Illusory contours activate specific regions in human visual cortex: Evidence from functional magnetic resonance imaging

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ABSTRACT The neural basis for perceptual grouping operations in the human visual system, including the processes which generate illusory contours, is fundamental to understanding human vision. We have employed functional magnetic resonance imaging to investigate these processes noninvasively. Images were acquired on a GE Signa 1.5T scanner equipped for echo planar imaging with an in-plane resolution of 1.5 x 1.5 mm and slice thicknesses of 3.0 or 5.0 mm. Visual stimuli included nonaligned inducers (pacmen) that created no perceptual contours, similar inducers at the corners of a Kanizsa square that created illusory contours, and a real square formed by continuous contours. Multiple contiguous axial slices were acquired during baseline, visual stimulation, and poststimulation periods. Activated regions were identified by a multistage statistical analysis of the activation for each volume element sampled and were compared across conditions. Specific brain regions were activated in extrastriate cortex when the illusory contours were perceived but not during conditions when the illusory contours were absent. These unique regions were found primarily in the right hemisphere for all four subjects and demonstrate that specific brain regions are activated during the kind of perceptual grouping operations involved in illusory contour perception.

Our goal is to identify areas of human cortex involved in the operation of perceptual grouping of local features into a global percept. We used functional magnetic resonance imaging (fMRI), a noninvasive neuroimaging technique which relies on local variations in blood supply and O$_2$ concentration during neural activity (1–3), to investigate these processes. Neural activation within the cerebral cortex is believed to be associated with an increase in blood flow that is out of proportion to the O$_2$ consumption, thus decreasing the capillary O$_2$ extraction fraction and delivering more oxyhemoglobin to the local venous circulation (4–7). The resulting decrease in the local capillary and venous deoxyhemoglobin concentration results in an increase in the $T_2^*$ weighted magnetic resonance signal due to the decreased paramagnetic effects of deoxyhemoglobin (8, 9). These local changes in blood chemistry can be observed without the use of exogenous contrast enhancing agents on clinical magnetic resonance scanners (3, 10–12), which has enabled fMRI localization of visual (10–16), motor (17–19), auditory (20), speech (21), taste (22), and olfactory (23) processing in the human brain. Since fMRI is now established as a method for exploring the functional organization of the human brain (24), we applied this technique to investigate the global processes of perceptual grouping in vision.

Borders between visual objects and their background are usually defined by changes in luminance or color. However, perceptual borders can be created by inducing elements distant from the perceived border, as in Kanizsa’s triangle (25). The phenomena of perceived visual borders not associated with net luminance or color changes across the border are collected under the heading of anomalous or illusory contours (we use the latter term). Though these illusory contours are shorter in nature and are of perceptual significance in signaling the occlusion of one surface by another (25). The neural mechanisms that produce the perception of illusory contours are crucial for normal image segmentation mechanisms and the active creation of the perceptual representation of visual surfaces. Since illusory contours are also a specific example of the general phenomenon of the global perceptual grouping of local image features, the neural mechanisms involved here will reveal much about the properties of grouping mechanisms that are needed for global form perception (26, 27).

The view that illusory contours reveal mechanisms of normal form perception is often, though not exclusively, associated with the “bottom-up” or physiological view of the contour-detecting mechanisms as being hardwired neural mechanisms that are excited involuntarily by any visual pattern. This view has gained support from experiments that indicate that there are physical limits to the spatial range of interpolation in illusory contours (28) and that manipulation of stimulus parameters like contrast and color contrast can prevent contours from being seen in situations in which a cognitive solution should be possible (25). Also, von der Heydt, Peters, and Baumgartner (29–31) have shown that some cells in the Macaque monkey’s secondary visual cortical area, V2, respond to illusory contours in a way that resembles human visual perception. More recently, Grosos et al. (32) found evidence for responses to illusory contours in V1, the earliest cortical stage of visual signal processing. Related work on spatial linking of local information in macaque V1 by Lamme et al. (33) and Purpura and Victor (34) indicates that perceptual grouping may begin already in V1. These neurophysiological results led us to investigate the illusory contours and perceptual grouping in human cerebral cortex with fMRI.

METHODS AND RESULTS

Images were acquired on a 1.5-Tesla magnetic resonance scanner (General Electric) that was retrofitted for echo planar imaging (Advanced NMR Instascan) located in the Department of Radiology at Memorial Sloan–Kettering Cancer Center. A gradient echo sequence [echo time (TE) = 60 ms; repetition time (TR) = 3 s; flip angle = 30°] and a standard quadrature head coil were employed to acquire T2*-weighted images.

Abbreviations: fMRI, functional magnetic resonance imaging; voxel, the smallest unit of volume sampled.

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images with an inplane resolution of 1.56 × 1.56 mm (128 × 256 matrix; 20 × 40 cm field of view). Four healthy subjects with no history of vision-related complaints participated in the experiment: subject A, right-handed male; subject B, left-handed male; subject C, right-handed male; and subject D, right-handed female. Handedness was determined by the Edinburgh handedness inventory (35). Slice thickness was either 3.0 mm (subject B) or 5.0 mm (subjects A, C, and D) and either 12 (subjects A, B, and C) or 16 (subject D) contiguous axial slices were acquired simultaneously. On the basis of a midsagittal view of a T1 image of the brain for each subject, slice positions were selected for the T2* image to cover the occipital lobe. For subjects A, B, and C, the slices were parallel to the anterior-to-posterior commissure (AC/PC) line (36), and for subject D, the slices were horizontal (approximately parallel to the calhorneal line). Light levels inside the scanner room were dim, and lights inside the scanner were off for subjects A and B.

Five kinds of visual stimuli were employed: (i) pacmen inducers positioned as if on the corners of a square but misaligned, such that no illusory contour was generated (Fig. 1A and B); (ii) pacmen inducers in the identical positions but aligned, such that an illusory Kanizsa square was formed (Fig. 1C and D); (iii) a real square either with (Fig. 1E) or without (Fig. 1F) the pacmen; (iv) simple bulletts along the vertical or horizontal meridians for retinotopic mapping; and (v) a fixation mark alone. All line segments and stimulus objects were white on a dark background. The presentation order of conditions varied across subjects, and all subjects were familiar with the stimuli prior to the experiment. Subjects viewed the stimuli through a slanted mirror incorporated into the head coil and located above the head. The stimuli were back projected onto a screen located at the foot of the scanner platform. Viewing distance from eye to center screen was 355 cm, and the stimulus field subtended approximately 6° × 6° of visual angle. The intersecting line segments of the fixation mark (crosshair) subtended 0.8° of visual angle. This crosshair was presented alone and also on all stimuli. Two forms of the pacmen were employed: solid pacmen (Fig. 1B and D), and lined pacmen (Fig. 1A and C). Each individual pacman subtended approximately 2.0° of visual angle in diameter, the centers of the pacmen were separated by 4.5° along the horizontal and vertical direction and were separated from the crosshair by 3.2°. Stimuli were flickered at a rate of approximately 4 Hz with a duty cycle of 50% for subjects A, C, and D; no flicker was used for subject B.

Two identical image acquisition runs, each lasting either 90 s and consisting of 30 images or 120 s and consisting of 40 images, were performed for each condition. The two indepen-

![Fig. 1. Illustrations of the contour stimuli for which functional data were acquired.](image-url)
that correspond to the central fixation stimulus. Therefore, the more medial areas of activity shared by all three conditions on slice 4 can be assumed to represent the peripheral pacmen common to all stimuli. The approximate location of the boundaries of Brodmann’s areas 17/18 and 18/19 were identified by the responses to the vertical and horizontal meridian stimuli, respectively (39–41). Activity related to the vertical meridian bullets coincided with much of the slice 2 activity as well as the medial regions of slice 6. Activity related to the horizontal meridian bullets coincided with a subset of activity on slices 3, 4, and 7. These landmarks suggest that the distinct illusory-contour-alone activity observed on slice 6 is within extrastriate and, in particular, Brodmann’s area 18 for subject A.

A distinct illusory-contour-alone region was located in the right hemisphere for all subjects as shown in Fig. 3. The color code is the same as described for Fig. 2. The location of each axial slice is indicated by the red line on the corresponding mid sagittal view. These single slices were selected to illustrate that specific occipital–cortical regions associated with illusory contour perception were predominantly located within the right hemisphere. However, as in Fig. 2, these regions were multifocal, and individual differences were observed. Note that no real contour condition was run on subject B and that the real contour stimulus for subject D did not include pacmen. These experimental differences may account for some of the variation among the four subjects. Expected variations in brain size and morphology (42–44), as well as small differences in slice angles, further contribute to the different appearances of these slices and activation patterns. Nonetheless, all subjects consistently demonstrated clustered, right-hemisphere, illusory-contour-alone activity. As in the case of subject A, the illusory-contour-alone regions were contiguous with activity on adjacent slices, and adjacent slices also indicated the presence of real contour activity for all subjects who ran that condition. The clustered responses strengthen the confidence levels of the findings (45). Although subject A was the only subject for which responses to both the horizontal and vertical meridians were obtained, responses to the vertical meridians (subjects B and C) and crosshair alone (subjects B and D) suggest that the unique illusory contour activity is in extrastriate regions of the visual cortex for these subjects as well. A three-dimensional reconstruction of all the brain slices imaged in subject A is shown in Fig. 4 and illustrates the extensive regions of visual cortex activated in response to illusory contours.

DISCUSSION

The perception of illusory contours is an example of a perceptual grouping process in human vision. Here, we are presenting evidence for cortical activation associated with such contour perception in the human visual system by using fMRI. Results from four subjects demonstrated that the illusory-contour stimuli (Fig. 1 C and D) generated fMRI responses distinct from the responses to the no-contour stimuli (Fig. 1 A and B). These no-contour stimuli were identical to the illusory-contour stimuli, except that the orientation of the inducers (pacmen) was varied, such that perceptual integration into a single shape bounded by illusory contours was impossible. We conclude that the areas activated when the subject perceived a unified shape and illusory contours represent the activity of a population of neurons associated with the process of grouping local features via perceptual contours.
FIG. 3. A representative slice for each subject illustrates the visual regions associated with the illusory-contour (IC) stimulus (yellow). Red and blue indicate active regions associated with no-contour (NC) and real-contour (RC) conditions, respectively. Right brain is designated by "R." The grid is the sampling matrix where each box contains a 5 x 5 array of pixels. The center locations of the acquired slices are indicated by the parallel lines shown on the corresponding midsagittal views from the T1-weighted images. Slice positions were selected to cover the inferior occipital lobe, and slices for subjects A, B, and C were oriented parallel to and on the anterior-to-posterior commissure line. The plane orientation for subject D was horizontal. Slice thickness was 5.0 mm for all subjects except for subject B, where the slice thickness was 3.0 mm. The red line indicates the location of the axial slice shown on the left.

Stimuli along the vertical and horizontal meridians and located at the fixation point served as functional markers for the approximate boundaries between Brodmann's areas 17/18 and 18/19, as well as the foveal representation. Comparison of these landmark responses with those of the most prominent illusory-contour-related responses places the location of the distinct illusory-contour-related activation in extrastriate regions for all subjects. However, the neuroanatomical locations for the illusory-contour-alone activity occur in multiple foci and may also include foci not resolved by our analysis. In particular, these observations do not rule out striate cortex as a participant in contour-related activity. For example, the medial and anterior (right hemisphere) regions shown on slice 6 (subject A; Fig. 2) are near the vertical meridian regions of activity and may implicate striate cortex involvement. For subject C, the vertical-meridian-related activity coincided with illusory-contour-related activity on slices 2, 4, 5, and 8–10, and for subject B, the illusory-contour- and vertical-meridian-related activity coincided on slices 3, 4, 6, and 11. To the extent that the vertical meridian serves as a landmark for the area 17/18 border, these coincident illusory contour and vertical meridian regions may suggest striate activity in contour-related processes. All subjects showed a predominance of illusory-contour-related activity in the right hemisphere. This finding may be consistent with clinical findings showing right hemisphere specialization for figural closure tasks (46, 47).

The results of these experiments do not rule out either higher level or lower level processes in the formation of illusory contours or in perceptual grouping (25). While our findings are consistent with a data-driven, bottom-up approach to illusory-contour perception, the effect of activity in other brain areas may modulate the responses in areas that we have observed. It is also possible that, in addition to activating distinct regions, illusory-contour responses may potentiate or diminish local responses to the inducing features at early levels of cortical image processing or may cause overt linking activity.

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