1 FROM VISION TO ACTION: HOW THE PRIMATE BRAIN ENCODES AND REMEMBERS VISUOMOTOR SPACE

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INTRODUCTION

In 1870, Fritsch and Hitzig first studied primary motor cortex in the monkey brain using electrical stimulation and, in 1881, Hermann Munk used lesion methods to localize the primary visual cortex in the occipital lobe (cited in Gross, 1998). Only now, more than 100 hundred years later, has neuroscience begun to identify the neuronal pathways that connect these two areas. We are finally beginning to understand the routes through which vision is transformed into action.

Some of the hypothesized visuomotor pathways through the monkey cortex are shown in Figure 1.1 (Desimone and Ungerleider, 1989; Felleman and Van Essen, 1991; Goodale *et al.*, 1994; Wise *et al.*, 1997; Graziano and Gross, 1998b). Information from the eye passes through the lateral geniculate nucleus to primary visual cortex, is processed further by extrastriate visual areas, and reaches the posterior parietal cortex (shown in black in Figure 1.1B). The various posterior parietal areas are thought to encode the movement and spatial locations of objects. This set of parietal areas projects to a variety of frontal lobe areas, such as the frontal and supplementary eye fields, involved in oculomotor control, and the premotor and supplementary motor areas, involved in movements of the head and limbs. These areas, in turn, modulate the activity of motor structures such as primary motor cortex, the spinal cord and eye movement generators in the midbrain and brainstem.

The line between sensory and motor traditionally lies at the central sulcus. A major advance of the past few years, however, is the realization that the planning of movement begins in specialized subregions of the parietal lobe itself (Snyder *et al.*, 1997), and that the processing of sensory space around the body continues into premotor cortex (Fogassi *et al.*, 1996; Graziano and Gross, 1998b). Indeed, there is accumulating evidence that premotor cortex may participate in a variety of complex sensory and cognitive functions that had never before been ascribed to it, such as visual attention (Graziano and Gross, 1998a) and memory of the locations of objects (Graziano *et al.*, 1997b). Recent evidence suggests that understanding the actions of other individuals may involve using the premotor cortex to process how those actions are coordinated (Gallese and Goldman, 1998).

In this chapter, we concentrate on the visuospatial properties of premotor cortex. In the following section, we describe how single neurons in the ventral part of premotor cortex of the monkey encode the visual, tactile, auditory and even mnemonic space near the body. These neurons represent the locations of nearby objects with respect to individual body parts, in 'body-part-centered' coordinates. This spatial representation is well suited to guide movements of the head and arms toward, away from or around nearby objects. We then consider psychophysical evidence to suggest that a similar, body-part-centered encoding of space is used for the control of movement in humans. In the final section, we briefly review the growing literature on the functional imaging of premotor cortex in the human brain.

REPRESENTATION OF SPACE IN VENTRAL PREMOTOR CORTEX

The ventral premotor cortex, or area PMv, is located in the frontal lobes just posterior to the arcuate sulcus and anterior to primary motor cortex (Figure 1.1). Sensory information can reach PMv through projections from the parietal lobe (Jones and Powell, 1970; Mesulam *et al.*, 1977; Kunzle, 1978; Matelli *et al.*, 1986; Cavada and Goldman-Rakic, 1989), and PMv

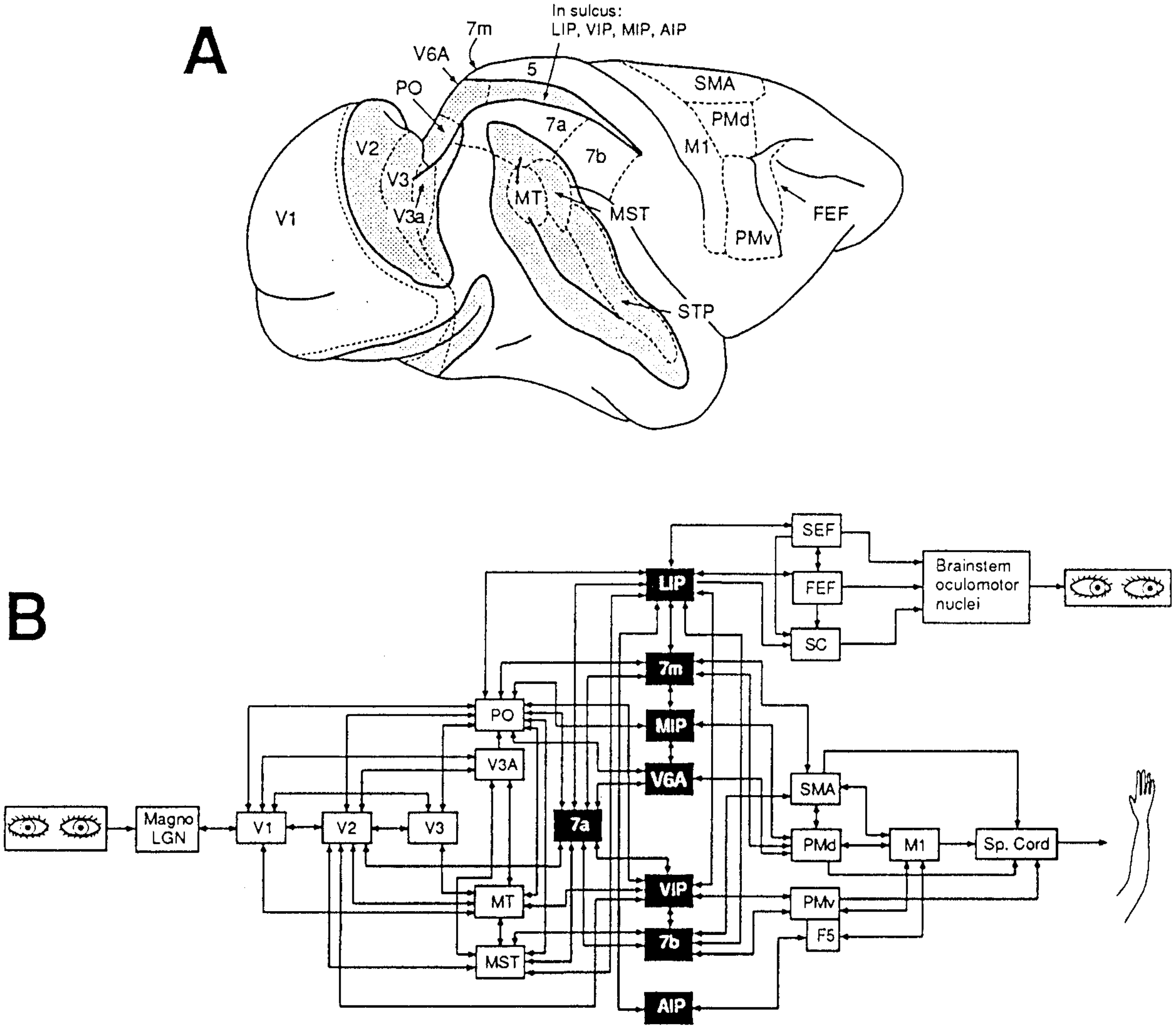

Figure 1.1. Visuomotor pathways of the monkey brain. Top: lateral view of macaque cerebral cortex showing some of the cortical areas involved in the representation of visual space and visuomotor coordination. Major posterior sulci have been 'opened up' to show the buried cortex in grey. Bottom: some of the neuronal pathways by which visual information entering the eye might guide movement of the eyes and limbs. Areas shown in black are in the posterior parietal lobe. SEF, supplementary eye fields; FEF, frontal eye fields; SC, superior colliculus; SMA, supplementary motor area; PMv, ventral premotor cortex; MDP, medial dorsal parietal area; LIP, lateral intraparietal area; VIP, ventral intraparietal area; MIP, medial intraparietal area; AIP, anterior intraparietal area. Adapted from Graziano and Gross (1998b).

can influence movement through its projections to primary motor cortex and the spinal cord (Matsumura and Kubota, 1979; Muakkassa and Strick, 1979; Godschalk *et al.*, 1984; Leichnetz, 1986; Matelli *et al.*, 1986; Barbas and Pandya, 1987; Dum and Strick, 1991; He *et al.*, 1993). Most neurons in PMv respond to tactile stimuli, and about 40% also respond to visual stimuli (Rizzolatti *et al.*, 1981; Graziano *et al.*, 1994, 1997a; Fogassi *et al.*, 1996). These bimodal, visual–tactile neurons are especially numerous in the posterior half of PMv, termed F4; while area F5, the anterior portion of PMv that extends into the posterior bank of the arcuate sulcus, is more involved in the musculature of the fingers and the control of grasp (Gentilucci *et al.*, 1988). Recent evidence (Fogassi *et al.*, 1999) suggests that the cortical region in which bimodal, visual–tactile neurons are found may extend upward from F4 into dorsal premotor cortex (PMd; see Figure 1.1). Here we confine the discussion to the bimodal neurons found in the posterior part of PMv, because they have been studied most extensively; however, similar properties may well exist in PMd.

For the bimodal cells in PMv, the tactile receptive field is located on the face, shoulder, arm or upper torso, and the visual receptive field extends from the approximate region of the tactile receptive field into the immediately adjacent space. PMv is organized somatotopically: from dorsal to ventral, the map progresses from the arm to the face to the inside of the mouth (Graziano *et al.*, 1997a). Visual responses are not found in the mouth representation. Figure 1.2 shows the tactile receptive fields (shaded) and the associated visual receptive fields for two typical bimodal neurons related to the face (Figure 1.1A) and arm (Figure 1.1B). About 20% of the bimodal neurons continue to respond to objects in the visual receptive field even after the lights are turned out and the object is no longer visible (Graziano *et al.*, 1997b). Such neurons apparently 'remember' the locations of nearby objects. Neurons with a tactile response on the side and back of the head often respond to auditory stimuli near the head (Graziano *et al.*, 1999). Regardless of the intensity of the sound, if the source is more than about 0.5 m from the head, these neurons do not respond. The multimodal neurons in PMv, therefore, represent the space immediately surrounding the body through touch, audition, vision and memory.

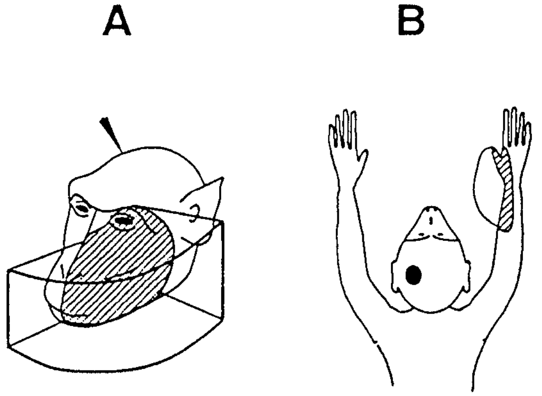

Figure 1.2. Receptive fields of two bimodal, visual–tactile neurons in PMv. (A) The tactile receptive field (shaded) is on the snout, mostly contralateral to the recording electrode (indicated by the arrowhead) but extending partially onto the ipsilateral side of the face. The visual receptive field (boxed) is contralateral and confined to a region of space within ~10 cm of the tactile receptive field. (B) The tactile receptive field for this neuron is on the hand and forearm contralateral to the recording electrode (indicated by the black dot), and the visual receptive field (outlined) surrounds the tactile receptive field. Adapted from Graziano and Gross (1998b).

For almost all bimodal cells with a tactile receptive field on the arm, when the arm is placed in different positions, the visual receptive field moves with the arm (Graziano *et al.*, 1994, 1997a). In contrast, when the eyes move, the visual receptive field does not move, but remains anchored to the arm (Gentilucci *et al.*, 1983; Fogassi *et al.*, 1992, 1996; Graziano *et al.*, 1994, 1997a; Graziano and Gross, 1998a). Thus these cells encode the locations of nearby visual stimuli with respect to the arm, i.e. in 'arm-centered' coordinates. Such information can be used to guide the arm toward or away from nearby objects. Some bimodal neurons have tactile receptive fields restricted to the forearm or upper arm. The adjacent visual receptive fields would be useful for guiding those portions of the arm, such as for avoiding or nudging an object or reaching around an obstacle. Other neurons have tactile receptive fields on the hand, and the associated visual receptive fields would be useful for reaching toward nearby objects. A high percentage of arm-related bimodal neurons in PMv are active during movements of the arm, and electrical stimulation of these neurons causes arm movements (Gentilucci *et al.*, 1988).

Other evidence from the monkey supports the hypothesis that reaching with the arm may be controlled in an arm-centered coordinate system. Caminiti *et al.* (1990) recorded from an area on the border of PMv, PMd and primary motor cortex, and found that each neuron responded best as the monkey reached in a particular direction, i.e. the neuron had a motor field. When the arm was moved to a different position, the motor field also moved, rotating roughly with the arm. On average, across the population of neurons, the motor fields were arm centered, moving by the same amount that the shoulder joint rotated, just as the visual receptive fields in our experiments were arm centered.

As described above, premotor cortex also contains a tactile representation of the face and a visual representation of the space near the face. For most bimodal cells with a tactile receptive field on the face, when the head is rotated, the visual receptive field moves with the head (Graziano *et al.*, 1997a). When the eyes move, the visual receptive fields do not move, but remain anchored to the head (Gentilucci *et al.*, 1983;

Fogassi *et al.*, 1992, 1996; Graziano *et al.*, 1994, 1997a; Graziano and Gross, 1998a). These visual receptive fields, therefore, encode the locations of nearby stimuli relative to the head, in 'head-centered' coordinates, and would be useful for guiding the head toward or away from nearby stimuli, such as for biting, kissing, or flinching. More than half of these head-related bimodal neurons respond during specific voluntary movements of the head (Graziano *et al.*, 1997a).

In summary, neurons in PMv represent the spatial locations of objects within about reaching distance of the body. Any object that enters that critical region of space will activate PMv, whether the monkey senses the object through touch, vision or audition, or even if the monkey is in the dark and 'remembers' that the object is present. The representation of space in PMv is not static, unitary or Euclidian, however. Instead, it is composed of sensory receptive fields anchored to different parts of the body, moving as those body parts move, i.e. in body-part-centered coordinates. We have suggested that such body-part-centered coordinates provide a general mechanism for sensory–motor integration (Graziano *et al.*, 1994, 1997a).

OTHER BODY-PART-CENTERED COORDINATES

Visual receptive fields that do not move with the eye have been reported in a number of different brain areas and species. Such cells have been found by Schlag *et al.* (1980) in the thalamus of the cat, by Pigarev and Rodionova (1988) in parietal cortex of the cat, by Galletti *et al.* (1993) in parietal area V6A of the monkey, and by Duhamel *et al.* (1997) in the ventral intraparietal area of the monkey. Although these visual receptive fields did not move with the eye, it was not clear what part of the body or world they did move with. Therefore, the spatial coordinate systems in these brain areas remain unknown. Wiersma (1966) found visual receptive fields in the crayfish that were influenced by the otolith organs. When the animal's whole body was rotated, the visual receptive fields remained constant with respect to the gravitational vertical. Visual fields influenced by the tilt of the body were also reported in striate cortex of the cat by Gabriel Horn, to whom this book is dedicated (Horn and Hill, 1969).

The frontal eye fields, lateral intraparietal area and the intermediate and deep layers of the superior colliculus all guide saccadic eye movements by means of visual and auditory receptive fields that are fixed to the retina (Bruce, 1990; Sparks, 1991; Duhamel *et al.*, 1992; Stricanne *et al.*, 1996). There is evidence that even the tactile receptive fields in the superior colliculus may be anchored to the eye (Groh and Sparks, 1996), i.e. the neurons in these areas encode the location of the target with respect to the fovea, in retinocentric coordinates, even if the target is not a visual one. Such information would be useful for guiding the fovea toward the target. These areas therefore use a type of body-part-centered coordinate system, the body part in this case being the eye ball. The advantage of body-part-centered coordinates is that sensory information about the location of the target can serve as a motor error signal guiding movement toward or away from the target.

EVIDENCE OF BODY-PART-CENTERED COORDINATES IN HUMANS

Is there any evidence that humans use body-part-centered coordinate systems to guide movement? Most studies of visuomotor integration in humans have concentrated on arm movements, specifically reaching toward visual targets. As we discuss below, a number of these studies suggest that the location of the target and the path of the hand movement are encoded in hand-, arm- or shoulder-centered coordinates. Thus humans do appear to use body-part-centered coordinates to guide reaching. We would suggest that these psychophysical results reflect the presence of body-part-centered visual receptive fields in premotor cortex.

Prablanc *et al.* (1986) showed that reaching toward a small visual target is more accurate when the target is visible throughout the reach than when the target is visible only briefly at the beginning of the reach. This result indicates that the reach is not pre-programmed, but depends on the continuous adjustment of the position of the hand relative to the target, i.e. the spatial information most relevant during reaching is body part centered: the relative location of target and hand.

Soechting and Flanders (1989) asked subjects to point to remembered targets, and analyzed the pattern of errors. They found that the errors were most systematic when plotted in a coordinate system whose origin was located roughly at the shoulder. This origin was somewhat variable between tests, ranging in location from the eye to the upper arm. Our hypothesis of body-part-centered coordinate systems, however, predicts that reaching with the hand should be guided by a coordinate system whose origin is fixed to the hand, not to the shoulder. It is important to note that visual information first enters the brain in retinal, or eye-centered, coordinates, and is presumably transformed through many intermediate stages before arriving at hand- or arm-centered coordinates in premotor cortex (Graziano and Gross, 1998b). Therefore, any errors in reaching toward a target may reflect an accumulation across many different coordinate frames. The exact parameters of the reaching task may bias which processing stage and, therefore, which coordinate system contributes most to the systematic errors. Indeed, Gordon *et al.* (1994), using a similar procedure involving reaching toward remembered targets, found different results from those of Soechting and Flanders and concluded that the errors were most systematic in a hand-centered coordinate frame. More recently, McIntyre *et al.* (1998) found that the pattern of errors during reaching supported both an eye-centered and an arm-centered reference frame. Thus, these studies, in which small errors in pointing are analyzed to determine the coordinate system involved in reaching, may well be measuring a summation of many different coordinate systems that lead up to the hand- or arm-centered coordinate systems found in premotor cortex. Taken together, they suggest that visually guided reaching makes use of arm-centered coordinates at some point in the processing sequence.

Tipper *et al.* (1992) found evidence that attention to visual stimuli during a reaching task may be arm centered. In their study, subjects reached for a target while avoiding a distracting stimulus. The reaction times were longer when the distractor lay roughly between the hand and the target. The critical region of visual space, in which the distractor had maximum effect, was anchored to the hand and moved if the hand was placed in different starting locations. This result could be explained by arm-centered visual-receptive fields such as those found in monkey premotor cortex.

The psychophysical studies discussed above all emphasize the control of reaching. The study by Tipper *et al.* (1992) investigates visual attention, but again in the context of visually guided reaching. There is evidence that motor planning, such as planning a reach or a saccadic eye movement to a particular location in space, may feed back on other parts of the brain and influence attention to that location in space (Rizzolatti *et al.*, 1987; Knowler *et al.*, 1994). In this view, covert motor planning is one of the many ways in which spatial attention is shifted from one location to another. If arm movements are planned in arm-centered coordinates, then it may be possible to demonstrate arm-centered spatial attention even when the subject is not explicitly performing a reaching task.

There are two studies that may show this effect of arm position on visual attention. Driver and Spence (1998) found that a touch on the hand enhanced processing of visual stimuli in the space near the hand. When the hand was placed in different locations, the enhanced region of visual space also moved, remaining anchored to the hand.

In another experiment on the relationship between arm position and visual attention, di Pellegrino *et al.* (1997) studied unilateral spatial deficits in stroke patients. In this type of patient, if a single stimulus is presented on the contralesional side, the subject can detect and report the stimulus. If two stimuli are presented simultaneously, one to each side, the patient ignores the contralesional stimulus and reports only the ipsilesional one. This phenomenon is called extinction, and is thought to be caused by an imbalance in attention in which the ipsilesional stimulus out-competes the contralesional one (see Duncan, Chapter 4). In the study by di Pellegrino *et al.* (1997), subjects were asked to detect a tactile stimulus applied to the contralesional hand. When a visual stimulus was presented near the ipsilesional hand, the subjects no longer reported the tactile stimulus, i.e. the tactile stimulus had been extinguished by the competing visual stimulus. The critical region of visual space, in which the competing stimulus was most effective, surrounded the ipsilesional hand and moved if the hand was moved.

In summary, there is accumulating evidence that the human brain uses arm-centered coordinates, both for visually guided reaching and for spatial attention in general. Other coordinate systems and other methods of spatial processing must also be used by the human brain. It is our hypothesis that arm-centered coordinates are especially relevant to the final stages of planning an arm movement under visual guidance, and that head, leg or other body-part-centered coordinate systems would be found if visually guided movements of those body parts were studied.

FUNCTIONAL IMAGING OF PREMOTOR CORTEX IN THE HUMAN BRAIN

Humans presumably have a homolog to the monkey PMv, but the exact location of the area in the human brain is not certain. Frontal lobe lesions produce spatial and visuomotor neglect, but the lesions are relatively large and sometimes include the parietal lobe (Husain and Kennard, 1996). The best evidence for the location of PMv in humans comes from functional imaging studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI; see also Dolan, Chapter 17). As described below, many studies that involve visuomotor guidance or visuospatial judgement about objects in relation to the body activate a ventral region in human premotor cortex (Brodmann's area 6). This region is in roughly the same anatomical location as the arm representation of monkey PMv.

In one such experiment using fMRI, Vallar *et al.* (1999) studied the encoding of body-centered space. Subjects viewed a stimulus that oscillated from side to side on a screen. The subjects pressed a button each time they judged the stimulus to be aligned with their own body midline. As a control task, the subjects pressed the button each time the stimulus changed direction at the edge of its trajectory. In comparison with the control task, the spatial judgement task activated regions of the parietal lobe and also a ventral part of premotor cortex. This result matches the single neuron findings in monkeys, in that ventral premotor cortex was active during the representation of space relative to the body.

A number of imaging studies have investigated spatially guided goal-directed movement. In one study using PET (Winstein *et al.*, 1997), subjects moved a stylus rapidly between two visual targets, tapping one and then the other. This study found activation in a range of motor and premotor areas, including the PMv. Several other studies have found activation in a similar ventral part of premotor cortex during observation of objects and motor imagery of grasping and manipulating those objects (Decety *et al.*, 1994; Stephan *et al.*, 1995). Observation of tools, silent naming of tools and silent naming of a tool's use all activated PMv (Martin *et al.*, 1995, 1996; Grafton *et al.*, 1997; Grabowski *et al.*, 1998). Perhaps the subjects imagined grasping the tool as they named it.

Many studies of motor and visuomotor function do not show activation in PMv. For example, studies investigating the preparation or execution of complex finger movement sequences (Rao *et al.*, 1993; Jenkins *et al.*, 1994), motor sequence learning (Grafton *et al.*, 1995; Deiber *et al.*, 1997; Hazeltine *et al.*, 1997; Honda *et al.*, 1998), pointing (Kawashima *et al.*, 1994; Inoue *et al.*, 1998), reaching (Grafton *et al.*, 1996) and several other motor tasks (Deiber *et al.*, 1991; Van Oostende *et al.*, 1997; Grafton *et al.*, 1998; Iacoboni *et al.*, 1998) found activity in more dorsal portions of human premotor cortex and the supplementary motor area but little activity in PMv. One possible reason why these tasks did not activate PMv, although many of them were visually cued, few were visually guided. The visual targets were often stationary or the motor actions simple enough and repeated often enough that they did not require constant sensory guidance.

In summary, a ventral region of premotor cortex in the human brain is active in at least some tasks that require spatial and visuomotor processing, suggesting that it may have similar functions to monkey PMv.

CONCLUSIONS

To represent the space around our bodies, and to move within that space, we must put together vision, touch, audition and proprioception, and integrate them with the control of movement. Studies in monkeys and humans are beginning to clarify where and how these signals are combined in the brain. Multisensory and motor signals converge in the posterior parietal lobe. The processing of space and movement continues in premotor areas in the frontal lobe. In particular, area PMv appears to represent the space immediately surrounding the face, arms and upper torso in body-part-centered coordinates. These body-part-centered coordinates can provide a general mechanism for guiding movements of the limbs and head toward, away from or around the everyday objects that surround us.

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