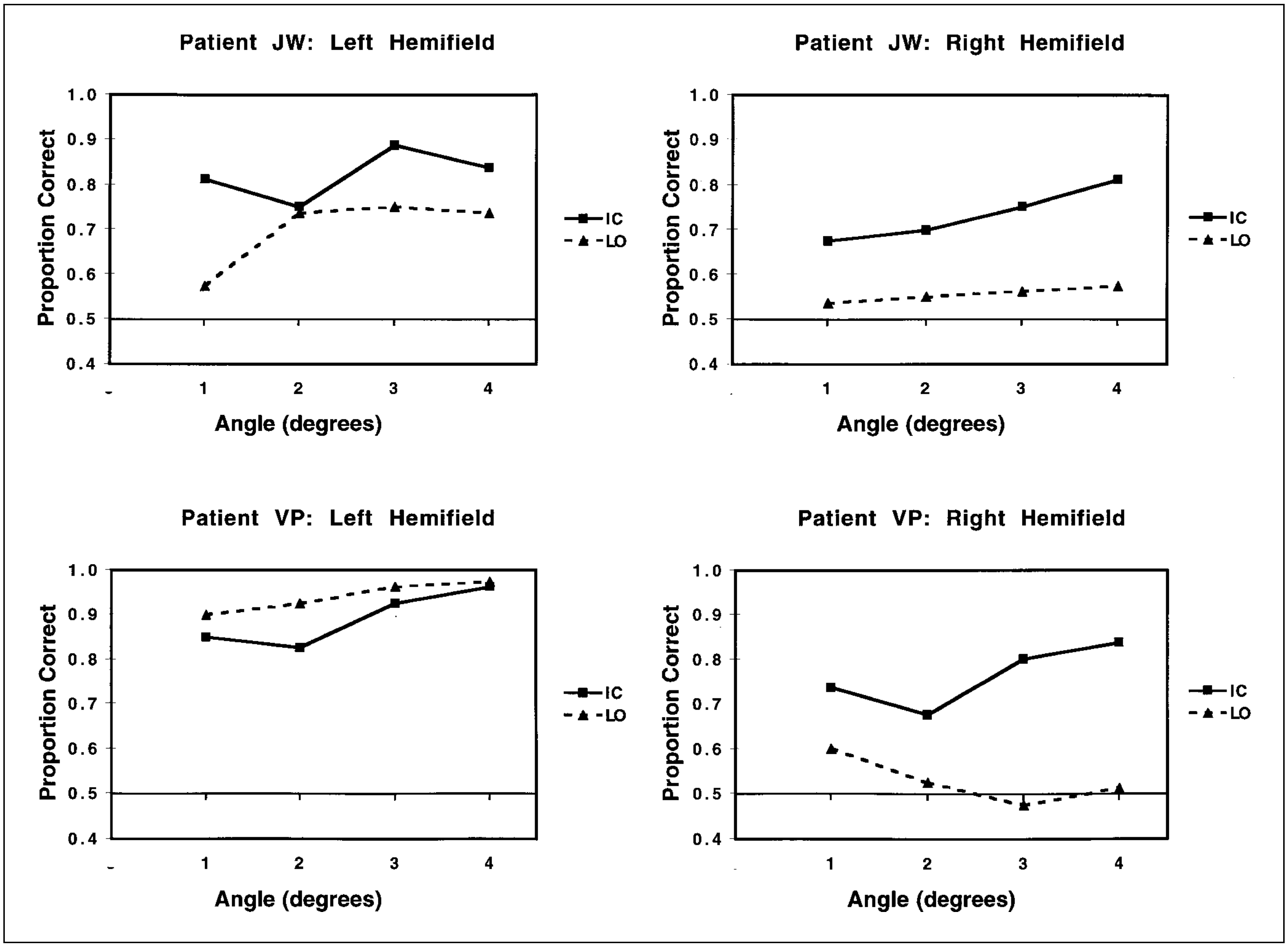

Figure 3. Psychometric functions showing percentage correct as a function of angular displacement of the pacman inducers for patients J.W. (top) and V.P. (bottom). Separate plots are shown for left and right hemifields and for the IC and LO tasks.

though his right hemisphere is better at angular discriminations, both of J.W.'s hemispheres could generate illusory contours, and both benefited to a similar extent from the presence of these contours. This finding contrasts with previous research linking illusory-contour perception with structures in the right hemisphere. J.W.'s data provide no evidence that a right-lateralized process underlies illusory-contour perception.

Illusory Contours vs. Amodal Completion

Figure 4 reveals that J.W. performed the IC task better than the AC task in both hemifields, but the difference between the two tasks was greater for RVF stimuli than for LVF stimuli. This raises the possibility that different mechanisms underlie the performance of the two tasks and that they are lateralized differently. Specifically, it appears that the mechanism responsible for performance of the AC task may be biased toward the right hemisphere. Once again, overall performance was better for LVF stimuli.

J.W.'s responses were again subjected to multidimensional-χ^2 analysis to assess the effects of task (IC versus AC), hemifield, angle, and stimulus condition on response choice. This analysis revealed a significant interaction between condition and response ($\chi^2(1) = 515.52, p < 0.001$), which indicated that J.W. was performing the task accurately and had understood the instructions (overall response accuracy was 0.723). A significant interaction between field, condition, and response ($\chi^2(1) = 75.83, p < 0.001$) confirmed the observation that J.W. was more accurate when the stimuli were presented in the left hemifield than when they were presented in the right hemifield (proportion correct = 0.809 for the LVF, 0.638 for the RVF). There was also a significant interaction between task, condition, and response ($\chi^2(1) = 26.31, p < 0.001$), which reflected the fact that J.W. was more accurate overall in the illusory-contour task than in the amodal-completion task (IC task accuracy = 0.773; AC task accuracy = 0.673). However, a significant four-way interaction between field, task, condition, and response ($\chi^2(1) = 6.28, p < 0.05$) revealed that the difference in performance between the IC and AC tasks was significantly greater for RVF stimuli than for LVF stimuli (in

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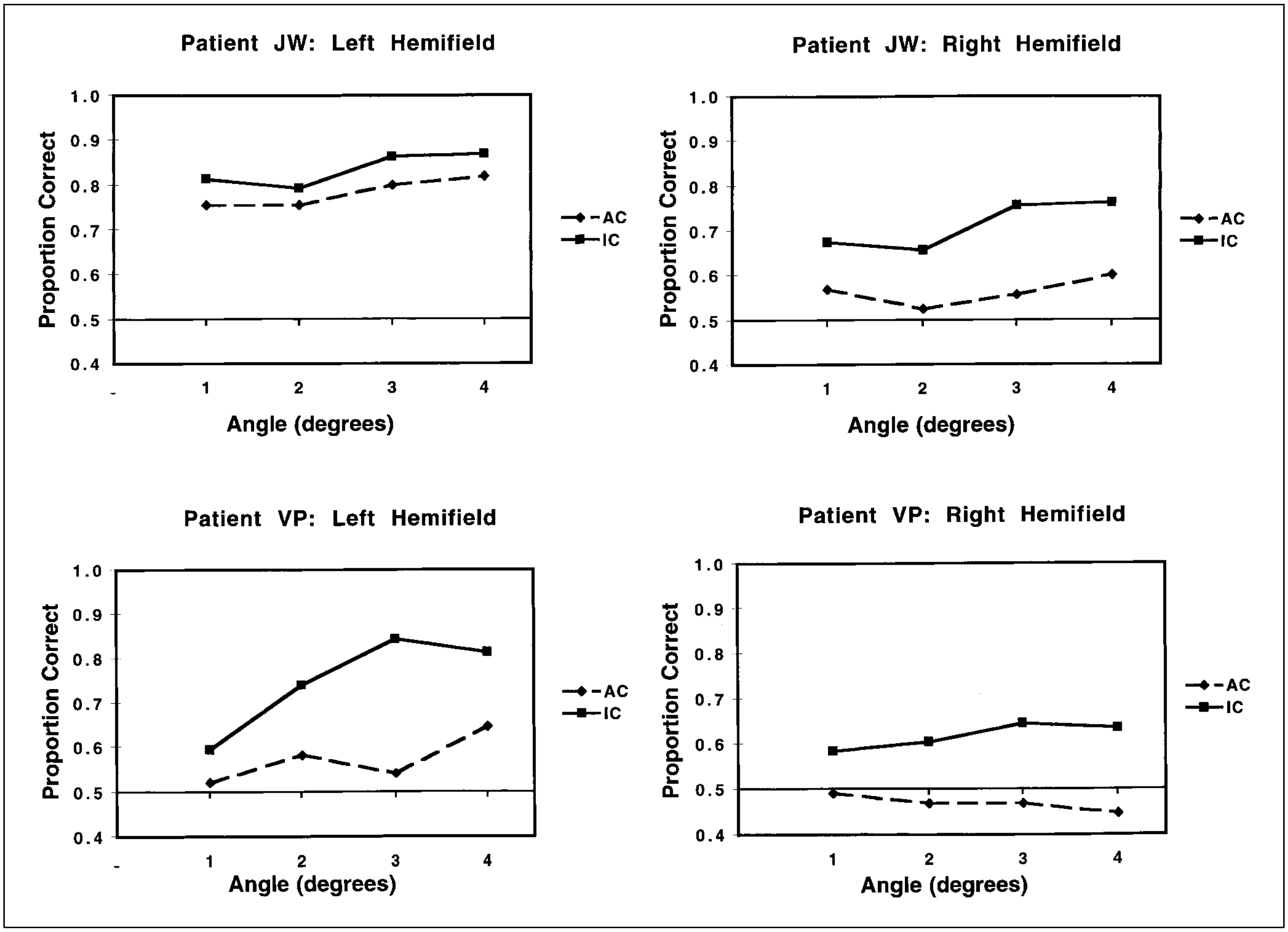

Figure 4. Psychometric functions showing percentage correct as a function of angular displacement of the pacman inducers for the IC and AC tasks for patients J.W. (top) and V.P. (bottom). Separate plots are shown for each hemifield and task.

the LVF this difference averaged 0.051; in the RVF it averaged 0.149). No interactions involving angle reached significance.

The performance of J.W.'s right hemisphere was similar for the IC and AC tasks, although the IC task was performed slightly better. In contrast, his left hemisphere was very poor when the task required amodal completion (i.e., in the AC task) but was reasonably accurate at the IC task. This finding is consistent with the idea raised above that the mechanism responsible for amodal completion may be preferentially lateralized to the right hemisphere, whereas both hemispheres are capable of perceiving illusory contours.

Patient V.P.

Illusory Contours vs. Local Orientation

As was the case with J.W., V.P.'s overall performance in both the IC and LO tasks was better in the LVF than the RVF. Figure 3 reveals that V.P.'s discrimination performance was better in the IC task than in the LO task for RVF stimuli and that her performance was similar in both tasks for LVF stimuli.

The multidimensional-χ^2 analysis revealed a significant condition by response ($\chi^2(1) = 406.87, p < 0.001$), which reflects the fact that V.P.'s overall accuracy was significantly greater than chance (overall response accuracy was 0.779). There were several significant higher-order interactions involving response accuracy (i.e., interactions involving condition and response). A significant interaction between task, condition, and response ($\chi^2(1) = 11.88, p < 0.01$) reflects the fact that V.P. was overall significantly more accurate in the IC task (0.827) than in the LO task (0.731). A significant interaction between field, condition, and response ($\chi^2(1) = 97.77$, $p < 0.001$) indicates that she was more accurate when the stimuli were presented in her LVF (0.916) than in her RVF (0.642). There was also a significant four-way interaction between field, task, condition, and response ($\chi^2(1) = 27.61, p < 0.001$). This indicates that the difference in accuracy between the two tasks differed for the left and right hemifields. For RVF stimuli, the IC task was performed reasonably accurately (0.762), whereas the

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LO task was performed poorly (0.522). In contrast, both tasks were performed well when the stimuli were presented in the LVF (IC task accuracy = 0.891; LO task accuracy = 0.941). In fact, the LO task was performed slightly (but not significantly) better than the IC task in the LVF.

The data from patient V.P. were less straightforward than those from J.W. Although V.P.'s right hemisphere is normally dominant for spatial processing (Fendrich & Gazzaniga, 1990), we could find no evidence for improved performance in the IC task relative to the LO task when the stimuli were presented in her left hemifield. This could be interpreted as suggesting that her right hemisphere is incapable of perceiving illusory contours. However, because V.P.'s performance in the LO task was so good in the left hemifield, any potential advantage in the IC task may have been masked by a ceiling effect. The data indicate that V.P.'s left hemisphere, at least, is capable of forming figure percepts by integrating spatially separated retinal inputs. At this point, there is therefore not sufficient evidence to reach a conclusion about the ability of her right hemisphere to perceive illusory contours, although there is little reason to suspect that it cannot.

Illusory Contours vs. Amodal Completion

Figure 4 shows that V.P.'s performance was considerably worse in the AC task than in the IC task in both hemifields. In fact, her RVF performance in the AC task was at chance. As in all the previous analyses, her overall performance in both tasks was better for LVF stimuli than for RVF stimuli.

Multidimensional-χ^2 analysis revealed a significant condition by response interaction ($\chi^2(1) = 64.60, p < 0.001$), which reflected above-chance performance overall (overall proportion correct was 0.602). There were also significant interactions between field, condition, and response ($\chi^2(1) = 19.84$, $p < 0.001$) and task, condition, and response ($\chi^2(1) = 40.95$, $p < 0.001$). The task by condition by response interaction reflects V.P.'s greater accuracy for the IC task than for the AC task (IC task accuracy = 0.682; AC task accuracy = 0.521). The four-way interaction between field, task, condition, and response was not significant ($\chi^2(1) = 0.128$, *n.s.*).

Interpretation of these data is made difficult by V.P.'s poor overall performance in the AC task. On one hand, we have some evidence to suggest that only the right hemisphere is capable of amodal completion, because V.P. was able to perform the AC task significantly better than chance in the LVF ($z = 2.86, p < 0.05$) but not in the RVF ($z = -1.22$, *n.s.*). This is consistent with the finding from patient J.W. that the mechanism responsible for amodal completion appears to be lateralized to the right hemisphere. This conclusion is somewhat mitigated, however, by the lack of a significant task by field by condition by response interaction. This indicates that the difference in performance between the IC and AC tasks was not discriminably different in the two hemispheres.

GENERAL DISCUSSION AND CONCLUSIONS

We set out to explore two issues in illusory-contour perception and amodal completion. The first was whether we could find evidence that the neural mechanism underlying illusory-contour perception is preferentially lateralized to the right cerebral hemisphere. The second question was whether we could find evidence for different mechanisms underlying illusory contour perception and amodal boundary completion.

The data from patient J.W. suggest that both hemispheres are equally capable of perceiving illusory contours or at least that both gained equal performance benefits from having them present to assist in the angular discrimination. The data from patient V.P. were harder to interpret, because her performance in the LVF was close to ceiling. This limitation notwithstanding, it seems evident that her left hemisphere, at least, is capable of perceiving illusory contours.

The comparison between the illusory-contour and amodal-completion tasks provides some evidence supporting the notion that different mechanisms underlie the generation of illusory contours and amodal completion. The data from patient J.W. suggest that amodal completion may be solved better by the right hemisphere than the left. V.P.'s results are more equivocal but provide some support for this idea. Taken as a whole, the data reported here provide evidence that the perceptual task of shape perception by boundary completion appears to be solved by multiple processes. In the right hemisphere, a specialized mechanism may serve to group together local shape fragments into global percepts, possibly drawing on prior visual experience. This results in amodal completion. However, automatic organizational processes that are equipotent in the hemispheres (and probably earlier in the visual pathway) seem to utilize basic attributes of the sensory input to extrapolate likely boundaries not actually present on the retina. This produces illusory contours. In the intact brain these processes can be difficult to distinguish due to their functional overlap. In the split brain, however, the difference between them is readily observable because one set of processes is lateralized and the other is not.

The finding that both hemispheres are able to perceive illusory contours contrasts with the report of Hirsch et al. (1995) that the perception of illusory contours is associated with a unilateral right-hemisphere activation, as well as with neuropsychological and psychophysical reports linking illusory-contour perception with right-hemisphere function (Atchley & Atchley, 1998; Wasserstein et al., 1987). In their study, Hirsch et al.

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compared a condition in which the pacman inducers were arranged to form a Kanisza square with a condition in which the inducers were misaligned so that no square was perceived. This display was intended to produce conditions in which the square was defined by illusory contours. However, the display would also have permitted the grouping processes that produce amodal completion to contribute to the figure percept. Therefore the perception of a unified shape did not actually depend on the perception of illusory contours. Our data raise the possibility that the right-hemisphere activation reported by Hirsch et al. might have reflected the operation of the mechanism underlying amodal completion rather than illusory contours per se. Similarly, the various psychophysical and neuropsychological reports of right-hemisphere specialization for the perception of illusory contours have all used stimuli that could have activated the processes responsible for amodal completion as well as those responsible for the formation of illusory contours.

Several researchers have suggested that the perception of illusory contours and amodal boundary completion are different manifestations of the same perceptual mechanisms (e.g., Kellman & Loukides, 1987; Kellman & Shipley, 1991; Minguzzi, 1987; Ringach & Shapley, 1996). The results reported in this paper suggest otherwise. We report data that suggest that modal and amodal completion rely on different, though partially overlapping, mechanisms with different patterns of lateralization that can be dissociated in the split brain.

METHODS

Subjects

Two callosotomy patients, J.W. and V.P., participated in this study. Both have been tested extensively and were familiar with the testing procedures used in this experiment.

Patient J.W. is a 42-year-old right-handed male who underwent a two-stage callosotomy for the relief of intractable epilepsy in 1979, when he was 25 years old (Sidtis, Volpe, Holtzman, Wilson, & Gazzaniga, 1981; Sidtis, Volpe, Wilson, Rayport, & Gazzaniga, 1981). The completeness of the callosal section has been confirmed by magnetic resonance imaging (Gazzaniga, Holtzman, Deck, and Lee, 1984). Testing of J.W. was carried out in February and March of 1997.

Patient V.P. is a 45-year-old right-handed female who underwent a two-stage callosotomy for the relief of intractable epilepsy in 1979, when she was 27 years old. Magnetic resonance imaging has revealed some spared fibers in the splenium and rostrum of the corpus callosum, although it appears that there is little or no transfer of visual information between the hemispheres (Funnell, Corballis, & Gazzaniga, unpublished data; Gazzaniga et al., 1984). Testing of V.P. was carried out in June of 1997 and February of 1999.

Apparatus and Stimuli

All stimuli were presented on a VGA monitor controlled by an IBM-compatible computer, which was also used to collect responses. All stimuli were presented in white on a black background.

IC stimuli were created by placing inducers (pacmen) at the four corners of an imaginary rectangle. The imaginary rectangle measured 3° (W) by 4° (H) of visual angle, and the pacmen each subtended 2°. This resulted in an illusory rectangle (Kanisza rectangle) with a support ratio[2] of 0.5 along the vertical sides and 0.67 along the horizontal sides. The pacmen were then rotated by 1, 2, 3, or 4° to create thin or fat illusory rectangles. AC stimuli were identical to the IC stimuli, except that the "mouths" of the pacmen were outlined by closed circles. LO control stimuli were similar to the IC stimuli except that all the pacmen were oriented the same direction. The pacmen were each rotated in the same direction by 1, 2, 3, or 4° to create up or down stimulus arrays. The mouths of the pacmen in the LO task were always on the bottom half of the inducer and always faced toward the midline (i.e., the mouth was on the bottom right of the pacman for stimuli in the left hemifield and on the bottom left for stimuli shown in the right hemifield). Examples of the stimuli are shown in Figure 2.

Tasks

Illusory Contour Task

On each trial a small fixation cross appeared in the center of the screen. After a 500-msec delay, an IC stimulus was flashed for 117 msec (seven screen refreshes), centered 4° to the left or right of fixation. The subject was instructed to indicate whether the rectangle looked thin or fat by pressing a key on the computer keyboard. The subject's response initiated the next trial after a delay of 2000 msec.

Four blocks of trials were run in two sessions. Each block consisted of 160 trials, made up as follows. The stimuli could appear in either the left or right hemifield, could be either thin or fat, and could be distorted by 1, 2, 3, or 4°. Each stimulus was repeated 10 times in each block. The subject was instructed to maintain fixation on the fixation cross throughout the block. The hand used to respond was counterbalanced between blocks.

Amodal Completion Task

The amodal completion task was identical to the illusory contour task, except that AC stimuli were used in place of IC stimuli.

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Local Orientation Task

The local orientation task was similar to the other tasks except that LO stimuli were presented, and the subject was instructed to indicate whether the stimulus appeared to tilt up or down.

Notes

1. This term reflects the notion that the shape of the figure is completed outside the visual mode (i.e., it has no perceptual "reality"). In contrast, illusory contours are completed in the visual mode. The process leading to their formation is sometimes referred to as "modal completion."
2. The support ratio is the ratio of the inducer's diameter to the length of the side of the illusory figure (Lesher & Mingolla, 1993; Ringach & Shapley, 1996).

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