

# Parietofrontal Circuits for Action and Space Perception in the Macaque Monkey

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**The classical view of the functional role of the posterior parietal cortex has been radically changed in recent years. The parietal lobe is formed by a multiplicity of functionally distinct areas strongly and reciprocally connected in a rather selective way with the various areas forming the agranular frontal cortex (motor cortex). These connections—parietofrontal circuits—mediate, in parallel, the sensorimotor transformation for the control of specific actions. According to this view, space coding is now believed to be the result of the construction of multiple space representations that may be related to a specific class of actions. Therefore, the concept of one single parietal master center for space perception is no more tenable.** © 2001 Academic Press

**Key Words:** posterior parietal cortex; motor cortex; sensorimotor transformation; monkey.

## INTRODUCTION

The posterior parietal cortex was classically considered as a large association region, target of information of different sensory modalities converging to construct a single spatial map of the world and a general scheme of the body. This view, recently, has been seriously challenged by a series of anatomical and functional data showing that the posterior parietal cortex is constituted by a multiplicity of architectonically and functionally defined areas, each of them involved in the analysis of different aspects of sensory information. Given the strong and specific connections of these parietal areas with the motor cortex, sensory information is then transformed into action (sensorimotor transformation). As a consequence, it is now widely accepted that there is not one single multipurpose area for perception of space, rather the brain constructs multiple space representations that may be related to a specific

class of actions (see Rizzolatti *et al.*, 1997; Colby 1999). Like the posterior parietal cortex also the agranular frontal cortex, here referred to as the motor cortex, is formed by a mosaic of at least seven anatomically and functionally distinct areas that appear to play different roles in motor control. Figure 1 shows a modern subdivision of the monkey motor cortex proposed by Matelli *et al.* (1985, 1991) based on architectonical data as well as on functional and hodological studies.

In the present article we briefly review hodological data collected in our laboratory in order to characterize the general pattern of cortical connections of each of the various motor areas and, in particular, those linking parietal and motor areas. For more details and a complete review of the literature, see Rizzolatti *et al.* (1998).

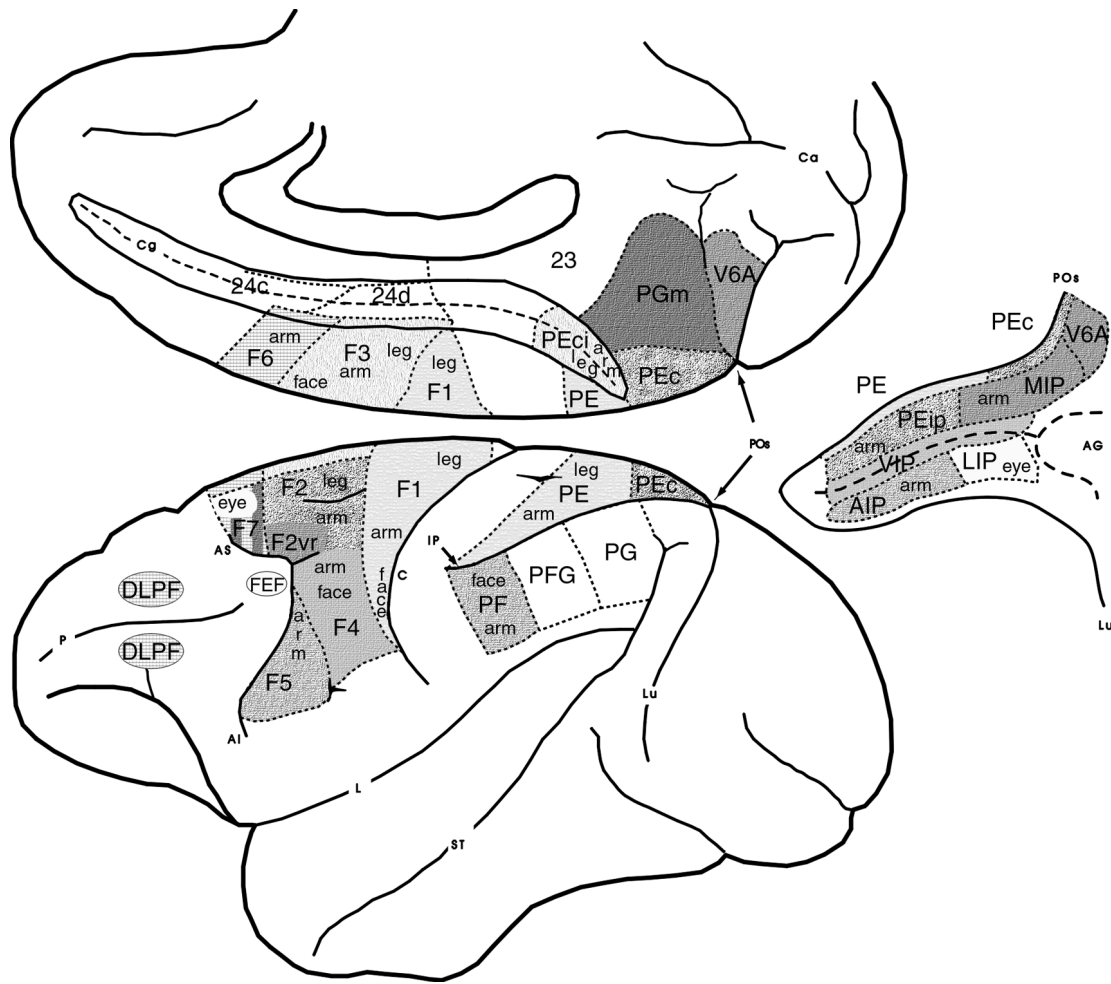
## THE GENERAL ORGANIZATION OF THE MOTOR CORTEX

The motor areas can be subdivided into two main classes: areas that receive their predominant cortical input from the parietal lobe (parieto-dependent motor areas) and areas that receive their predominant cortical input from the prefrontal and the cingulate cortex (fronto-dependent motor areas, see Table 1). Areas F1, F2, F3, F4, and F5 belong to the first class and areas F6 and F7 to the second class.

The organization of corticospinal projections is in accord with this subdivision (He *et al.*, 1993, 1995). The parieto-dependent areas have a direct access to the spinal cord, whereas the fronto-dependent areas send their output only to the brain stem. Furthermore, the parieto-dependent areas have direct connections with F1, whereas the fronto-dependent areas lack this link.

Within the parieto-dependent group of premotor areas, each area is the target of a different set of parietal areas. Typically, each premotor area receives strong afferents from a single parietal area. Conversely, each parietal area projects predominantly (but not exclusively) to a single premotor area. Functional data, when available, indicate that parietal and motor areas linked by predominant connections may share common functional proper-

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**FIG. 1.** Mesial and lateral views of the macaque brain showing the parcellations of the frontal motor cortex and of the posterior parietal cortex. Areas buried within the intraparietal sulcus are shown in an unfolded view of the sulcus. For the nomenclature and definition of motor, posterior parietal, and cingulate areas, see Rizzolatti *et al.* (1998). On the basis of the available data, the various body part representations in the motor and parietal cortices are also reported. Single motor areas and their major source of cortical afferents are indicated with the same gray tones. Abbreviations used: AG, annectant gyrus; AI, inferior arcuate sulcus; AS, superior arcuate sulcus; C, central sulcus; Ca, calcarine fissure; Cg, cingulate sulcus; DLPF, dorsolateral prefrontal cortex; FEF, frontal eye field; IP, intraparietal sulcus; L, lateral fissure; Lu, lunate sulcus; P, principal sulcus; POS, parieto-occipital sulcus; ST, superior temporal sulcus.

ties. Thus, the parietal and premotor areas form a series of anatomical circuits largely independent one from another (Table 2). In the next sections parietofrontal circuits involving parietal visual areas, possibly involved in different aspects of visuomotor transformations for action, will be examined in more details.

#### VISUOMOTOR PARIETOFRONTAL CIRCUITS INVOLVING THE DORSAL PREMOTOR CORTEX (VENTRAL AREA F7 AND VENTRAL AND ROSTRAL AREA F2)

The agranular frontal cortex sector located dorsal to the level of the spur and the superior limb of the arcuate sulcus is frequently referred to as the "dorsal premotor cortex" (PMd) and is formed by areas F2 and F7 (Fig. 1).

F2 is electrically excitable and has a rough somatotopic organization with a leg and an arm representation located dorsal and ventral to the superior precentral dimple, respectively. Not much is known about F2 sensory properties. Available evidence indicates, however, that many F2 neurons respond to somatosensory stimuli and in particular to the proprioceptive ones. Recent observations from our laboratory showed that there are also F2 neurons driven by 3-D visual stimuli (Fogassi *et al.*, 1999). These neurons are located essentially in its rostral and ventral part (F2vr). Furthermore, a recent study showed that in this part of F2 information about the target location and the arm to be used can be integrated at single neuron level, to plan a forthcoming action (Hoshi and Tanji, 2000). Parietal afferents are very rich and differentially distributed within area

**TABLE 1**

Quantitative Analysis of Intrinsic (Motor) and Extrinsic (Prefrontal and Parietal) Connections of the Premotor Areas in the Macaque Monkey

Injected area	Caudal premotor areas					Rostral premotor areas		
	Area F2 Dimple	Area F2 vr	Area F3	Area F4	Area F5	Area F6	Area F7 vc	Area F7 SEF
No. of cases	1	2	4	2	2	2	2	1
Prefrontal (%)	0.93	3.04	0	0.72	0.87	19.95	23.46	69.06
Motor (%)	62.27	52.87	60.7	74.7	64.61	54.55	60.98	11.87
Parietal (%)	33.84	26.28	18.35	11.97	25.46	2.6	12.97	0.87
Others (%)	2.96	17.81	20.95	12.61	9.06	22.9	2.59	18.2
Total (%)	100	100	100	100	100	100	100	100

*Note.* Data are expressed as percentages of the total number of retrogradely labeled cells in the cerebral cortex with the exclusion of the injected area. The term “others” includes cingulate, opercular, and temporal connections.

F2. That part of F2 that is located around the superior precentral dimple is a major target of areas PEc and PEip. These two areas are involved in higher order somatosensory elaboration. In contrast, F2vr (the part where visually responsive neurons are located) is a major target of areas MIP and V6A and is also target of minor projections from the dorsal area 46. Area MIP is located in the caudal part of the medial bank of the intraparietal sulcus (see Colby, 1999). Neurons in this area respond to stimuli within reaching distance and show responses to pure visual stimuli or to both visual and somatosensory stimuli (bimodal neurons). In particular, bimodal neurons are strongly activated when the monkey reaches for a visual target and can be specific for the location of the target and for the arm that is used for reaching the target. Some purely visual neurons show an increase of their discharge when the target is moved to within the reaching distance. Area V6A is located in the dorsal part of the anterior bank of the parietooccipital sulcus (Galletti *et al.*, 1999). In this area neurons have visual receptive fields (RFs) mostly organized in retinotopic coordinates, many of them showing activity modulated by gaze direction, many responding to complex visual stimuli. In addition to purely visual neurons, V6A is characterized by the presence of non visual neurons discharging during active arm movements. Arm related neurons are often directionally selective and frequently driven also by somatosensory stimuli. One possible function of the MIP/V6A–F2vr circuit is the transformation of somatosensory and visual information for the control of the transport phase of the hand toward the target.

Much less is known about the functional properties of F7, with the exception of its dorsal part which contains the “supplementary eye field” (SEF). The SEF is an oculomotor field that can be identified with intracortical microstimulation and that, anatomically, is richly connected with the frontal eye field

(FEF). The remaining part of F7 is scarcely excitable and has been object of few functional studies (Vaadia *et al.*, 1986; di Pellegrino and Wise, 1991; Fuji *et al.*, 2000). Some F7 neurons have visual responses even when the stimulus is not instructing a subsequent movement. Others have visual responses when the location of the stimulus matches with the target of an arm movement. F7 is target of predominant projections from the dorsal prefrontal cortex, which has been suggested to play a role in spatial memory (Wilson *et al.*, 1993). F7 is also target of specific, but minor parietal afferents originating from area PGm, an area located on the mesial wall of the hemisphere. PGm is connected with PG and with extrastriate visual areas and it has been suggested that it is involved in the localization of objects in space (Ferraina *et al.*, 1997). Area F7, therefore, is part of a cortical circuit that could be involved in coding object locations in space for orienting and coordinated arm-body movements.

**TABLE 2**

Predominant and Additional Cortical Connections of the Motor Areas in the Macaque Monkey

Motor areas	Predominant connections	Additional connections
F1	PE	SI
F2 dimple	PEc, PEip,	CGp
F2vr	<b>MIP</b>	<b>V6A, PFG</b>
F3	PEci, 24d	PE, SII, SI, <b>PFG</b>
F4	<b>VIP</b>	<b>PF</b> , PEip, SII
F5	<b>AIP, PF</b>	<b>PFG</b> , SII
F6	DLPF, 24c	<b>PFG</b> , PG
F7	DLPF	<b>PGm, V6A</b> , CGp
F7 (SEF)	FEF	DLPF, <b>LIP</b>
FEF	<b>LIP, MST, MT<sup>a</sup></b>	

*Note.* Parietal visual areas are typed in italic, and parietal bimodal visual and somatosensory areas are typed in bold italic.

<sup>a</sup> Schall *et al.* (1995).

### VISUOMOTOR PARIETOFRONTAL CIRCUITS INVOLVING THE VENTRAL PREMOTOR CORTEX (AREA F4 AND AREA F5)

The agranular frontal cortex sector located ventral to the level of the spur and the inferior limb of the arcuate sulcus is frequently referred to as the "ventral premotor cortex" (PMv) and is formed by areas F4 and F5 (Fig. 1).

Microstimulation experiments showed that F4 contains representations of arm, neck, face, and mouth movements. F4 neurons discharge during the execution of specific actions, such as movements toward the mouth, or when the arm is moved toward a given spatial location. Their directional specificity is broad. Most of F4 neurons respond to sensory stimuli. According to the effective sensory stimulus, F4 neurons were subdivided into two categories: pure somatosensory neurons and bimodal, somatosensory and visual neurons (Gentilucci *et al.*, 1988; Graziano *et al.*, 1994; Fogassi *et al.*, 1996). Bimodal neurons have large somatosensory RFs located on the face, chest, arms and hands. Visual RFs are formed by tridimensional portions of space located around the animal. They are generally limited in depth (from few centimeters to about 40 from the tactile RFs) and almost always originate from the skin, thus forming an extension in space of the tactile RFs. Visual responses are very often selective for stimuli moving toward the tactile RFs and do not depend on the retinal position of the stimulus. Visual RFs remain anchored to the tactile ones regardless of gaze position, indicating that the space coding in F4 is based on an egocentric body part-centered frame of reference. F4 is a major target of an area located along the fundus of the intraparietal sulcus and termed VIP (ventral intraparietal area). Area VIP shares many functional properties with F4 (see Colby, 1999). Also in this area there are bimodal, visual and tactile neurons, most of them centered on the face and, as in F4, visual RFs are in register with the tactile ones and limited to the peripersonal space. In at least one third of these neurons visual RFs appear to be coded in egocentric coordinates. Therefore, the VIP-F4 circuit seems to be involved in encoding peripersonal space according to a body part-centered frame of reference and in transforming object locations into appropriate movements toward them.

Area F5 is electrically excitable and contains a movement representation of the hand and the mouth (see Rizzolatti *et al.*, 1998). F5 neurons typically code goal-directed motor acts, such as grasping, holding, tearing or manipulating objects. Most of the "grasping neurons" code specific types of hand prehension, such as precision grip (thumb and index finger opposition), whole hand prehension and finger prehension. A consistent population of F5 neurons responds also to the presentation of 3-D objects even when no action upon

the object is requested. F5 receives a modest projection from the ventral part of the dorsolateral prefrontal cortex. Its main connections are with a parietal area located within the intraparietal sulcus, area AIP (anterior intraparietal area) and with area PF. AIP neurons have functional properties similar to those of the canonical F5 neurons. They have motor responses coding selective hand manipulation, grasping movements and visual responses to the physical characteristics of the objects. On the basis of these data, it has been suggested that the AIP-F5 circuit is involved in the creation of a "pragmatic" representation of the object, in which the object intrinsic properties (size, shape, and orientation) are coded in order to select the most appropriate way to grasp it (Jeannerod *et al.*, 1995).

### VISUOMOTOR PARIETOFRONTAL CIRCUITS INVOLVING THE PREARCUATE CORTEX (FEF)

The LIP-FEF circuit (see Table 2) contains neurons with similar properties that can be grouped into three main categories: visual neurons, movement neurons, and visuomovement neurons (Bruce and Goldberg, 1984; Andersen *et al.*, 1997; Colby, 1999). Visual neurons are strongly activated by stationary stimuli and, usually, have large RFs. Movement neurons discharge in relation to eye movements and many of them are active before the saccade onset. Visuomovement neurons show both visual and saccade-related activity and their visual RFs are in register with the end-point of the effective saccade. Although most of the visual responsive neurons in area LIP have retinotopic receptive fields, the intensity of their discharge is modulated by the position of the eye in the orbit ("planar gain fields"). This important property may allow the LIP-FEF circuit to use eye position and retinotopic information for calculating an absolute position in space (transformation of a retinocentric into a craniocentric frame of reference) and for programming eye movements.

If one compares the properties of LIP-FEF circuit with those of VIP-F4 circuit, some analogies are immediately evident. Both circuits code space specifically for a particular motor goal: eye movements in the case of LIP-FEF circuit, body part movements in the case of VIP-F4 circuit. The differences possibly concern the different type of movements they control and the different sensory demands that eye movements and body part movements pose. The way in which space is coded in the two circuits follows the same logic. A rather simple system based on retinotopic neurons, calculating also eye position, is sufficient for programming eye movements that are executed under the same load condition and, therefore, are stereotyped. The organization of body part movements, which are characterized by a large variability in terms of load, speed and degree of freedom, requires multiple different frames of

references. Explicit space coding at the single neuron level, using different frames of reference according to the body part used, leaves the frequency of the neuronal discharge free to carry additional information on stimulus properties providing a considerable advantage for this system.

### FUNCTIONAL CONSIDERATIONS

As reviewed in the previous sections, each parieto-dependent premotor area is part of largely segregated parietofrontal circuits. It has been proposed that the functional correlate of this anatomical organization is that each parieto-premotor circuit is dedicated to a specific sensorimotor transformation (see Rizzolatti *et al.*, 1998). These circuits, then, represent the basic elements of the cortical motor system.

The visuomotor transformations for action may imply simultaneous control of different visual mechanisms. For example, the kinematic description of a reaching-grasping movement requires the occurrence of several submovements: transporting the hand to the object, orienting the wrist, and preshaping the fingers. Therefore, visuomotor transformation for reaching-grasping movements should include the coding of the location of the object in space, the control of the arm trajectory during reaching, the coding of the orientation, size and shape of the objects. The anatomical organization of the parietofrontal connections suggest that the cortical motor system is able to process in parallel all these aspects related to the control of arm and hand movements. Such parallel processing would reduce the time required for movement planning and execution and may explain why a multiplicity of body movement representations is present in both the motor and parietal cortices.

How is visual information transformed into action along these circuits? A model of such type of an operation has been proposed for the AIP-F5 circuits by Fagg and Arbib (1998). According to this model, AIP provides a multiple pragmatic description of 3-D objects, thus "proposes" several grasping "possibilities" to F5. F5, in turn, selects the most appropriate type of grip on the basis of contextual information (e.g., purpose of the action, motivation, etc.). This information is then sent to F1, for motor execution and, simultaneously back to AIP neurons that code the selected grip in order to keep them active during movement execution. Visuomotor transformation is then the result of a collaboration between a parietal and a frontal area forming any given parietofrontal circuit, in which motor and sensory signals are fully integrated at both levels. According to this view, space coding would be, therefore, a secondary result of the activity of some of these circuits in which the spatial location of an object is coded according to its own motor purposes. These circuits construct multiple space representations that

can be selectively affected by restricted cortical and subcortical lesions (see Rizzolatti and Gallese, 1988). Therefore, the existence of a single, multipurpose space area is supported neither by anatomical data nor by lesion studies.

The result of the sensorimotor transformations processed by the various parietofrontal circuits is the generation of a "potential motor action," which is of a representation of an action that may or may not be executed. The transformation of such a potential action into an actual movement should be the result of different cortical circuits. Most probably the fronto-dependent motor area F6 is responsible for this operation. Area F6 has almost no connections with the parietal lobe, but is strongly connected with the dorsal and ventral sectors of prefrontal area 46 and with the rostral cingulate cortex (area 24c). There is consensus that these prefrontal sectors are not involved in the analysis of sensory stimuli, but rather play a role in cognitive functions, such as working memory and temporal planning of actions. It is possible, therefore, that F6 relays this information to the parieto-dependent premotor areas, so that the potential motor actions are either executed or not.

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### REFERENCES

- di Pellegrino, G., and Wise, S. P. 1991. A neurophysiological comparison of three distinct regions of the primate frontal lobe. *Brain* **114**: 951-978.
- Fagg, A. H., and Arbib, M. A., 1998. Modeling parietal-premotor interactions in primate control of grasping. *Neural Netw.* **11**: 1277-1303.
- Ferraina, S., Johnson, P. B., Garasto, M. R., Battaglia-Mayer, A., Ercolani, L., Bianchi, L., Lacquaniti, F., and Caminiti, R. 1997. Combination of hand and gaze signals during reaching: Activity in parietal area 7m of the monkey. *J. Neurophysiol.* **77**: 1034-1038.
- Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., and Rizzolatti, G. 1996. Coding of peripersonal space in inferior premotor cortex (area F4). *J. Neurophysiol.* **76**: 141-157.
- Fogassi, L., Raos, V., Franchi, G., Gallese, V., Luppino, G., and Matelli, M. 1999. Visual responses in the dorsal premotor area F2 of the macaque monkey. *Exp. Brain Res.* **128**: 194-199.
- Fujii, N., Mushiake, H., and Tanji, J. 2000. Rostrocaudal distinction of the dorsal premotor area based on oculomotor involvement. *J. Neurophysiol.* **83**: 1764-1769.
- Galletti, C., Fattori, P., Kutz, D. F., and Gamberini, M. 1999. Brain location and visual topography of cortical area V6A in the macaque monkey. *Eur. J. Neurosci.* **11**: 575-582.
- Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., Camarda, R., and Rizzolatti, G. 1988. Functional organization of inferior area 6 in the macaque monkey: I. Somatotopy and the control of proximal movements. *Exp. Brain Res.* **71**: 475-490.
- Graziano, M. S. A., Yap, G. S., and Gross, C. G. 1994. Coding of visual space by premotor neurons. *Science* **266**: 1054-1057.

- Jeannerod, M., Arbib, M. A., Rizzolatti, G., and Sakata, H. 1995. Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends Neurosci.* **18**: 314–320.
- He, S. Q., Dum, R. P., and Strick, P. L. 1993. Topographic organization of corticospinal projections from the frontal lobe: Motor areas on the lateral surface of the hemisphere. *J. Neurosci.* **13**: 952–980.
- He, S. Q., Dum, R. P., and Strick, P. L. 1995. Topographic organization of corticospinal projections from the frontal lobe: Motor areas on the medial surface of the hemisphere. *J. Neurosci.* **15**: 3284–3306.
- Hoshi, E., and Tanji, J. 2000. Integration of target and body-part information in the premotor cortex when planning action. *Nature* **408**: 466–470.
- Matelli, M., Luppino, G., and Rizzolatti, G. 1985. Patterns of cytochrome oxidase activity in the frontal agranular cortex of macaque monkey. *Behav. Brain Res.* **18**: 125–137.
- Matelli, M., Luppino, G., and Rizzolatti, G. 1991. Architecture of superior and mesial area 6 and of the adjacent cingulate cortex. *J. Comp. Neurol.* **311**: 445–462.
- Rizzolatti, G., and Gallese, V. 1988. Mechanisms and theories of spatial neglect. In *Handbook of Neuropsychology* (F. Boller and J. Grafman, Eds.), Vol. 1, pp. 223–246. Elsevier, Amsterdam.
- Rizzolatti, G., Fogassi, L., and Gallese, V. 1997. Parietal cortex: From sight to action. *Curr. Opin. Neurobiol.* **7**: 562–567.
- Rizzolatti, G., Luppino, G., and Matelli, M. 1998. The organization of the cortical motor system: New concepts. *Electroencephalogr. Clin. Neurol.* **106**: 283–296.
- Schall, J. D., Morel, A., King, D. J., and Bullier, J. 1995. Topography of visual cortex connections with frontal eye field in macaque: Convergence and segregation of processing streams. *J. Neurosci.* **15**: 4464–4487.
- Vaadia, E., Benson, D. A., Hienz, R. D., and Goldstein, M. H. 1986. Unit study of monkey frontal cortex: Active localization of auditory and visual stimuli. *J. Neurophysiol.* **56**: 934–952.
- Wilson, F. A., Scalaidhe, S. P., and Goldman-Rakic, P. S. 1993. Dissociation of object and spatial processing domains in primate prefrontal cortex. *Science* **260**: 1955–1958.