Shape processing area LO and illusory contours

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Abstract:

Recent functional MRI has highlighted that illusory contours can activate the primary visual cortex. Our investigation sought to demonstrate whether this correlation reflects computations performed in the primary visual cortex or feedback effects from shape processing area LO. We explored this in a patient who has a bilateral lesion to LO, but a functionally spared V1. Our data indicate that illusory contours are unable to influence behaviour without visual area LO. Whilst we would not claim that our data provide evidence for the 'cognitive' nature of illusory contours, they certainly suggest that illusory contours are dependent upon the computations involved in extracting shape representations in LO. Our data highlight the importance of neuropsychological data in interpreting the role of feedforward and feedback effects in the generation of visual illusions.

Typical illusory contours result when the visual system modally completes a surface whose presence is implied by the removal of corners from real objects (see Figure 1 for the example of the stimuli used in the current study). It is unclear whether these illusions result from local computations involved in the visual system's attempt to extract edges from the visual scene or from a higher-level interpretation of the possible shapes that could cause that pattern of visual input ("cognitive contours": Gregory 1972). Recent neuroimaging studies, using stimuli identical to those employed in this paper, have shifted the debate on illusory contours by demonstrating that they activate early visual areas (Seghier et. al., 2000). Of course this result does not preclude the possibility that these activations develop from feedback arising at higher levels of the visual system.
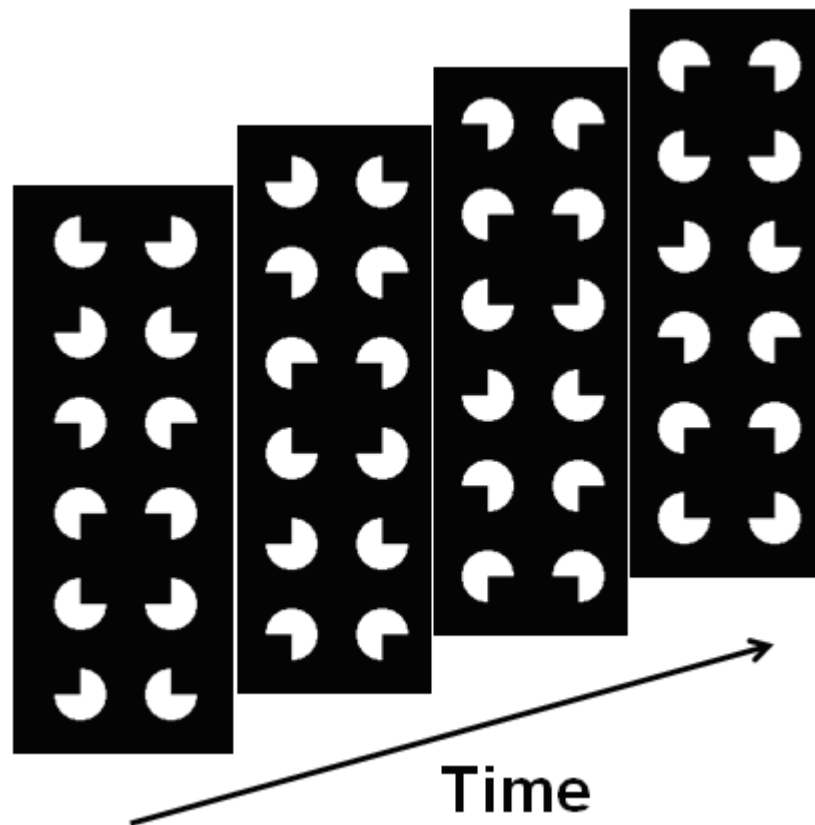

Figure 1: Moving Kanizsa Stimulus.

The stimuli were displayed on a Taxan Ergovision 8855LR (600 x 800 pixels) monitor, driven by a Cambridge Research Systems VSG 2/5 graphics system at 100 Hz. Each frame was presented in the centre of a black screen for 300ms. Each "pac-man" subtended 1.5 degrees of visual angle.

The neurological patient D.F. provides an opportunity to test the role of different areas in computing illusory contours. D.F. has a visual form agnosia resulting from bilateral damage to the putative shape processing area LO (James et al. 2003). D.F.'s ability to perceive visual form is extremely limited, and her perceptual system is unable to make even very basic form discriminations. On the other hand it is also clear that D.F.'s primary visual cortex is functionally spared, and is able to perform a number of important computations: it can supply information to guide manual actions (Milner and Goodale 1995), enables the perception of motion direction, the segmentation of figure-ground relationships (Carey et al., 2006) and the integration of chromatic and orientation information (Humphrey et al., 1991).

This pattern of impaired and preserved function allows us to ask whether computations performed in the primary visual cortex are sufficient for creating illusory contours. Indeed D.F.'s preserved motion perception allows us to use a variation of the illusory contour phenomenon in which the contours give rise to a percept of motion (see Figure 1). If orientation and segmentation processing in D.F.'s primary visual cortex are sufficient to generate this illusory stimulus then they should evoke, or at least influence, her motion perception.

Before exploring D.F.'s ability to perceive the motion of an illusory square, it was necessary to establish that she can perceive the motion of a real black square (presented without the 'pac-men' inducers, at the same speed and size as the illusory square). D.F. was not perfect at this, but did achieve an accuracy of 90% on 2 blocks of 24 trials. She was then presented with 4 blocks of 24 trials of illusory motion. D.F. certainly did not experience the compelling perception of motion experienced by normal observers – she felt she was guessing. Her guesses were, however, above chance, averaging 60.4%. On a two-tailed binomial test this performance is almost significant (N=96, p=0.082). Thus D.F.'s pattern of performance could be taken to suggest that despite the complete bilateral disruption to LO, she is still able to extract sufficient information to represent illusory contours and for those contours to bias her motion discrimination.

In the next series of observations we had two aims: the first was to establish the reliability of the trend reported above. The second aim was to establish whether or not this near-significant performance could be explained by any means other than the extraction of illusory contours.
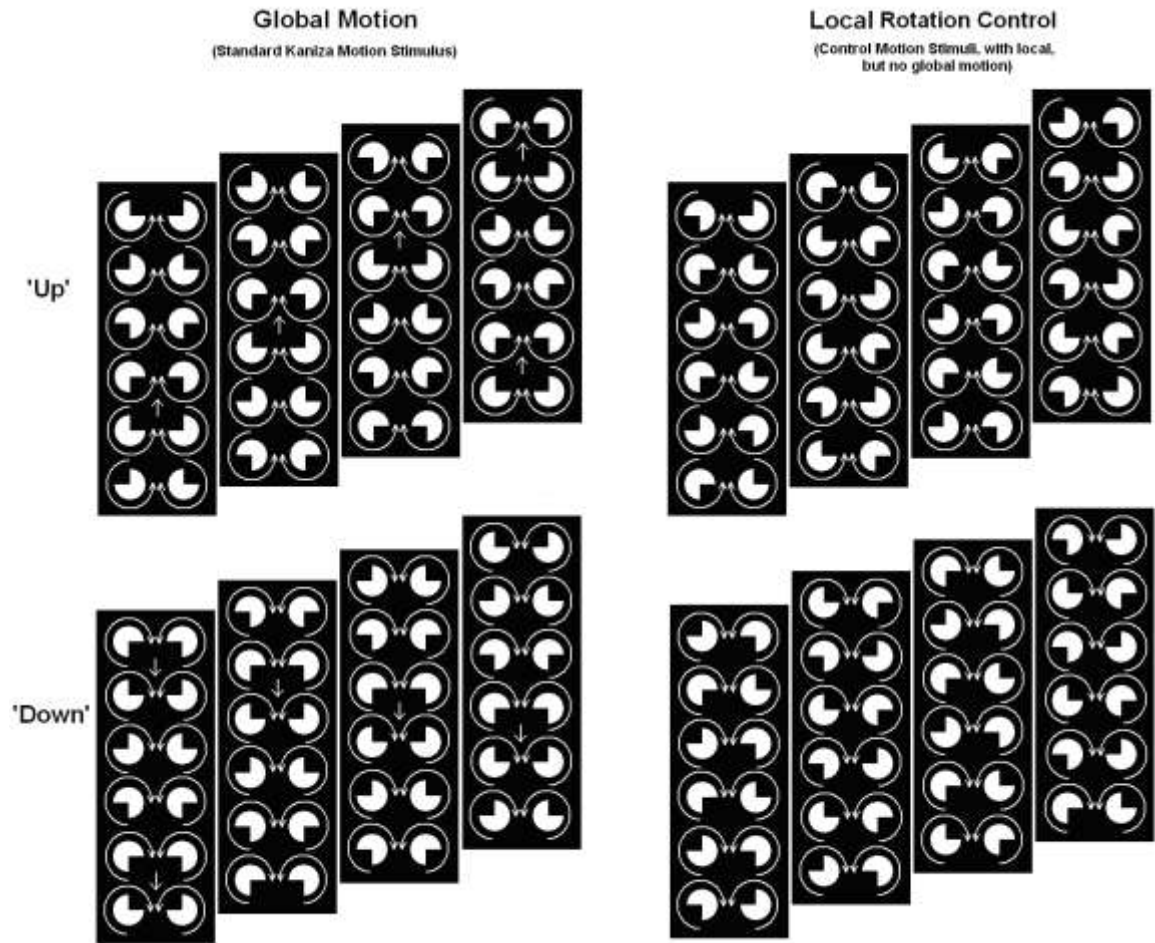
Figure 2: The local rotation confound in the motion stimulus of Figure 1.

The control stimuli on the right contain a local rotation cue but no subjective square.

On viewing Figure 2 it becomes apparent that when the illusory square moves up the screen all the "pac-men" on the left rotate anti-clockwise while those on the right rotate clockwise, and vice-versa when the illusory square is seen to move down the screen. We therefore constructed a control stimulus in which this local rotation confound remains present, but there is no global illusory motion. If D.F.'s performance on the

global motion stimulus is in fact based on this local rotational cue than she should also be above-chance in her judgement of the local rotation control stimulus.

D.F. was presented with 11 blocks of 24 trials using the original illusory motion stimulus. Her performance was slightly lower than previously (58%), but with the larger sample a two tailed binomial test revealed that this reached significance (N=246, p=0.011). However when presented with 19[1] blocks of 24 trials employing the local rotation cue alone D.F. was also able to perform significantly above chance (57%, N=432, p=0.004). Critically a Fisher's exact test between the performance associated with each stimulus type revealed that her performance on the two tasks did not differ (N=696, p=0.813).

Thus whilst D.F. has a functioning primary visual cortex that enables her to perceive figure-ground relationships and enables an implicit processing of orientation, she is unable to perceive this normally compelling motion illusion generated by illusory contours. Indeed D.F. is not only unable to perceive this illusion she is also unable to guess at the direction of motion, when an appropriate stimulus is used as a control baseline. In reviewing fMRI studies of the neural substrates activated by illusory contours, Seghier and Vuilleumier (2006) highlight a range of different areas, including V1, area LO, and the right fusiform gyrus. Although informative, these neuroimaging data cannot tell us where the critical computations responsible for the illusion take place. D.F. shows functional activations in both V1 (James et al. 2003) and right fusiform gyrus (Steeves et al., 2006) but has a clear anatomical disruption to, and indeed shows no functional activation in, area LO (James et al. 2003). The current findings therefore

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[1] The uneven number of blocks (11 for the original and 19 for this control) occurred because of time constraints in testing the patient.

suggest that area LO is critical to the generation of illusory contours. The orientation

processing and segmentation mechanisms evidently supported by D.F.'s primary visual

cortex are insufficient in themselves to support the formation of illusory contours. Thus

although Seghier and colleagues (2000) have demonstrated that moving illusory contours

activate the primary visual cortex, our data suggest that this activation may reflect

feedback from the results of computations performed at higher stages of information

processing. Indeed this conclusion, based on human neuropsychology, is complementary

to lesion work with monkeys (Huxlin, et al. 2000) suggesting that the inferior temporal

cortex (considered the monkey homologue to human LO) is required for the monkey's

visual system to generate illusory contours. We contend that this work highlights the

value of neuropsychological research for teasing out the role of feed-forward and

feedback effects in the human visual system.

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