Progress in Understanding Spatial Coordinate Systems in the Primate Brain

A new study in this issue of Neuron shows that when monkeys reach to a visual target, neurons in the dorsal premotor cortex compare the location of the target, the hand, and the point of visual fixation. The neurons therefore encode space through a combination of eye-centered and hand-centered coordinates.

We act on the world by reaching, grasping, manipulating, looking, avoiding, and performing hundreds of other actions on the objects around us. These behaviors depend on computing the relative spatial locations of objects and body parts. How does the brain coordinate spatially accurate behavior? The dorsal premotor cortex (PMD) of the monkey brain, and more specifically the caudal division of PMd (PMDc; see Figure 1), is densely connected to a network of motor structures, including the spinal cord, and is involved in the control of reaching. In a new study, Pesaran et al. (2006) show in this issue of Neuron that PMDc may guide the arm by means of a simultaneous comparison of hand location, eye location, and target location. Here I outline some of the previous experimental steps in understanding the representation of space in parietal and frontal cortical areas and discuss how the present finding significantly extends this line of research.

Retinal Receptive Fields Modulated by Extraretinal Factors

One of the first accounts of how neurons represent space was proposed by Andersen et al. (1985). They described visually responsive neurons in area 7a of the posterior parietal lobe of monkeys. Like classical visual neurons at most stages of the visual system, each neuron in area 7a had a visual receptive field on the retina. The magnitude of the response of a 7a neuron, however, was modulated by the angle of the eyes in the orbit. When the eyes were angled one direction, the neuron might become relatively unresponsive. When the eyes were angled another direction, the neuron might become highly responsive to visual stimuli. The two pieces of information that influenced the neurons, the location of the stimulus on the retina and the location of the eyes in the orbit, could in principle provide the location of an object with respect to the head.

Further work by Andersen and colleagues (Brotchie et al., 1995; Snyder et al., 1998) revealed that not only the angle of the eyes in the orbit, but also the angle of the head on the trunk, and vestibular information about the position of the head in the world, also modulated the responsiveness of the “gain” of neurons in posterior parietal areas. From this work, a general model of spatial coding emerged. In this model, neurons have receptive fields on the retina, explicitly encoding space in eye-centered coordinates. The response gain of the neurons, however, is modulated by additional spatial factors. As a result, the pattern of activity across a population of neurons carries information about the location of a visual stimulus with respect to the eye, the head, the trunk, and the external world.
neurons here have a tactile receptive field on the arm and a visual receptive field on the body surface (Graziano and Gross, 1998).

In the experiment by Pesaran et al. (2006), monkeys reached to a set of targets while the starting hand and eye positions were varied. Each neuron responded when the monkey prepared to reach into a restricted region of space, the neuron’s reach field. The primary finding was that the reach fields were not anchored to the eye, nor were they anchored to the hand. Indeed, these reach fields were not strictly anchored to one reference point. Rather, the firing rate of the neurons was a function of the spatial relationship between the target and the eye, the target and the hand, and the eye and the hand.

This elegant study shows that there is no simple answer to the coordinate frame question. PMDc neurons
do not appear to encode reach targets in a hand-centered coordinate frame or in an eye-centered one. A different conception may be necessary, in which there is no single spatial coordinate system. Rather, a diverse set of spatial information that is normally used during the act of reaching is multiplexed in the response profile of these neurons. To the extent that hand-centered spatial information is required, it is present. But eye-centered information is also present, perhaps because reaching normally involves a close interaction between the hand and the eye.

Different Spatial Representations Optimized for Different Types of Actions?
Reaching to a target is only one type of spatially guided action. Monkeys and humans perform other actions, such as manipulating objects that are already grasped, bringing objects to the mouth, or avoiding contact with potentially dangerous objects. Each of these actions has its own idiosyncratic properties and requires its own mixture of spatial information. For example, consider the problem of avoiding an object, such as a bee, flying toward the body surface. The spatial relationship between the bee and the projected point of contact on the body is of paramount importance. In this case, hand-centered coordinates and eye-centered coordinates may be less important than side-of-the-neck-centered coordinates, if that is where the bee is headed. The standard defensive reaction might involve a rapid lifting of the shoulder, ducking of the head, and withdrawal of the body. The sensorimotor problem here is quite different from the problem of reaching the hand to a target.

As described above, neurons in a polysensory zone in the ventral premotor cortex have tactile receptive fields typically on the upper body and visual receptive fields apparently anchored to the body surface at the site of the tactile receptive field. Our initial hypothesis regarding these neurons was that they might contribute to the general sensory guidance of movement (Graziano and Gross, 1998). However, when we electrically stimulated these polysensory sites in cortex, we consistently evoked apparent defensive movements including ducking, withdrawing, lifting the shoulders, and lifting the arm as if to block a threat (Graziano and Cooke, 2006). Even under anesthesia, we evoked movements that appeared to defend the site of the tactile receptive field on the body. In contrast, stimulation in PMd tended to evoke an opening of the hand and a projecting movement of the arm consistent with reaching.

The stimulation evidence suggests that different subregions of motor cortex may partially specialize in different categories of action. These subregions of cortex, therefore, may encode the space around the body in different ways, optimized for different types of action.

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Selected Reading

Cognitive Control Signals in Visual Cortex: Flashes Meet Spotlights

At the intersection of two intensely belabored fields, primary visual cortex (V1) function and neural mechanisms of cognitive control, Jack et al. (in this issue of Neuron) report a neural signal that is neither related to stimulus representation nor spatial attention. Instead, this endogenous signal correlates with task structure and raises new questions.

Across several species, primary visual cortex (V1) is arguably the most heavily studied and best understood brain area. The investigation of its functional response properties was heralded by the seminal work of Hubel and Wiesel who were first in eliciting reliable and selective responses of single neurons to sensory stimuli. These stimulus-related response properties included retinotopic receptive fields and orientation selectivity and have appeared in every neuroscience textbook. Along these lines, V1 is still often thought of as a camera-like device that provides a somewhat distorted and fractured but fairly veridical representation of the retinal image. Yet its neurons seem to be involved in functions going beyond mere image representation.

This insight comes as no surprise if one considers the anatomical connectivity of V1 and realizes that retino-geniculo-cortical afferents provide only a fraction of its input (Casagrande and Kaas, 1994). Despite these anatomical clues, it has proven more difficult to evoke V1 responses by mechanisms other than sensory stimulation, as for instance by visual imagery or spatial attention, cognitive processes that are associated with strong activity changes elsewhere in the brain. Following initial sparse electrophysiological reports of attentional V1 activity modulation, significant progress came from functional magnetic resonance imaging (fMRI) studies that mapped activations during covert spatial attention to corresponding retinotopic representations of the attended visual field locations (reviewed in Posner and Gilbert, 1999).