Brain Activity Related to the Perception of Illusory Contours

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We have addressed the question of whether the brain's capacity to resolve an ambiguous retinal image depends upon the activity of early visual areas or whether it involves the investment of the received image with higher order cognitive hypotheses. To resolve the issue, we have used the technique of positron emission tomography to detect increases in regional cerebral blood flow (rCBF) in the brains of humans while they perceive the simple figures described by Schumann (1900) and by Kanizsa (1979). These figures produce striking percepts of surfaces or contours variously described as illusory, subjective, cognitive, or anomalous because they depend upon the brain's ability to complete the figures. If such completion is due to higher order cognitive processes or a combination of higher order and early areas, then, one might expect areas of increased rCBF outside the occipital lobe when subjects perceive these figures. However, if completion is mediated entirely by early visual areas, then the increases in rCBF will be restricted to these regions. Our results show that the perception of subjective contours is associated with significant activity in early visual areas only, particularly in area V2, leading us to conclude that the occipital cortex can contribute to the perception of these stimuli without higher order cognitive influence specific to the completion task.

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INTRODUCTION

The human brain interprets, apparently effortlessly, many incomplete figures by investing them with forms. Examples are provided by the famous Kanizsa figures, where the arrangement of simple components induces the perception of contours and shapes which are more than the sum of the parts in the stimuli themselves. Figure 1A illustrates how a particular configuration of incomplete black circles and squares can induce the appearance of a superimposed triangle, whiter than the background. In essential details, the triangle thus produced is identical to a real triangle constructed by the addition of six small lines that bridge the discontinuities in the "illusory" figure (Fig. 1B). If the black shapes of Fig. 1A are rearranged (Fig. 1C), a triangle is no longer recognizable. It is thus evident that the perception of the triangle depends, in part at least, upon an interpretation that the brain imposes upon the particular arrangement of the black shapes, and it has been postulated that this interpretation is critically dependent upon higher order cognitive processes (Gregory, 1972; Rock and Anson, 1979). On the other hand, electrophysiological studies have identified cells in V1 (Grosof et al., 1993; Shapley, 1994) and V2 that respond to illusory lines (von der Heydt et al., 1984; von der Heydt and Peterhans, 1989; Peterhans and von der Heydt, 1989). Although such studies do not exclude a cognitive contribution from higher areas, they support the evidence of psychophysical studies (Smith and Over, 1979) that activity in these early visual areas themselves invest such Kanizsa figures with "anomalous" contours. The PET method provides a quick way of establishing the contribution of both higher and lower areas to the perception of a Kanizsa figure.

METHODS

The experimental design required to answer this question was not straightforward. An obvious experiment would be to compare the pattern of regional cerebral blood flow (rCBF) elicited by the illusory triangle (Fig. 1A) with that of the real triangle (Fig. 1B) and identify those cortical regions required for completion. However, if the same regions of the brain were involved in the perception of all triangles, no matter what their derivation, the positron emission tomography (PET) analysis, which reveals only differential activation, would fail to identify them. An alternative strategy, and the one that we used in this study, was to compare the activity produced by the illusory triangle (Fig. 1A) as well as the real triangle (Fig. 1B) with the activity produced by a control (Fig. 1C). By examining the difference between the two comparisons (illusory
Figure 2A shows that, compared to the control, the illusory triangle activated two symmetrical strips of the occipital cortex, one on either side of the midline, each with a statistical significance that withstood correction for multiple comparisons (Friston et al., 1995a) (Left: \( z = 4.54, P(n_{\text{max}} > k) = 0.003 \); \( z = 4.41, P(n_{\text{max}} > k) = 0.017 \), \( z = 0.032 \)). Coregistration with the average MRI derived from the same brains showed that the activity on each side is situated in the vertically oriented lunate sulcus lateral to the occipital pole (Ono et al., 1990); it did not extend onto the pole or along the calcarine fissure (Fig. 2B). Based upon human anatomical (Brindley, 1972; Clarke, 1994) and imaging (Shipp et al., 1995; Sereno et al., 1995) evidence, the most likely location of this activity is the representation of the central visual field in human area V2, although it may also include the representation of the central visual field in neighboring area V3. There were no significant activations in any brain region in the control condition with respect to the illusory triangle.

The activity in these zones might be the result of the triangle itself, the completion processing, or a combination of the two. If the activation was simply a response to the triangle, then one might expect the real triangle to produce an equivalent or even greater activity in the identical regions. In fact, the real triangle versus control comparison did not lead to significant activity in any cortical regions. We are aware, however, that the corrected significance threshold we use is very rigorous and obscures the fact that the real triangle activated the same areas as the illusory triangle (Left: \( z = 3.92, P(n_{\text{max}} > k) = 0.142 \); \( z = 3.41, P(n_{\text{max}} > k) = 0.329 \); Right: \( z = 3.41, P(n_{\text{max}} > k) = 0.956 \), \( z = 0.019 \)), although the activity is weaker in the real triangle condition (real triangle 1.7% increase in rCBF; illusory triangle 3.1% increase). One consequence of the similarity in the pattern of activity elicited by the illusory and real triangles is that the SPM analysis can detect no differences between the two, even at the lower, uncorrected threshold of \( P < 0.001 \). We conclude therefore that, while both real and illusory triangles activate V2, it is the illusory triangle that is the more potent stimulus.

If the activity in the region of V2 was secondary to a higher order hypothesis, one might expect to find evidence of the primary “cognitive” activity. However,
FIG. 2. (A) Areas of activation in the illusory triangle versus control comparison. A statistical parametric map is displayed in a maximum intensity projection viewed from the right-hand side, the back, and the top of the brain. The anatomical space corresponds to the atlas of Talairach and Tournoux (1988) and the map has been thresholded at $z = 3.09$. A table of the regions of increased rCBF is shown below with the region size in voxels, the location in the anatomical space, the $z$ score, the uncorrected significance and the significance corrected for multiple comparisons based on spatial extent $[P(n_{\text{max}} > k)]$, and the highest $z$ value $[P(z_{\text{max}} > u)]$ (Friston et al., 1995a). (B) Three horizontal slices from the average MRI of two of the four subjects normalized into the same anatomical space as the PET images. The level of each slice with respect to the AC PC plane ($z = 0$) is given above each image. The PET activity is superimposed and shown in white. PET images were obtained using a CTI 953B scanner. Permission for the administration of radioactive substances was given by the Administration of Radioactive Substances Advisory Committee of the UK Health Department. In each scan $H_2^{15}O$ was infused through an antecubital vein using a slow bolus technique (Silbersweig et al., 1993). On average, subjects received 11.2 mCi for each of the 12 scans, giving a whole body radiation dose of about 5 mSv. After backprojection, the images were realigned, transformed into stereotaxic space (Friston et al., 1995b), and smoothed (FWHM 16 mm) prior to statistical analysis using software from the Wellcome Department of Cognitive Neurology. (C) Areas of activation for the first three presentations of the illusory triangle and control. Conventions are as in A. (D) Eigenimage analysis of illusory triangle versus control comparison showing covarying regions of activity (Friston, 1994).
with the exception of a small region in the temporal lobe that did not withstand correction and was present only in the real triangle condition, there was no activity outside the occipital lobe at, or above, an uncorrected threshold of \( P < 0.001 \) in either the illusory triangle versus control or the real triangle versus control comparison. This observation implies that the completion processing necessary to perceive the illusory triangle occurs entirely within this early visual region. Such a surprising result made us wonder whether the task was too easy and whether the higher order, extraoccipital processes were active only in the first few scans. To test for this we reanalyzed the results using only the first three presentations of illusory triangle and control. Figure 2C shows that, even in these early scans, there is no extraoccipital activity. We also performed an eigenimage analysis (Friston, 1994) to identify all brain areas that did not withstand correction and were present only in the real triangle condition, with no activity outside the occipital lobe at, or above, a threshold of \( P > 0.05 \). In particular, the prefrontal cortex, covaried with the occipital regions, they did so in both the real triangle and in the illusory triangle conditions. We conclude that if the prefrontal activity reflects higher order processing, it is not a specific requirement for completion and is equally prominent during the perception of a real or an illusory figure.

**DISCUSSION**

Area V2 is well suited to respond to an “illusory” stimulus, with some 32–44\% of its cells responding to both real contours and their illusory counterparts (von der Heydt and Peters, 1989; Peters and von der Heydt, 1989). Cells in V1 may respond to virtual lines produced by abutting gratings (Grosof et al., 1993; Shapley, 1994) but have not been shown to respond to illusory bars, as do the cells of V2 (Peters and von der Heydt, 1989), which might explain why no extra activity was identified in V1 in this study. Area V3 has not been studied in this respect. One explanation for the different potency of the two triangles in activating the occipital areas is that the experiments performed identify those areas executing the completion task. In the real triangle condition, the completion processing is not abolished but is merely attenuated by the addition of genuine contours, resulting in a smaller increase in rCBF. An alternative explanation is that area V2 serves a dual role. First, V2 might be instrumental in the processing of simple shapes (in this study a triangle, although we believe other simple shapes would give the same result), leading to a greater activity in this region while viewing the real or illusory triangles than while viewing the control. Second, V2 may also play a role in the completion of simple shapes, thus recruiting an additional set of neurones while viewing the illusory triangle, with a consequent greater increase in rCBF. Whatever the functional significance of the V2 activity, our results demonstrate that the largest changes in rCBF associated with the perception of an illusory triangle fall within the territory of well defined and relatively early visual areas and that, while cognitive processing may be occurring in other cortical regions, any “higher order” activities specific to the completion task are restricted to the occipital lobe. This result further supports the notion that activity in a given cortical area can lead to both the sensing and the comprehension of a stimulus, without the need for separating the two processes cortically (Zeki, 1993).

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**REFERENCES**


**APPENDIX**

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