

## Journal Club

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## Seeing Things: Illusory Contours in the Human Visual Brain

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Review of Montaser-Kouhsari et al. (<http://www.jneurosci.org/cgi/content/full/27/9/2186>)

Visual illusions are fascinating. They raise a fundamental question: how is it that our perception can be so profoundly different from reality? Visual illusions have proven to be a fruitful strategy to investigate the constructive nature of vision. Illusory contours in particular have captured researchers' attention ever since they were introduced by Gaetano Kanisza in 1976 (Kanisza, 1976). In contrast to "real" contours, which are defined by luminance or chromaticity, "illusory contours" are perceived in the absence of any luminance or chromaticity gradient. One example is the "abutting-line grating" illusion (Fig. 1A) in which displaced line gratings induce the perception of an illusory boundary.

Despite intense study, the underlying neuronal mechanisms of illusory percepts are still not fully understood (Seghier and Vuilleumier, 2006). Electrophysiological investigations in monkeys have focused on early visual areas V1 and V2. Illusory-related activity can be consistently observed in V2 neurons. The story is more complicated and still under debate whether V1 neurons also respond to illusory contours, and if so, whether the signal is generated by V1 neurons or reflects a feedback signal from V2 or even higher visual areas. In contrast, functional neuroimaging studies in humans show

illusory-related activity mainly in higher visual areas, although some evidence exists for involvement of early visual areas. Montaser-Kouhsari et al. (2007) have recently made a significant contribution to the search for neuronal correlates of illusory contour perception using functional magnetic resonance imaging (fMRI) in a study published in *The Journal of Neuroscience*.

The authors presented subjects abutting line gratings that elicited either vertical or horizontal illusory contours (Fig. 1A) [Montaser-Kouhsari et al. (2007), their Fig. 1A (<http://www.jneurosci.org/cgi/content/full/27/9/2186/F1>)]. To localize orientation-selective neuronal responses to these illusory contours, Montaser-Kouhsari et al. (2007) used an fMRI adaptation paradigm. In a typical event-related fMRI adaptation paradigm, two stimuli ("adapter" and "test stimulus") were presented sequentially. The adapter and the test stimulus had either the same ("parallel") or a perpendicular ("orthogonal") illusory-contour orientation (Fig. 1A) [Montaser-Kouhsari et al. (2007), their Figure 2A (<http://www.jneurosci.org/cgi/content/full/27/9/2186/F2>)]. The great advantage of such an fMRI design is that it allows assessing the functional characteristics of brain regions at the level of neuronal subpopulations. If fMRI responses for test stimuli parallel to the adapter are smaller than for test stimuli orthogonal to the adapter (Fig. 1B), one may assume that the region contains neurons selective for the orientation of the illusory contour. In their straight-

forward analysis, Montaser-Kouhsari et al. (2007) defined a number of visual areas based on the retinotopic organization and measured the orientation-selective fMRI responses to the illusory contours.

Orientation-selective adaptation to illusory contours was observed in all retinotopic visual areas [Montaser-Kouhsari et al. (2007), their Figs. 4 (<http://www.jneurosci.org/cgi/content/full/27/9/2186/F4>), 5 (<http://www.jneurosci.org/cgi/content/full/27/9/2186/F5>)]. The authors calculated an adaptation index to quantify the difference between fMRI responses to parallel and orthogonal trials, taking into account the overall response amplitude in each visual area. Most interestingly, this analysis revealed that the amount of adaptation increased from early to higher visual areas [Montaser-Kouhsari et al. (2007), their Fig. 7A (<http://www.jneurosci.org/cgi/content/full/27/9/2186/F7>)]. The authors took great care in controlling for confounding effects. Potential adaptation to the inducing line grating was avoided by changing the orientation of the inducers every 160 ms during both the adaptation and test period. To control for attention-related effects, subjects were engaged in a demanding center task. Two experiments were conducted to ensure that the observed adaptation effects were actually based on the illusory percept and not on low-level features of the stimuli. In one experiment, the line gratings were misplaced to eliminate the percept of illusory contours, and in the other experiment, the adapter stimulus was a random-noise pattern with a phase spectrum that differed

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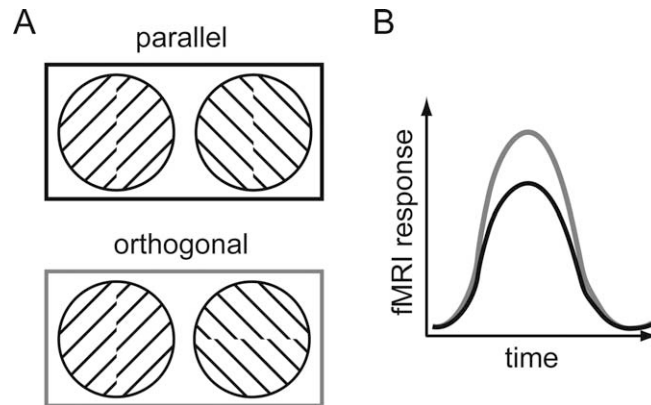
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from that of the test stimulus [Montaser-Kouhsari et al. (2007), their Fig. 1A, (<http://www.jneurosci.org/cgi/content/full/27/9/2186/F1>)]. No orientation-selective adaptation to the control stimuli was observable in any of the visual areas under study [Montaser-Kouhsari et al. (2007), their Fig. 6B,C (<http://www.jneurosci.org/cgi/content/full/27/9/2186/F6>)].

In summary, Montaser-Kouhsari et al. (2007) show in a series of elegant experiments that fMRI adaptation detected orientation-selective responses to illusory contours in multiple visual areas. The authors thereby bridge previous electrophysiological and neuroimaging findings. Moreover, their study demonstrates nicely the potential of fMRI adaptation in disentangling neuronal subpopulations that are not separable using conventional fMRI.

Although the current investigation advances our understanding of the neuronal correlates of visual illusions, a key question remains unanswered: which brain areas are really necessary to produce the illusory percept? As shown by Montaser-Kouhsari et al. (2007), almost all visual areas are involved in the processing of il-

lusory contours; however, their exact interplay in constructing the perceptual illusion is still open. More precisely, it is still hotly debated whether a feedforward model alone is sufficient to give rise to conscious perception or whether feedback activity from higher areas to the primary cortices have to be taken into account (Lamme, 2006). Additional empirical investigations are needed before we can really answer the vexing question: how can it be that we see something that is not really there?



**Figure 1.** Experimental design. **A**, Schematic illustration of the two main experimental conditions. **B**, Schematic illustration of hypothesized brain fMRI responses to the different experimental conditions.

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