unique shape and orientation, are all essential components for understanding tooth formation in these worms.

The discovery of magnetite in the teeth of chitons initiated a series of investigations that contributed significantly to our understanding of basic processes of biomineralization. The discovery of this copper chloride mineral in the teeth of another invertebrate may well do the same. There is still much to learn about the mechanisms involved in controlled mineral formation.

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Table S1

PERSPECTIVES: NEUROSCIENCE

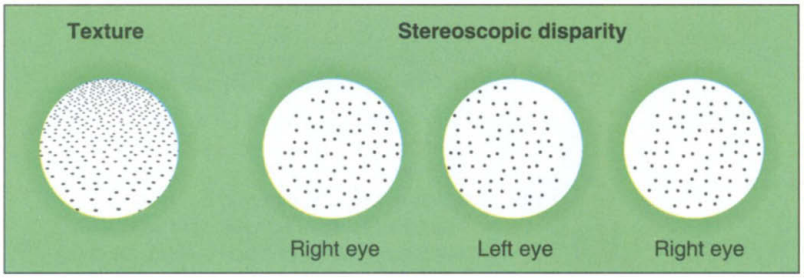
Reconstructing a 3D World

Charles E. Connor

Information in the visual system starts out as a two-dimensional (2D) pattern of neural activity across the retina. Yet the world we perceive is three-dimensional (3D). The neural mechanisms for reconstructing this 3D reality from 2D sensory inputs have long fascinated scientists. Much research has focused on stereopsis—inferring depth position from small image disparities between the right and left eyes. Neurons in the primary visual cortex (V1), V2, and many other visual areas are sensitive to such disparities, providing the signals that enable us to perceive depth stereoscopically (*1*–*3*). However, even without stereopsis—for example, when viewing photographs or movies—we still obtain vivid impressions of depth. This kind of nonstereoscopic 3D perception depends on other cues such as shading, perspective, texture gradients, and motion parallax. Two articles in this issue, one by Tsutsui *et al.* on page 409 (*4*) and one by Vanduffel *et al.* on page 413 (*5*), break new ground in understanding how the brain uses such cues to infer 3D structure.

Tsutsui and colleagues (*4*) used electrophysiological recording to study responses of single neurons in the caudal intraparietal sulcus (CIP) of the monkey brain. CIP is part of the dorsal visual pathway, which processes large-scale spatial information. This group has already shown that CIP neurons are tuned for 3D surface orientation defined by stereoscopic disparity and perspective cues (*6*, *7*). Here, they report that CIP neurons are also sensitive to texture-based depth cues. Texture gradients convey 3D orientation through gradual changes in the size, shape, and spacing of small surface elements (see the figure).

One striking aspect of the Tsutsui *et al.* results is that most cells showed identical tuning for surfaces defined by texture gradients and for surfaces defined by purely stereoscopic cues. The figure shows how texture and stereopsis suggest the same surface orientation in different ways. The majority of CIP neurons tested with both of these very different cues showed consistent selectivity for the same surface orientations. Such convergence of coherent information from different sources is unlikely to occur by chance. Thus, these investigators provide unusually strong evidence for CIP's involvement in 3D surface perception.



Making 3D a reality. The figure shows how texture and stereopsis suggest the same surface orientation in different ways. **(Left)** The gradual bottom-to-top decrease in texture element size and spacing implies that the surface is slanting away toward the top. **(Right)** A random dot stereogram, with no changes in texture size or spacing, but with a bottom-to-top gradient in dot position disparity (between the right and left eye images). Readers can either uncross their eyes to view the right pair of circles or cross their eyes to view the left pair. This stereogram produces the same percept of surface slant.

3D surface orientation tuning has also been demonstrated in region MT/V5, another dorsal visual pathway area, using random dot stimuli with stereoscopic disparity (*8*) and motion parallax (*9*) cues. In contrast, many neurons in area V4, part of the object-related ventral visual pathway, are tuned for the 3D orientation of elongated stimuli (rectangular bars) but not continuous surfaces (*10*). It may be that the dorsal (spatial) pathway is specialized for representing 3D surfaces, which can pertain to objects but can also define the large-scale spatial structure of landscapes and buildings. (The ground, for example, usually slants away from the viewer in the direction shown in the figure.) The ventral (object) pathway may be more concerned with 3D contours (edges and lines), which contain the most information about object shape.

The importance of electrophysiological studies in monkeys, exemplified by the Tsutsui *et al.* work, lies partly in their implications for human vision. Monkeys have long been considered a good model for human vision because of their similar visual capacities and evolutionary proximity. The relationship has turned out to be even closer, as shown by functional magnetic resonance imaging (fMRI) studies of visually evoked neural activity in humans. These studies reveal a similar arrangement of retinotopic maps (that is, retinal maps of visual space) and specialized responses across the surface of the visual cortex in the two species. As a result, there is a strong case for homology between monkey and human areas V1, V2, V3, V3A, VP, V4v (ventral V4), and MT/V5 (*11*, *12*). Thus, it is now possible to study detailed neural mechanisms in the monkey and point to specific areas of the human brain where the same processing may occur.

Such cross-species comparisons usually rely on electrophysiology in monkeys and fMRI in humans. Vanduffel and colleagues, in their study of motion-based 3D perception (*5*), have taken the more direct approach of using fMRI on awake subjects of both species. This has the obvious advantage of closer technical equivalence between experiments. It also overcomes the

The author is in the Department of Neuroscience and the Zanvyl Krieger Mind/Brain Institute, Johns Hopkins University, Baltimore, MD 21218, USA. E-mail: connor@jhu.edu

data limitations of monkey electrophysiology, which is ideal for examining circuit-level information processing but slow and indirect for measuring neuronal population activity in multiple brain areas. Vanduffel *et al.* used this parallel fMRI approach to show that organization of motion-based 3D processing in monkeys and humans is partly analogous, but also has some striking dissimilarities that may reflect functional differences in higher level visual areas.

The stimuli used by Vanduffel *et al.* were "bent paper clip" figures undergoing rotation in depth, which produces 2D image transformations that convey 3D shape (*13*) [see their online movie (*5*) or reproduce the phenomenon yourself by twirling a bent paper clip and observing its shadow]. The control stimuli were the same bent paper clip figures translating back and forth across the image plane. The contrast between fMRI responses to 3D rotation and 2D translation was used to identify brain regions sensitive to 3D shape-from-motion.

Vanduffel and colleagues report that several areas are sensitive to 3D shape-from-motion in both species: V2, V3, and MT/V5, all of which are known to process motion and depth information. In the monkey, FST (fundus of the superior temporal sulcus) and V4 also responded preferentially to 3D stimuli. Area FST has no identified homolog in humans. Human V4 has been partially identified: The ventral portion (V4v), representing the upper visual field, has been localized with retinotopic mapping (*11*, *12*). Human V4v does not appear to have been differentially activated in this study. The expected location for dorsal human V4 (V4d) would be posterior to MT/V5, although retinotopic mapping suggests that no V4d homolog exists in this location (*14*). This area (labeled LOS by Vanduffel *et al.*) did respond preferentially to motion-based 3D shape. Previous fMRI studies have shown that this region is also sensitive to motion-defined boundaries (*14–16*).

The most striking interspecies differences were found in the intraparietal sulcus (IPS). There were four distinct foci in human intraparietal cortex. These corresponded to previously identified regions sensitive to motion and shape-from-motion (*17*, *18*). In the monkey, no differential activity was observed in IPS. The homology between human and monkey parietal areas is uncertain, but the complete lack of activity in monkey IPS suggests a strong species difference.

In contrast with these results, a previous study in anesthetized monkeys by Sereno and colleagues (*19*) revealed several foci in the IPS with preferential responses to motion-based (and texture-based) 3D shape. Sereno *et al.* also found activity in middle and anterior STS (superior temporal sulcus), which Vanduffel *et al.* did not. On the other hand, Vanduffel *et al.* found activity in V4, whereas Sereno *et al.* did not. Some of these discrepancies could reflect different significance criteria. There are certainly differences between anesthetized and awake visual responses, but one would expect higher level visual areas in IPS and STS to be less sensitive rather than more sensitive to 3D structure under anesthesia. The most likely cause for the widely discrepant activation patterns is stimulus differences. Sereno *et al.*'s shapes were composed of surfaces (defined by moving dots), which may be more effective stimuli for dorsal pathway areas in IPS and STS (upper bank) as discussed above. Vanduffel *et al.* presented their subjects with bent paper clip stimuli composed of 3D-oriented limbs, which may be more effective for stimulating ventral pathway areas like V4 (*10*).

More surprising are the discrepancies between these two fMRI studies and a number of electrophysiological studies, including those by Tsutsui *et al.* There is now electrophysiological evidence for 3D surface orientation tuning in CIP (*4*, 6, *7*) (based on stereoscopic, texture gradient, and perspective cues) and in MT/V5 (*8*, *9*) (based on stereoscopic and motion parallax cues). There is also evidence for 3D bar orientation tuning in V4 (*10*) (stereoscopic cues) and 3D shape tuning in IT (inferotemporal) cortex (*20*, *21*) (stereoscopic cues). MT/V5 has also been specifically implicated in 3D shape-from-motion processing (*22*). One might predict that all of these areas would be differentially sensitive to 2D versus 3D shapes, but only MT/V5 gave a positive result in both fMRI experiments. The inconsistencies could be due to depth cue differences—the fMRI studies were based on motion, whereas the electrophysiological studies were based on stereoscopic disparity, texture gradients, and perspective. However, one would expect that visual areas processing 3D structure would, like CIP, take advantage of multiple cues (*4*, 6, *7*).

The more general explanation for these discrepancies may be that information processing at the local circuit level does not necessarily correlate with neuronal population activity measured by fMRI. Electrophysiology strongly indicates 3D processing in CIP (*4*, *6*, *7*) and IT cortex (*20*, *21*), but this need not entail enhanced population-level responses to 3D stimuli. If positive and negative response changes at the local level balance out on a larger scale, CIP and IT cortex would exhibit equivalent overall responses to 2D and 3D stimuli, as observed by Vanduffel and co-workers.

Conversely, differential population activity does not necessarily imply any specific kind of information processing—preference for 3D stimuli does not have to signify tuning for 3D structure. A given area may represent non-3D information but still respond best to 3D stimuli, perhaps because they are more complex, coherent, realistic, or object-like. Conclusions about 3D processing depend on careful controls (Vanduffel *et al.* specifically controlled for the effects of 2D rotation and expansion/contraction; Sereno *et al.* controlled for local motion coherence and 2D boundary shape differences) and electrophysiological confirmation at the local circuit level.

All of this highlights the need for an evolving interplay between large-scale imaging studies (like that of Vanduffel *et al.*) and fine-scale analysis of neural mechanisms (like that of Tsutsui *et al.*). Imaging techniques can be used to assess whole-brain activity, and they provide the critical link between monkey and human vision. Electrophysiology addresses circuit-level information processing and remains important for interpreting the population-level differences revealed by fMRI. Every imaging result poses questions for a future electrophysiological experiment, and vice versa. Imaging and electrophysiological experiments with equivalent stimuli and perceptual conditions will be required to fully elucidate how the brain constructs a 3D reality from its 2D sensory inputs.

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