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The Nature of Illusory Contour Computation

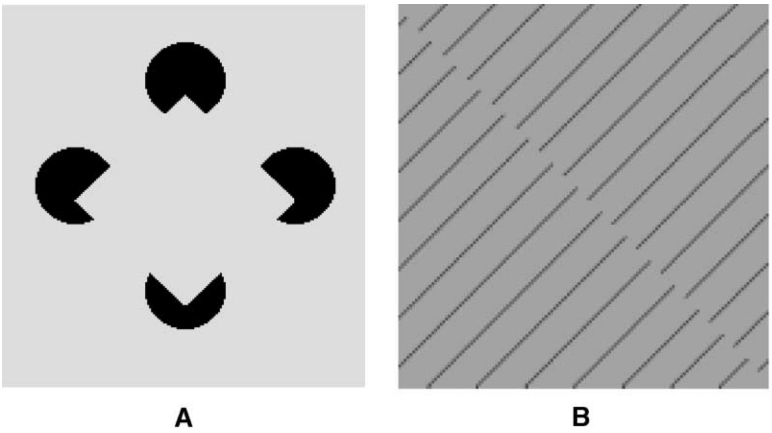
Neural correlates of illusory contour perception have been found in both the early and the higher visual areas. But the locus and the mechanism for its computation remain elusive. Psychophysical evidence provided in this issue of *Neuron* shows that perceptual contour completion is likely done in the early visual cortex in a cascade manner using horizontal connections.

An organizing principle underlying many visual computations is postulated to be the need for producing a parsimonious and simple description of the visual scene. The process for fulfilling this need is called perceptual organization. The perception of illusory contour in Kanizsa figures (Figure, panel A) underscores the workings of this principle. Rather than describing the picture as an accidental arrangement of four pacmen in some peculiar orientations, it is much simpler to interpret it as a diamond in front of four circular discs. This interpretation implies a surface or depth discontinuity between the diamond and the background. The vivid perception of illusory contour suggests this surface or depth discontinuity may be represented in the visual system explicitly, even at locations where there is no direct physical evidence for it. Psychophysical and neurophysiological studies of illusory contour perception are therefore important for understanding the neural mechanisms responsible for contour completion, in particular, and perceptual organization, in general.

Single unit neurophysiology, in recent years, has provided direct evidence that the early visual areas (V1 and V2) are involved in representing illusory contour. Since only the early visual areas contain neurons with small receptive fields for encoding information with high spatial precision and feature resolution, these areas are ideal for representing the perceived sharp contours explicitly. In their ground-breaking experiment, von der Heydt et al. (1984) found that a moving illusory bar could excite V2 neurons in monkeys even when there was nothing inside the receptive field of the neurons. Lee and Nguyen (2001) studied the temporal evolution of neuronal activities in V1 and V2 in response to the static display of Kanizsa figures. They found that the response to illusory contour emerged in V1 at about 100 ms, significantly later than the emergence of illusory contour response in V2. Other single unit and optical imaging studies involving the illusory contour defined by abutting gratings, as shown in the Figure, panel B, also implicated V1 and V2 in the representation of illusory contour (Grosof et al., 1993; Sheth et al., 1996; Ramsden et al., 2001).

However, a recent functional imaging experiment by Mendola et al. (1999) found Kanizsa figures elicited significant responses in the lateral occipital (LOC) region, but only weak, if any, response in the human early visual areas. This finding, along with the observation by Huxlin et al. (2000) on the impairment of a monkey's ability to see illusory contours as a result of a lesion in the inferotemporal cortex (IT), ignited a debate on whether the illusory contour computation is an early or a late process. While single unit studies have confirmed that the early visual cortex participates in the representation of illusory contour, they did not pinpoint the locus or the mechanism of the illusory contour computation. Computational models on illusory contour completion offered several possible solutions. Some suggested an intracortical mechanism within the early visual cortex through algorithms based on horizontal interaction (Geiger et al., 1996). Others argued for a computation that is based on successive feedforward conjunctions of elementary features (Heitger and von der Heydt, 1993). Grossberg and Mingola's (1985) model involved both intracortical and intercortical interaction.

Pillow and Rubin (2002), in this issue of *Neuron*, reported a series of careful psychophysical experiments to dissect these issues. They asked observers to discriminate the shapes of slightly deformed Kanizsa-type illusory figures. They found that, if the stimuli is exposed only for 97 ms, followed by a blank screen and then a mask, the subjects are more sensitive to the curvature of the illusory contour when the inducers (pacmen) are within a visual hemifield than when the inducers are on opposite sides of the vertical meridian. This asymmetry in sensitivity increases dramatically with an increase in gap size between the inducers. Crossing the hemispheric divide through the corpus callosum apparently has incurred an extra cost that is gap size dependent. If the computation is purely feedforward and completed in IT, one would expect the extra cost for interhemispheric transfer to be more or less fixed, independent of the gap size. The finding that the cost of interhemi-



Illusory Figures and Illusory Contours

spheric transfer increases with gap size is therefore consistent with the idea that illusory contour completion is accomplished by cascade propagation of contour signals. Neurons in the higher visual areas, such as LOC and IT, have very large receptive fields and often are not arranged in retinotopic coordinates. It is thus difficult to imagine that cascade computations of this nature would be carried out in these areas. On the other hand, early visual areas are ideal for such cascade computations to take place because the receptive fields of their neurons are small and spatially localized in retinotopic coordinates, with well-known local horizontal connections (Gilbert, 1998). Pillow and Rubin's (2002) results support models of contour completion that are based on cascade computation in the early visual cortex, thereby helping to illuminate the nature of the illusory computation.

However, Pillow and Rubin's data are not inconsistent with the idea that feedback from higher areas may also play a very important role in guiding the contour completion process in the early visual cortex. The computation of subjective contour, illusory or real, cannot be robust without the successful inference of depth and surface structures, figure-ground organization, global shape, and curvature recognition. Perceptual organization is likely an interactive process that occurs at multiple brain areas at the same time. Inferences at the different levels constrain one another through the recurrent connections. The most probable scenario is one that information rapidly propagates to IT through direct feedforward computation, which generates rough hypotheses about the shapes and figures in the scene. These hypotheses or contextual information then propagate down the visual hierarchy to guide the early visual areas to work out the details, constructing a precise representation of illusory contour using the intrinsic circuitry in V1 and V2. As the illusory contour becomes clear and precise in the early visual cortex, the global shape percept of the illusory figure starts to emerge in the higher visual areas. From this perspective, the computation of illusory contour involves both the early and the late processes.

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Toward an Understanding of the Brain Substrates of Reward in Humans

"If you ever get close to a human and human emotion, you better get ready to get confused."

—Bjork

A network of brain regions has been implicated in food-reward processing. O'Doherty et al. (2002) now provide evidence that this network is differentially modulated by anticipation versus receipt of a food