Published in final edited form as:
Cogn Neurosci. 2013 ; 4(1): 49–50. doi:10.1080/17588928.2012.748024.

Neurophysiological constraints on models of illusory contours

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Kogo and Wagemans present a lucid discussion of the various models that have been proposed to explain the phenomenon of illusory contours, pointing out that models need to explain not only the illusory contours where they appear, but also why they do not appear in other situations. I agree in particular with their point that simple interpolation models fail these criteria. A demonstration that makes this immediately obvious is the Ehrenstein illusion in which radial lines induce a circular illusory contour (the 4-armed version is shown in Fig.1A right). In this figure, interpolation of the lines would produce a cross rather than a circle. I wonder why Kogo and Wagemans (2010) and other authors did not test their model on this illusion. It might be thought that the pacman figure (Fig. 1A left) and the Ehrenstein illusion (right) involve different mechanisms. However, the neurophysiology tells otherwise. In our study of illusory contour representation in monkey visual cortex, Esther Peterhans and I used two different types of stimuli, one in which an illusory contour is produced by abutting gratings of thin lines, and a configuration in which an illusory bar is induced by two solid shapes (von der Heydt and Peterhans, 1989;Peterhans and von der Heydt, 1989). In the latter configuration, the illusory contours are collinear interpolations of given edges, like in the pacman figure. But in the abutting gratings, the illusory contour is orthogonal to the inducing lines, like in the Ehrenstein figure. We compared both types of contour in a sample of neurons and found that the results correlated: Of 15 cells that signaled an illusory contour with the abutting grating stimulus, 9 also signaled one in the illusory bar configuration, and of 23 cells that were unresponsive to the former, 22 were also unresponsive to the latter. Thus, the two tests produced correlated results ($p<0.001$). The simplest explanation for this is that the illusory contour signals in the two situations are produced by the same mechanism. It is a challenge to produce the correct illusory contours in the pacman figure as well as the Ehrenstein figure with the same model, because one calls for interpolation, whereas the other prohibits it (see Fig. 1A). To reconcile these conflicting demands was a main consideration in the model by Heitger et al. (1998), results of which are shown in Fig. 1B.

Also from the neurophysiological perspective I have reservations with the claim that illusory contours and border ownership must be treated together and that the former cannot be explained without the latter, which is the main point of the review. I agree that both are related. Illusory contours reflect mechanisms for the detection of occlusion, and occlusion implies border ownership. But some findings indicate that the underlying neural mechanisms are different. Illusory contour responses, as recorded in area V2, show a limited range of context integration. Typically, these responses drop to zero when the gap between the inducing elements is wider than about 3 deg (Peterhans and von der Heydt, 1989). By comparison, border ownership selectivity, also found in V2, shows context integration over distances of 10 deg or more. Also different from illusory contours, border ownership modulation does not require “relatability” (Kellman and Shipley, 1991): even a figure edge parallel to the edge in the receptive field contributes border ownership modulation (Zhang and von der Heydt, 2010). Together, these studies suggest that illusory contour responses might be generated by relatively local integration of signals, possibly in feed-forward fashion (e.g., Heitger et al., 1998), whereas border ownership modulation might involve feedback from a higher level (Zhang and von der Heydt, 2010; Sugihara et al., 2011). Both mechanisms might contribute their shares to the strength of illusory contours as measured in perceptual studies, depending on configuration and paradigm. The wide range of context integration seen in border ownership signals and their short latencies are important constraints on modeling. Kogo & Wagemans do not discuss these constraints and how the influence of global configuration, as sketched in their Fig. 7F, can propagate so fast over large distances in cortex. This might be a problem, especially since their model uses an iterative algorithm in which signals have to travel back and forth multiple times.

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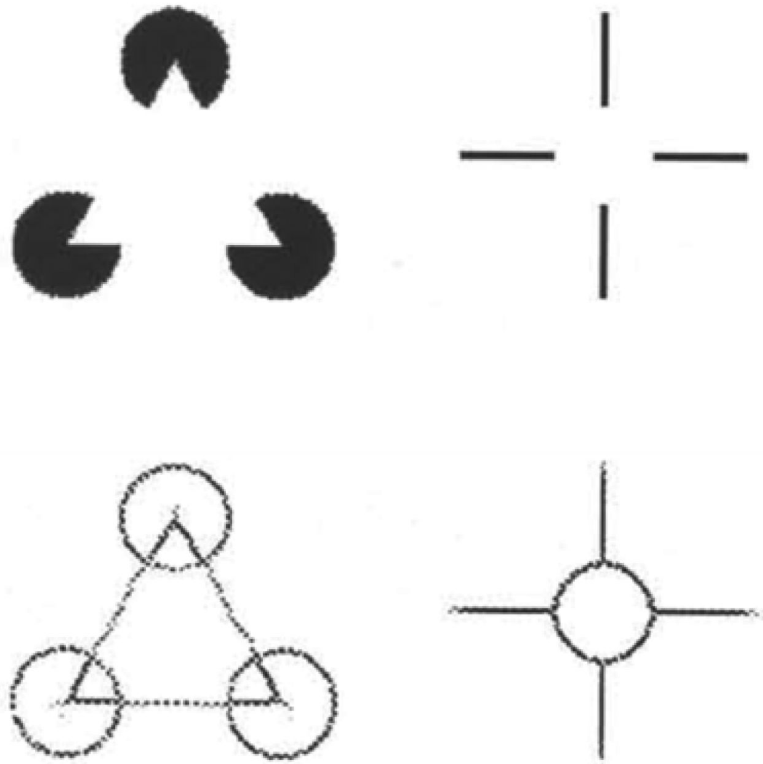

Fig. 1.

A, Illusory contours can appear as interpolations between edges of the inducing elements (pacman figure, left), or can be orthogonal to the inducing elements (Ehrenstein figure, right). B, Contours produced by the model of Heitger et al. 1998. Modified from Heitger et al. 1998.