PERSPECTIVES: NEUROSCIENCE

Moving Through the Landscape

David Bradley

The brain, like any other organ, is composed of proteins, lipids, and carbohydrates. It is made of cells, which have membranes, organelles, and nuclei. It has connective tissue and vasculature, and consumes oxygen. And yet the brain possesses an extraordinary property that no other organ has: It thinks. It computes.

Computational neuroscience is a brand of neurobiology that tries to understand how the brain computes. Although mathematical modeling is an important discipline within computational neuroscience, solid experimental work is also essential. Without it—without new information—computational theories tend to spin circles around their own logic. Unfortunately, experimental work is sometimes perceived as being less creative, less intellectual, than theory. On the contrary, experimental design often requires highly creative and logical thought. A good example of this is the study reported by Froehler and Duffy (*1*) on page 2462 of this issue. These authors have devised a difficult experiment to demonstrate that neurons in the visual cortex of the primate brain monitor locomotion through the environment in a variety of ways.

In the early 1950s, Gibson suggested that heading perception—the moment-to-moment sense of where we are going—is based on a mental analysis of image expansion (*2*). Less intuitive than the idea of reckoning with visual landmarks, Gibson's theory proposes that we derive our heading by extracting information about the origin (focus) of the expanding image that falls upon the retina as we move through the environment (see the figure). Decades after Gibson's original suggestion, carefully controlled psychophysical experiments showed that humans do in fact sense their heading by tracking the image focus (*3*). Around the same time, cortical neurons that respond selectively to image expansion were discovered (*4*). These cells, which are clustered in a region of the brain called MST (medial superior temporal), also detect the position of the expansion focus and even correct for the displacement of that focus each time the eyes move. Several years ago, it was shown that monkeys trained to report their direction of heading can be biased toward a certain direction by electrical stimulation of their MST cells (*5*).

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These findings leave little doubt that MST is crucial for heading perception. But, as Froehler and Duffy now show, the behavior of MST neurons appears even more sophisticated than previously thought. The investigators put monkeys on a motorized sled that moved them in a circular trajectory. The monkeys were always facing the front of the room, and the walls were illuminated with small white lights. As the monkeys moved on their circular paths, they had two kinds of information available to them: visual (from the retina) and vestibular (from the vestibular apparatus of the inner ear, which senses acceleration). From these cues, one could potentially compute the instantaneous direction of heading, the instantaneous location in the room, or the path. In these tests, the path was always circular but could be either in the clockwise or counterclockwise direction.

While all of this was happening, microelectrodes recorded electrical discharges, called spikes, from the monkey's MST neurons. The frequency of spikes is a measure of a neuron's activity. The activity of many MST neurons increased when the monkey moved in a certain direction, regardless of its path or location in the room. But in some cases, neuronal activity also depended on the way a given direction was approached—that is, whether the path was clockwise or counterclockwise. Finally, some neurons had quite different activities depending on the monkey's location in the room.

Conceivably, the effects driving neuronal activity could confound one another. For example, as a moving object's location must depend on its direction in the preceding moments, perhaps the apparent effect of location on MST activities was in reality due to the neurons' sensitivity to heading direction. The investigators addressed this potential problem with separate experiments where monkeys sat stationary in different parts of the room. Some cells responded differently, depending on the monkey's location, and this dependence was consistent with location effects during circular motion. Therefore, the relation between neuronal activity and location could not be due to the correlation between location and heading.

The authors also showed that for cells whose activity depended on heading direction, location could not have been a confounding factor. They demonstrated this by holding animals in a single spot while displaying a video simulation of what the monkeys would have seen during a circular movement. In that case, neuronal activity still depended on the (simulated) direction of heading. Therefore, correlations between cell activity and heading direction were not the indirect consequence of location in the room.

Although early evidence suggested that MST neurons encode our direction of heading, the Froehler and Duffy results indicate that MST encodes much more than this. As we move through the environment, we can think of the raw information available to us as a distribution of events over space and time. For example, the variation in location of a stimulus on the retina over time tells us about its motion. From these basic events we can compute other things, such as our direction of heading, our location, and the shape of our path. Different derivations may be useful at different times. For example, if we move in a straight line, our heading is sufficient to tell us where we will soon be. But if we are turning, instantaneous heading alone is not sufficient; in this case our path—the change in our heading as we go along—must be known.

Of course, different events could be computed in different parts of the brain. Notably, the hippocampus is thought to keep track of

Path and place. When we move through the environment, the image falling on our retina expands, although we rarely notice this. The expanding image has a point of origin, or focus, from which all image motion seems to radiate. The focus, marked by the yellow cross on the tree, corresponds to our direction of heading. Neurons in a region of the brain called MST are responsible for encoding information about heading, path, and place, which is combined with visual cortex inputs to provide perception of heading during self-movement.

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our position in the environment. If similar information appears in MST, it is not necessarily redundant; instead it may reflect the need to combine positional information with information about heading or path. In fact, MST neurons may be informed about position through connections with the hippocampus. Conversely, hippocampal cells may compute location by integrating path information, derived from MST, over time. Whatever the case, the involvement of MST in our ability to move about is clearly at a more sophisticated level than previously thought. The work of Froehler and Duffy suggests that our exploration of computational mechanisms in MST is only just beginning.

References

1. M. T. Froehler, C. J. Duffy, *Science* **295**, 2462 (2002).
2. J. J. Gibson, in *Perception of the Visual World* (Houghton-Mifflin, Boston, 1950).
3. W. H. Warren Jr., D. J. Hannon, *Nature* **336**, 162 (1988).
4. H. Saito *et al.*, *J. Neurosci* **6**, 145 (1986).
5. K. H. Britten, R. J. A. van Wezel, *Nature Neurosci.* **1**, 59 (1998).

PERSPECTIVES: MATERIALS SCIENCE

Deformation of Nanostructures

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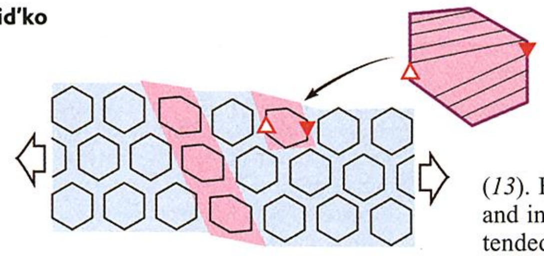
Materials based on nanometer-sized structural elements exhibit unique electronic, optical, magnetic, and mechanical properties, opening up a range of new applications (*1*, *2*). The mechanical behavior of nanocrystalline materials—solids composed of nanometer-scale crystallites divided by interfaces (see the figure)—is of particular interest. Such materials are often extremely hard and brittle, but several examples of substantial ductility under mechanical load have been reported (*3*). Some nanocrystalline metals, ceramics, and alloys even exhibit superplasticity—the ability of a solid to endure large elongations (100% or more) without failure—at relatively low temperatures and high strain rates (*4, 5*).

These remarkable mechanical properties of nanocrystalline materials are highly desirable for structural applications. To optimize the mechanical behavior, it is important to identify its underlying mechanisms. One of these mechanisms has now been revealed in an atomic-level experiment. On page 2433 of this issue, Murayama *et al.* (*6*) provide evidence for a rotational deformation mechanism (see the figure), considered in theoretical models (*7*, *8*), which resembles turbulence in fluids as well as the formation of rotational vortices in liquid crystals, superfluids, and magnetic and biological systems (*9*).

The appearance of rotational phenomena in deformed nanocrystalline materials can be understood in terms of their structural peculiarities. The materials are composed of nanometer-scale crystallites (grains) divided by interfaces (grain boundaries) (see the figure). Each crystallite is intermediate in size between individual atoms and conventional microstructures, leading to distinct properties. In addition, each crystallite is so small that a large fraction of its atoms (up to 50%) are located at interfaces. These combined nanometer-scale and interface effects are responsible for the unique properties of nanocrystalline materials (*1*, *2*) and give rise to their rotational deformation.



Rotational deformation in nanostructures. Nanocrystalline solid, consisting of nanometer-scale grains (hexagons) divided by grain boundaries, under mechanical tension. Rotational deformation occurs via motion of dipoles of disclinations (triangles), causing crystal lattice rotation behind them.

The primary carriers of the rotational plastic deformation in solids are believed to be dipoles of grain boundary disclinations (*7, 8*). A disclination is a line defect characterized by a rotation of the crystalline lattice around its line (*7*). A disclination dipole consists of two disclinations causing crystal lattice rotation between them; such dipoles are energetically permitted only for disclinations that are close to each other.

Motion of a disclination dipole along grain boundaries causes plastic flow accompanied by crystal lattice rotation behind the disclinations (see the figure). The disclination dipole motion has been suggested to be intensive in nanocrystalline materials, where the volume fraction of grain boundaries is high and disclinations are close to each other (*8*). Murayama *et al.*'s atomic-level observation of disclination dipoles in deformed nanocrystalline materials (*6*) provides experimental support for this suggestion.

In addition to the rotational deformation, other deformation mechanisms can occur effectively in nanocrystalline materials that usually do not play an important role in conventional materials. Examples are grain boundary sliding and stress-induced mass transfer, which occurs via enhanced diffusion along grain boundaries (*10–12*). These mechanisms are conducted by grain boundaries and compete effectively with conventional dislocation slip (shear) in crystallites, the mechanism that dominates in conventional materials.

Unusual deformation mechanisms also occur in strained semiconductor nanocrystallites, called quantum dots, whose deformation behavior is essential for their functional stability as laser elements (*13*). For instance, as a result of nanoscale and interface effects, nonconventional, extended dislocations cause effective strain relaxation in such nanocrystallites (*14*).

Different deformation mechanisms, most of which only occur in nanostructured matter, thus compete in mechanically loaded nanocrystalline materials. This competition causes the unique deformation behavior of nanocrystalline materials. Further research focusing on the fundamental laws that govern the competition is crucial for progress in fabrication, design, and processing of nanocrystalline materials with enhanced mechanical characteristics. Some of the remaining experimental and theoretical challenges include identifying (new) deformation mechanisms, elucidating the influence of plastic deformation on structural transformations (including structural stability against grain growth), and understanding the role of distinct structural elements of grain boundaries in deformation processes in nanocrystalline materials.

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References and Notes

1. M. C. Roco, R. S. Williams, P. Alivisatos, Eds., *Nanotechnology Research Directions* (Kluwer, Dordrecht, Netherlands, 2000).
2. G.-M. Chow, I. A. Ovid'ko, T. Tsakalakos, Eds., *Nanostructured Films and Coatings* (Kluwer, Dordrecht, Netherlands, 2000).
3. C. C. Koch *et al.*, *MRS Bull.* **24**, 54 (1999).
4. M. J. Mayo, *Nanostruct. Mater.* **9**, 717 (1997).
5. S. X. McFadden *et al.*, *Nature* **398**, 684 (1999).
6. M. Murayama *et al.*, *Science* **295**, 2433 (2002).
7. P. Klimanek *et al.*, *Adv. Eng. Mater.* **3**, 877 (2001).
8. M. Yu. Gutkin *et al.*, *J. Metast. Nanocryst. Mater.* **12**, 47 (2002).
9. M. Kléman, *Points, Lines and Walls* (Wiley, New York, 1983).
10. R. A. Masumura, P. M. Hazzledine, C. S. Pande, *Acta Mater.* **46**, 4527 (1998)
11. M. Yu. Gutkin, I. A. Ovid'ko, C. S. Pande, *Rev. Adv. Mater. Sci.* **2**, 80 (2001).
12. H. S. Kim, Y. Estrin, M. B. Bush, *Acta Mater.* **48**, 493 (2000).
13. P. Mulvaney, *MRS Bull.* **26**, 1009 (2001).
14. I. A. Ovid'ko, *Phys. Rev. Lett.* **88**, 046103 (2002).

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