

Spatial maps for the control of movement

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Neurons in the ventral premotor cortex of the monkey encode the locations of visual, tactile, auditory and remembered stimuli. Some of these neurons encode the locations of stimuli with respect to the arm, and may be useful for guiding movements of the arm. Others encode the locations of stimuli with respect to the head, and may be useful for guiding movements of the head. We suggest that a general principle of sensory-motor integration is that the space surrounding the body is represented in body-part-centered coordinates. That is, there are multiple coordinate systems used to guide movement, each one attached to a different part of the body. This and other recent evidence from both monkeys and humans suggest that the formation of spatial maps in the brain and the guidance of limb and body movements do not proceed in separate stages but are closely integrated in both the parietal and frontal lobes.

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Current Opinion in Neurobiology 1998, 8:195–201

<http://biomednet.com/elecref/0959438800800195>

© Current Biology Ltd ISSN 0959-4388

Abbreviations

AIP	anterior intraparietal area
LIP	lateral intraparietal area
MIP	medial intraparietal area
PMd	dorsal premotor area
PMv	ventral premotor area
VIP	ventral intraparietal area

Introduction

A scholar sits at her desk and reaches for a pen. Later, she turns in her chair, avoids upsetting the tea mug with her elbow, and pulls a book from a nearby shelf. She scratches her forearm by rubbing it carefully against the edge of the desk. At lunch, she holds her sandwich and reaches with her mouth toward a dangling piece of bologna. Most studies of visuomotor coordination have concentrated on how the hand is guided toward a visual target; the brain, however, solves a more general problem, involving guidance of the hand, elbow, shoulder, head and torso during reaching, biting, hitting, nudging and avoiding. Neurons in the ventral premotor cortex (PMv) have properties that may account for this versatility of action.

In this review, we summarize recent evidence on the properties of PMv neurons in the monkey brain and how they might help guide movement. We then describe how visual information can reach PMv along a sequence

of cortical areas, including portions of the superior and inferior parietal lobe. Finally, we describe evidence from brain-damaged and normal subjects showing that similar mechanisms exist in humans.

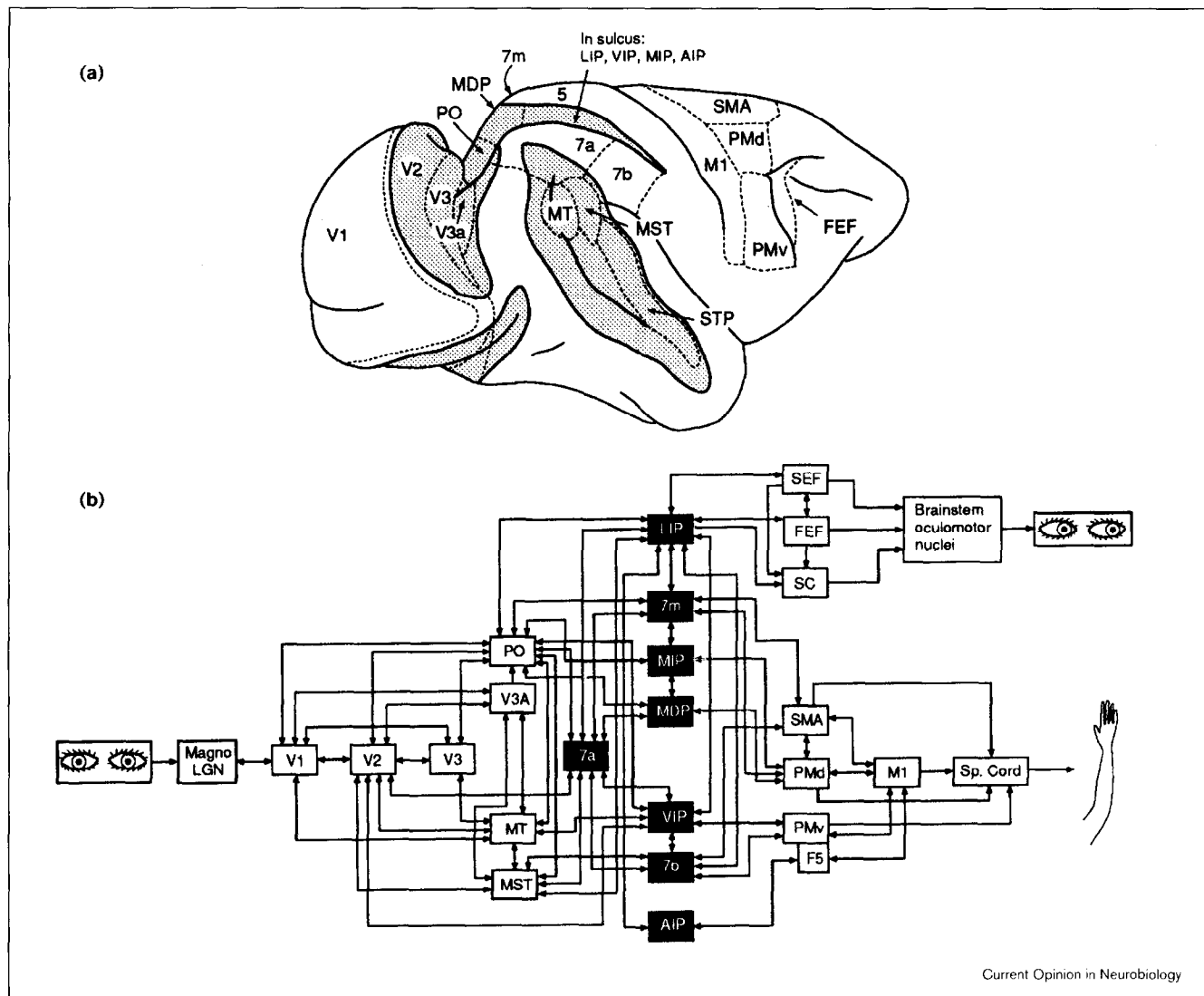
Body-part-centered coordinates in ventral premotor cortex

The ventral premotor cortex, or area PMv, is located in the frontal lobes just posterior to the arcuate sulcus and anterior to the primary motor cortex (Figure 1). Area PMv approximately matches area F4 of Rizzolatti and colleagues [1]. Sensory information can reach PMv through projections from the parietal lobe [2–6], and PMv can influence movement through its projections to primary motor cortex and the spinal cord [5,7–13]. Most neurons in PMv respond to tactile stimuli, and about 40% also respond to visual stimuli [14*,15,16*,17]. For these bimodal cells, 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.

Figure 2 shows the tactile receptive fields (striped) and the associated visual receptive fields for two typical bimodal neurons related to the face (Figure 2a) and arm (Figure 2b). 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 [18*]. 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 ([18*]; MSA Graziano, LA Jin, CG Gross, *Soc Neurosci Abstr* 1997, 23:2066). If the source is more than about half a meter from the head, these neurons do not respond, regardless of the intensity of the sound. This wide range of multimodal neurons in PMv represents the space immediately surrounding the body through touch, audition, vision and memory.

For almost all bimodal cells with a tactile receptive field on the arm, the visual receptive field moves with the arm when the arm is placed in different positions [15,16*]. In contrast, when the eyes move, the visual receptive field does not move, but remains anchored to the arm [14*,15,16*,19*,20,21]. Thus, these cells encode the locations of nearby visual stimuli with respect to the arm, that is, 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, and the adjacent visual receptive fields would be useful for guiding those portions of the arm, such as for nudging an object or reaching around an obstacle. A high percentage of arm-related bimodal neurons in PMv are active during

Figure 1



Visuomotor pathways of the monkey brain. **(a)** 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 (shaded in gray). **(b)** 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. FEF, frontal eye field; LGN, lateral geniculate nucleus; MDP, medial dorsal parietal area; MST, medial superior temporal area; MT, middle temporal area; SC, superior colliculus; SEF, supplementary eye field; SMA, supplementary motor area; Sp. cord, spinal cord; STP, superior temporal polysensory area; V, visual area.

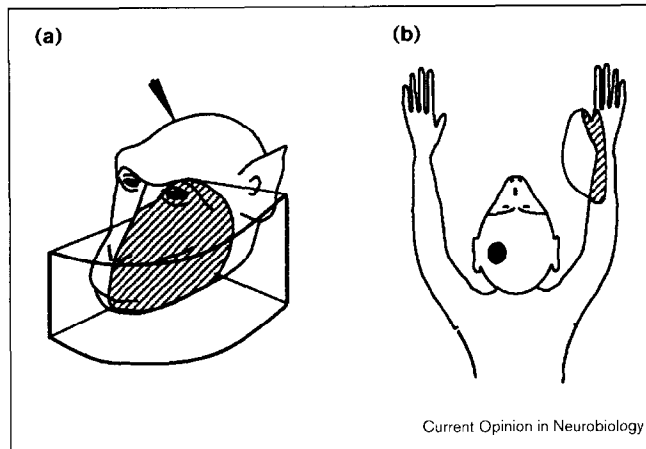
movements of the arm, and electrical stimulation of these neurons causes arm movements [1].

Similarly, 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 [16•]. When the eyes move, the visual receptive fields do not move, but remain anchored to the head [14•,15,16•,19•,20,21]. 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 [16•].

We have suggested that sensory receptive fields anchored to different parts of the body, that is, in body-part-centered coordinates, provide a general mechanism for sensory-motor integration [15,22•]. Not only movements of the arm and head, but also movements of the eye appear to be organized in body-part-centered coordinates. In areas of the brain that control eye movements, the visual, auditory and even tactile receptive fields move when the eye moves, representing the locations of saccade targets in eye-centered coordinates [23,24,25•,26,27•,28•,29,30•].

Figure 2



Receptive fields of two bimodal, visual-tactile neurons in PMv. **(a)** The tactile receptive field (striped) is on the snout, mostly contralateral to the recording electrode (indicated by the arrowhead) but extends partially onto the ipsilateral side of the face. The visual receptive field (boxed) is contralateral and confined to a region of space within about 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.

We predict that movements of any body part are guided by receptive fields anchored to that body part. The advantage of body-part-centered coordinates is that sensory information about the location of the target can serve as a motor signal, guiding movement of the body part toward or away from the target.

How are body-part-centered coordinates computed by neurons? Specifically, how does the brain construct a visual receptive field that is anchored to the body surface instead of to the retina? Such neurons require both visual information about the position of the stimulus on the retina and proprioceptive information about the position of the body parts. In the next section, we discuss the inputs to premotor cortex and the computational steps by which body-part-centered coordinates might be formed.

Pathways from parietal cortex to premotor cortex

Figure 1b shows some of the pathways by which visuospatial information might reach PMv and other premotor and motor areas. Regions in the parietal lobe (filled boxes) receive convergent visual, tactile, proprioceptive and efference copy input [31•,32–34] and, therefore, could serve as a source of information for the bimodal neurons in PMv. Neurons in area 7a and the lateral intraparietal area (LIP), for example, combine visual responses with proprioceptive information about the position of the eyes and the head [35–37]. Andersen and colleagues [31•] have argued that these neurons may encode the locations of objects in head-centered, trunk-centered or, possibly, world-centered space, while Goldberg and

colleagues have argued that the same neurons encode space in eye-centered coordinates (see [24,38•]). Our view is that these parietal neurons do not form any single spatial coordinate system; rather they carry the raw information necessary for other brain areas to construct spatial coordinate systems [22•]. Neural network models demonstrate that the neuronal outputs from areas 7a and LIP could indeed be used as the basis of the body-part-centered receptive fields found in PMv [39•,40].

Area 7a and LIP project to the ventral intraparietal area (VIP) and area 7b, which in turn project to PMv ([2,3,5,6,41]; M Matelli, G Luppino, A Murata, H Sakata, *Soc Neurosci Abstr* 1994, 20:984). The neuron properties in VIP and 7b are somewhat similar to those in PMv. As in PMv, a high percentage of neurons in VIP and 7b are bimodal, visual and tactile, and the visual receptive fields are generally restricted to the space near the body [42–49]. However, the visual receptive fields are not as closely linked to the body surface as in PMv. In 7b, for bimodal cells with a tactile response on the arm, the visual receptive fields do not move when the arm is moved ([50]; MSA Graziano, T Fernandez, CG Gross, *Soc Neurosci Abstr* 1996, 22:398). In VIP, only a small proportion of the visual receptive fields do not move when the eyes move [51•]. These two areas would therefore seem to form a processing stage immediately before the body-part-centered visual receptive fields in PMv.

Another route by which spatial information might reach premotor cortex and guide movement is through parietal areas PO, MDP, medial intraparietal (MIP) and 7m. These areas receive visual, proprioceptive and tactile input and project to the frontal lobe, mainly to the supplementary motor area and the dorsal premotor area (PMd) [52,53•,54•]. Caminiti and colleagues [52,53•] have suggested that this anatomical pathway underlies spatially guided reaching. Neurons in all of these areas respond during reaches of the contralateral arm, and in PMd the proportion is close to 100% [54•,55]. However, PMd notably lacks the visual receptive fields in the space near the body that are so common in PMv. Instead, the neurons respond to arbitrary instructional signals, such as colored spots of light, but only when the monkey is trained to move in response to those stimuli [56,57]. One suggestion, therefore, is that PMd helps to perform complex and arbitrary sensory-motor mappings, while PMv coordinates more spatially directed movements [54•,58,59]. Another possibility is that PMd is specific for projecting the hand toward a target, while PMv controls a greater range of spatially guided movements involving the arms, chest and head.

In the traditional view, the parietal lobe contains a general-purpose map of visual space, and this spatial information is then relayed to the motor areas of the frontal lobe to guide behavior. However, the planning and coordination of movement appears to begin in the parietal

lobe itself. Not only are reaching movements represented in parietal areas 7m and MIP, but eye movements are represented in LIP [60*,61*] and grasping movements in the anterior intraparietal area (AIP) [62,63*]. The motor functions of 7b and VIP, the main parietal sources of input to PMv, have not yet been systematically studied, but there is some indication that 7b may be involved in control of arm movements and VIP in control of the head and mouth [46,47]. These motor-specific parietal areas project to corresponding specific premotor areas in the frontal lobe (see Figure 1). We suggest that the premotor areas are the final stations where spatial maps for guiding movement are constructed. That is, motor processing and spatial processing overlap extensively, and the highest levels of spatial processing lie quite deep within the motor system. This integration of logically separable functions is not unusual and appears to be a common property of neuronal systems. For example, the inferior temporal cortex processes sensory information about shape and color, but is equally involved in storage of the same types of stimulus features [64]. Although psychology has traditionally divided the mind into separate functions, such as perception, memory, spatial representation and motor control, these logical categories do not appear to be biologically valid and often cannot be found in separate locations in the brain.

Multiple spatial coordinate frames in humans

The view of the spatial control of movement described above is based largely on single-neuron evidence from the monkey. Is there evidence that similar mechanisms exist in humans?

People with lesions of the parietal lobe have severe visuospatial and visuomotor impairments. They show deficits in reaching, fixating a target, remembering routes, judging spatial relations, localizing a touch on the body and attending to the contralateral side of space [65–71]. Visuospatial deficits have also been observed after frontal lesions [72*,73]. One major goal of current neuropsychological research is to determine the spatial coordinate system that is disrupted in these patients. For patients who neglect half of space, do they neglect the space to one side of the retina, the head, the body, the room in which they are sitting or the object to which they are attending? According to traditional notions of parietal function, the neglect should reflect damage to a single, supramodal map of space anchored to the body, either to the head or the trunk. According to the notion of multiple coordinate systems described above, neglect should vary depending on the specific portions of parietal or frontal cortex that are damaged and should reflect a complicated mixture of different coordinate frames. The evidence clearly supports this second view. Different patients and different tests on the same patient can demonstrate spatial deficits that are centered on the eye, the body or the attended object [71]. Neglect can involve primarily the space within reaching distance or more distant space

[74–77]. Distractors presented in the tactile modality can exacerbate neglect symptoms in the visual modality and vice versa, demonstrating a close link between the representation of visual space near the body and tactile space on the body [78*].

The position of the arm can also influence the symptoms of neglect. In one experiment involving cross-modal extinction [79*], subjects were asked to detect a tactile stimulus applied to the hand contralateral to the lesion. When a visual stimulus was presented near the other hand, the subjects no longer reported the tactile stimulus. That is, 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. This result can be explained by hand-centered visual receptive fields, such as we found in monkey PMv [16*].

Normal subjects also show evidence of a hand-centered coordinate system. In an experiment by Tipper *et al.* [80], when subjects reached for a target while avoiding a distracting stimulus, the reaction times were elevated when the distractor lay roughly between the hand and the target. Again, the critical region of visual space, in which the distractor had maximum effect, was anchored to the hand and moved if the hand was moved. In another experiment, Driver and Spence (see their review, in this issue, pp 245–253) found that a touch on the hand could enhance processing of visual stimuli in the space near the hand. When the hand was placed in different locations, the enhanced region of visual space remained anchored to the hand. These results demonstrate the existence of body-part-centered coordinate systems in the human brain.

Conclusions

To understand and represent the space around our bodies, we must put together vision, touch and proprioception, as well as vestibular sensation and audition. These signals are initially combined in the parietal lobe. The parietal areas also appear to begin the process of planning and coordinating movements. Different parietal areas are specialized for different motor outputs, such as those for eye, arm and hand movements. These parietal areas project to premotor areas in the frontal lobe, in which the processing of space and movement continues. 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.

Acknowledgements

Our work is supported by National Institutes of Health grant EY11347-27 and McDonnell-Pew grant 90-16.

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