

'My most true mind thus makes mine eye untrue'

It should come as no surprise that the way you see the world is not correlated perfectly with the image on your retina. A myriad of 'extraretinal' factors, including memory, attention, motivation and motor activity, supplement the retinal image, and contribute to the illuminating experience we call visual perception. In recognition of this, and the potential it holds for understanding the mechanisms of perception, there have been a number of attempts to investigate the underlying neural structures and events. One of the most recent is a remarkable study by Assad and Maunsell¹, who discovered a population of neurons that responded as though signaling the motion of a target moving behind an opaque occluder – despite the fact that the target's motion was not present in the retinal image.

In evaluating the significance of this new result, it is useful to consider the distinction between the classical definitions of sensation and perception, and the manner in which extraretinal influences bear upon that distinction. The concepts behind this distinction were made explicit in the mid-19th century by the English philosopher John Stuart Mill², who viewed perception as a mental representation of the 'permanent possibilities of sensation'. Whereas the retinal image offers data from the visual environment, those data are, by nature, fleeting and discontinuous. Perception reclaims the enduring structural and relational qualities of the external environment. It follows that perception includes inferences and expectations about parts of that environment in the absence of direct sensation, that is, awareness of the possibility of sensation. Mill's ideas were elaborated greatly by William James³ in his concept of the "perception of 'things'". In their essential qualities, these ideas have carried the discipline of perceptual psychology through to the present day.

Viewed in this manner, one type of extraretinal influence on visual perception

simply consists of internalized representations of environmental structure and events suggested by context, that is, sensory data received at another time or place. To put it in James' terms, these are the 'farther facts' associated with the object of sensation'. However reasonable this view might seem intuitively, 'internalized possibilities' and 'farther facts' are concepts perhaps too vague for modern neurobiology, and they raised the question of how such environmental inferences and expectations are represented in the brain. James took the question to heart but he and his contemporaries lacked the means to address it properly. The question has resurfaced in the last quarter of the 20th century at the core of the 'imagery debate'.⁴

The Jamesian view holds that imagery is part-and-parcel of perception, and that the experiential differences between the things that are called visual imagery and visual perception can be traced to the remoteness of sensory context³. My perception of the rooftop contour beyond my window has a direct link to sensory events. My no-less-real perception of the continuation of that rooftop behind the wall between two windows, in the absence of direct sensory data, is elicited by proximal context. My ability to perceive the same rooftop contour when I turn my back to the window stems from contextual cues that are slightly more remote in both space and time. And so on. Common to all of these internal states is the ability to direct a behavioral response to the perceived (or imagined, if you prefer) object, suggesting the existence of a common neuronal representation.

These arguments for parsimony lead us to consider the form of the representation. The polar views of the imagery debate hold that the representation is either depictive, in which the possibilities of sensation are represented in the same neuronal currency as sensation itself, or a propositional framework that captures the

structure of the scene (for example, 'surface *a* extends behind surface *b*')⁵. The foregoing discussion suggests a strategy for distinguishing between these two alternatives: the depictive hypothesis predicts that representational invariance should parallel perceptual constancy across different degrees of contextual remoteness. This predicted representational invariance should have measurable manifestations in neuronal activity. This proposition can be evaluated by examining the different ways in which context determines the relationship between sensory and perceptual events.

Three sensation-perception relationships

One type of relationship has set the standard for a depictive representation, and is characterized by perceptual events that have a direct and immediate link to sensory events. For example, the presence of an isolated oriented contour in the retinal image gives rise, rather directly, to a percept of the same. The response of a cortical orientation-selective neuron under these circumstances thus exemplifies a depictive representation of environmental structure. It might be argued that direct sensation-perception relationships never occur when viewing natural scenes because such sensory events always occur in a spatiotemporal context. However, it is possible to approximate a direct relationship in the laboratory using visual stimuli that are devoid of proximal context. Because stimuli of this sort have long been 'tools' in experimental studies of neuronal representations, it is in fact this type of sensation-perception relationship for which we have the greatest knowledge of neural substrates⁶.

In addition to direct relationships, both James³ and Kanizsa⁷ identified two fundamental ways in which perception breaks the bonds of sensory events routinely. In the first case, what is seen is not present in the sensory input, but the experience is indistinguishable from the direct perceptual

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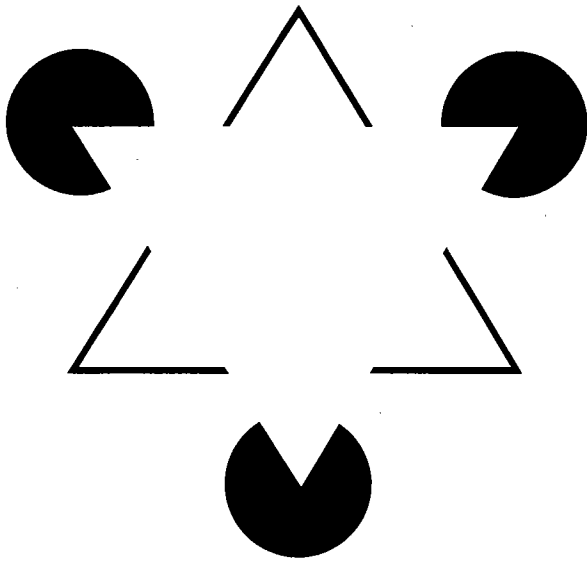


Fig. 1. Illusory contours are a salient and oft-noted example of one type of break between sensory events and perceptual state. The percept has a sensory-like quality or 'modal presence'⁷, and is indicative of environmental structure (overlapping surfaces). It is heavily dependent upon spatial context. Neurophysiological experiments indicate that such percepts are served by the same depictive neuronal representation that underlies more direct sensory-perceptual events⁸. G. Kanizsa, *Organization in Vision*, reprinted with permission of Greenwood Publishing Group, Inc., Westport, CT. © 1979.

effects of sensation. Kanizsa⁷ spoke of things perceived in this manner as having a 'modal presence', in reference to the fact that they appear to have resulted from stimulation of the visual modality, and they are what are thought of commonly as illusions. Many effects of this sort, such as illusory contours (Fig. 1) and illusions of lightness, can be 'explained' by appealing to internalized environmental structure⁷ – the presence of occluding surfaces and particular conditions of illumination. They can also be explained by reference to spatial context – other sensory events that occur at different retinal locations at the same time. Regardless of the explanatory level that is adopted, neuronal activity that is associated with these illusory perceptual events is almost indistinguishable from neuronal responses to the real thing⁸. This indicates the existence of a common depictive neuronal representation.

The second general class of sensation-perception schism recalls directly Mill's notion of belief in the permanent possibilities of sensation. As identified by James, this relationship is one in which a percept is elicited by indirect sensation because the 'mind is full of the thought of [the object]¹³. Restricting our discussion to a limited range of such percepts, this class consists of environmental structures or events that are occluded from immediate view but are nonetheless believed to exist. It is in this manner that I perceive the rooftop contour of the adjacent building as it passes from my view. Kanizsa⁷

called such perceptual interpolation 'amodal completion', in reference to the fact that 'perceptual existence is not verified by any sensory modality'. Amodal perceptual completion is, nonetheless, linked to sensory input by context, and it is fundamentally a process in which environmental surfaces are identified and ordered in depth' (Fig. 2).

Neuronal representations of things perceived but not sensed

Perceptual completion of occluded environmental structures is sufficiently regular and stereotyped to offer an ideal opportunity to explore neuronal representations of things perceived but not sensed directly. Of crucial importance is determining whether this type of perception is associated with the same depictive neuronal representation that underlies direct or modal sensation-perception relationships. The recent experiment by Assad and Maunsell¹ addresses this question directly. These investigators trained rhesus monkeys to view three different stimuli. One stimulus consisted of a small spot that was moved from a peripheral visual field location toward the center of gaze. The percept of a moving target elicited by this 'full-vision' condition bears a direct relationship to the sensory stimulus, and it constitutes an example of the first class of sensation-perception relationship identified above. A second stimulus in the experiment began with a stationary target that appeared at a peripheral location (12° from center of gaze). After a brief delay, during which no target was visible, the target reappeared and moved the short distance that remained

(2°) between the point of reappearance and the center of gaze. The visible target positions and the timing of the intervening delay were consistent with target motion occurring behind an opaque occluder, along a path that was identical to the real movement of the full-vision condition. This 'occlusion' condition should elicit amodal perceptual completion of the target's motion, as constrained by context (that is, the visible endpoints, and the motion path seen previously). The predictive quality of this perceptual experience is precisely that of Mill's 'permanent possibilities of sensation'. A third 'blink' stimulus was included as a control for sensitivity to the static target: the target appeared at a peripheral location, disappeared briefly, and reappeared at the same peripheral location. All three conditions were presented in blocks of similar stimulus type, which allowed perception to be informed by the context of trial expectations.

The full-vision and occlusion conditions were thus expected to elicit a common percept of target motion, despite different sensory input. By assessing the activity of motion-sensitive cortical neurons under these different stimulus conditions, Assad and Maunsell were able to determine whether these percepts are grounded in a common neuronal representation. For each cell studied in posterior parietal cortex, full-vision and occlusion conditions were viewed such that the path of motion, real and inferred, was aligned to traverse the neuron's receptive field, moving in the preferred direction. Predictably, each neuron responded to real target motion. Approximately half of the sampled cells also responded during the period

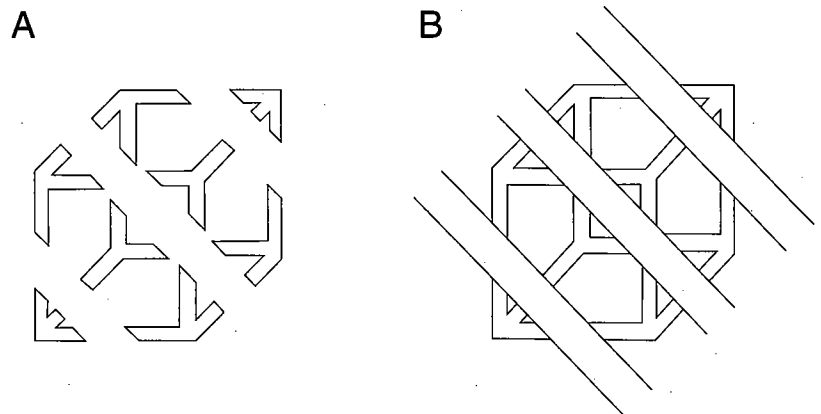


Fig. 2. 'Amodal perceptual completion'. Amodal perceptual completion constitutes a second type of break between sensory events and perceptual state, and it is a ubiquitous characteristic of visual perception. It is also dependent upon contextual cues. Simple continuity of line (compare A with B), for example, implies the existence of a foreground surface that elicits, in turn, perceptual completion of other partially occluded surfaces. In this manner, given prior knowledge of environmental attributes and a minimal set of structural rules, context implies the possibility of sensation. The recent results of Assad and Maunsell¹ indicate that amodal perceptual completion of the motion trajectory of an occluded object is served by the same depictive neuronal representation that underlies more direct sensory-perceptual events. G. Kanizsa, *Organization in Vision*, reprinted with permission of Greenwood Publishing Group, Inc., Westport, CT. © 1979.

between the two target presentations in the occlusion condition - precisely the interval during which the target would have been expected to move behind the occluder. In other words, these neurons responded in a manner that was consistent with environmental events suggested by context, despite the fact that no retinal motion was sensed. Notably, no sampled neurons responded during the delay period of the blink condition, which did not present contextual cues appropriate for inferred motion, even though blink and occlusion trials were identical before target reappearance.

This experiment is pioneering in two important respects. First, by manipulating crucial contextual cues, the investigators have cut the direct links between sensory and perceptual events that are characteristic of most neurophysiological studies of the primate visual system. In doing so, the results provide a glimpse of the neuronal structures and events that underlie perception in the broad sense of the term as expounded by Mill. Second, the results confirm that a depictive form of the neuronal representation remains invariant despite the increasing remoteness of sensory context.

But can we extend this experimental approach, and the knowledge gained, to the aspects of the mind's eye where 'imagination has lost the force of fact'³? Skeptics will surely note that as perception becomes increasingly remote from sensory events, so declines our ability to identify reliably the perceptual state of others. (This is, of course, a caveat that applies when interpreting the results of Assad and Maunsell.) While this is a concern for which appropriate precautions must be taken, it seems unlikely that such a promising approach will come to a grinding halt under the 'weight' of solipsism. There are ways of obtaining complex perceptual reports from non-human primates and, as we have seen from the work of Assad and Maunsell, data that are obtained from single neurons can be tremendously revealing. However, in some ways the human brain seems an easier target as we find it comparatively straightforward to convince ourselves of the perceptual states of our conspecifics. New techniques for estimating human neuronal activity have already yielded convincing evidence to support James' conjecture³ that visual imagery is carried out in the same neuronal structures that subserve more direct

perceptual events⁹. As these techniques begin to offer finer spatial and temporal resolution, we might soon grasp more fully how neuronal representations figure into the visual life of the mind - how 'the most sweet favor or deformed'st creature,...it shapes them to your feature. Incapable of more, replete with you, My most true mind thus makes mine eye untrue'¹⁰.

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