

## Spatial representations for action in parietal cortex

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### 1. Introduction

We live in an ever-changing sensory world. As we move our eyes and move through the environment, new images are continuously presented to the brain. Given such constantly changing input, it is remarkable how easily we are able to keep track of where things are. We can reach for an object, or look at it, or even kick it without making a conscious effort to assess its location in space.

The traditional view of spatial perception, strongly supported by subjective experience, is that we know where things are in some absolute, world-based frame of reference and use this spatial information to guide our movements. In this standard and intuitively plausible view, spatial perception is a monolithic process: the brain forms a single spatial representation of each object regardless of what action is going to be performed in relation to that object.

A new and somewhat counterintuitive view is that the brain represents the spatial location of an object many times over in different cortical areas and each representation is suited to certain kinds of behavioral responses [7,15,23]. Neurophysiological research carried out in monkeys indicates that in areas responsible for controlling head movements, visually sensitive neurons encode the location of an object relative to the head [7–9,31]. In contrast, areas involved in limb movement have neurons which encode object location relative to limb position [16–18,22,32] and, in areas controlling eye movements, visually sensitive neurons encode the location of an object relative to the center of gaze [14,20,21].

Three cortical areas with distinctive spatial representations have been discovered in the intraparietal sulcus of rhesus monkeys [7]. Neurons in each area are selective for particular stimulus dimensions and particular regions of space. They signal not only where an object is but how to act on it. The representation of space in a given area reflects a particular motor output by which a stimulus can be acquired or avoided. These results suggest that parietal cortex contains multiple action-based spatial representations. In the scheme emerging from these studies, spatial perception is a modular process. A single object may be multiply represented in terms of the actions that can be performed on it. While this new view seems implausible at first glance, it is analogous to current views of visual perception. When we see a red bouncing ball, we perceive a single object, even though its shape, color and direction of motion are analyzed separately. Likewise, beneath the apparent unity of subjective spatial experience, may lie a diversity of spatial representations, each with specific knowledge of how to act on an object.

### 2. Visual areas of the intraparietal sulcus

Posterior parietal cortex is divided into a number of separate areas. Unlike lower level extrastriate visual areas, these parietal areas do not typically contain simple retinotopic maps and their borders cannot be defined with reference to ventral or horizontal meridian representations. Parietal areas have instead been initially identified on the basis of their connections with other cortical areas [1,2,10,29]. Connections alone, however, are not sufficient to define an area. For instance, both the lateral and the ventral intraparietal areas (LIP and VIP) receive strong projections from area MT, in the superior temporal sulcus [34]. The most reliable guide to areal boundaries in parietal

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cortex is the response properties of the neurons. Because many features of parietal neurons are observable only in alert animals [4,6,30,33] we did a behavioral mapping of parietal cortex in which neural activity was examined in relation to a large set of tasks. Our standard protocol included tests for visual and somatosensory responsiveness, attentional modulation of these responses, and for oculomotor and somatomotor activity. Previous efforts to map parietal cortex have also used alert animals and shown clear evidence for a regional distribution of distinct functional cell types [26]. In the current experiments, we controlled the monkey's behavior by rewarding the animal for fixation or eye movements or selective attention to particular stimuli. A second advance over previous mapping experiments was the use of a recording grid which allowed us to record from identified locations repeatedly and allowed precise reconstruction of the location of recording sites [11]. This reconstruction is especially important because recordings were carried out over a long period of time and because these mapping experiments have focused on cortex buried in the intraparietal sulcus. Accurate reconstruction of recording sites is critical for establishing the location of borders between physiologically defined areas.

An overall view of the functional organization of intraparietal sulcus is presented in Fig. 1. Of the many different kinds of cells observed, each has a restricted distribution within the sulcus. In moving from one region of the sulcus

to the next, the probability of encountering any particular cell type changes systematically. In some regions of the sulcus, such as that near the fundus, the borders between areas are sharply defined by sudden changes in the predominant cell type. In other regions, such as on the medial bank, the boundaries are apparently less sharp and there is a more gradual shift in the response characteristics of the cells. The following sections will describe response properties of neurons in three intraparietal areas and how they contribute to a different spatial representations.

### 3. Spatial representation in area LIP

Neurons in the lateral intraparietal area are active in relation to both visual and oculomotor events [8,9,19,21]. They discharge when a visual stimulus appears in the receptive field and, for about half the population, discharge again when the monkey executes a saccade to the location cued by the stimulus (Fig. 2). The strength of the visual response is modulated by the behavioral set induced by the task. When the monkey must attend to the stimulus, the amplitude of the visual response is enhanced, compared to the response seen when the stimulus is irrelevant for the monkey's behavior [4,21,33]. In addition to these visual, attentional and presaccadic signals, many LIP neurons also carry a memory signal [7,19]. These tonically active neurons continue to respond to a visual stimulus in the remem-

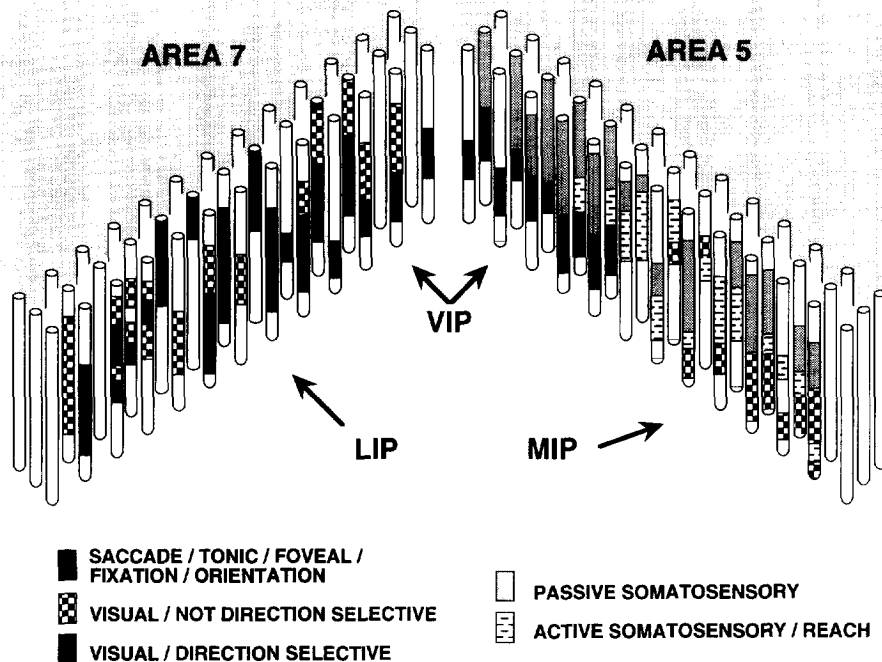


Fig. 1. Distribution of neuronal response properties in rhesus monkey intraparietal sulcus. Each column represents a single 10 mm penetration along the lateral or medial bank of the sulcus. Two rows of penetrations spaced 1 mm apart are shown for each bank. The anterior part of the sulcus is shown at the top of the figure. The posterior portion of the sulcus is shown at the bottom of the figure, where the banks of the sulcus have been separated.

bered saccade task during the interval between the appearance of the stimulus and the onset of the saccade. There is no visual stimulus present in the receptive field during this interval. In order to perform the task accurately, the monkey must retain an image of the stimulus location during the delay interval. Tonic activity during the delay reflects a memory trace of stimulus location.

These results on multiple sources of activation in LIP underscore the importance of studying single neurons in different behavioral tasks. The results from multiple tasks indicate that the responses of LIP neurons do not depend exclusively on either vision or movement. The single point of intersection of the various activations observed is the receptive field itself. We hypothesize that LIP neurons encode spatial locations. Further, their activity is modulated by attention to a spatial locus that is defined not by a stimulus or by a movement, but by the spatial vector that could describe either. In essence, the activity of an LIP neuron encodes an attended spatial location.

If LIP is encoding space, rather than visual perception or specific behaviors, it is important to understand the coordinate system in which it operates. There are three plausible coordinate frames for representing stimulus position. For a neuron operating in retinal coordinates, neural

activity signals where the stimulus is on the retina. In a head-centered coordinate frame, neural activity signals where the stimulus is relative to the head, regardless of where the eyes are looking. In oculocentric coordinates, neural activity signals the saccade necessary to foveate the stimulus. We have been able to discriminate among these three possibilities by observing what happens to memory-related activity in LIP when the monkey makes a saccade [14].

Every time an eye movement occurs, the projection of the visual world changes on the retina and, by implication, in all the retinotopically mapped areas of the brain. If it is to be useful, visual information currently being processed in LIP must be remapped in conjunction with each saccade. We have discovered that LIP neurons remap the memory trace of a previous stimulus event (Fig. 3). While the monkey fixates, a stimulus is briefly presented (50 ms) at a location well outside the receptive field of the neuron (Fig. 3B). A new fixation point appears, and the monkey makes a saccade to it. Because the stimulus flash is so brief, the stimulus is no longer present at the time of the saccade. The effect of the saccade is to bring the receptive field to the location that was previously stimulated. If the neuron had continued to encode events at the original

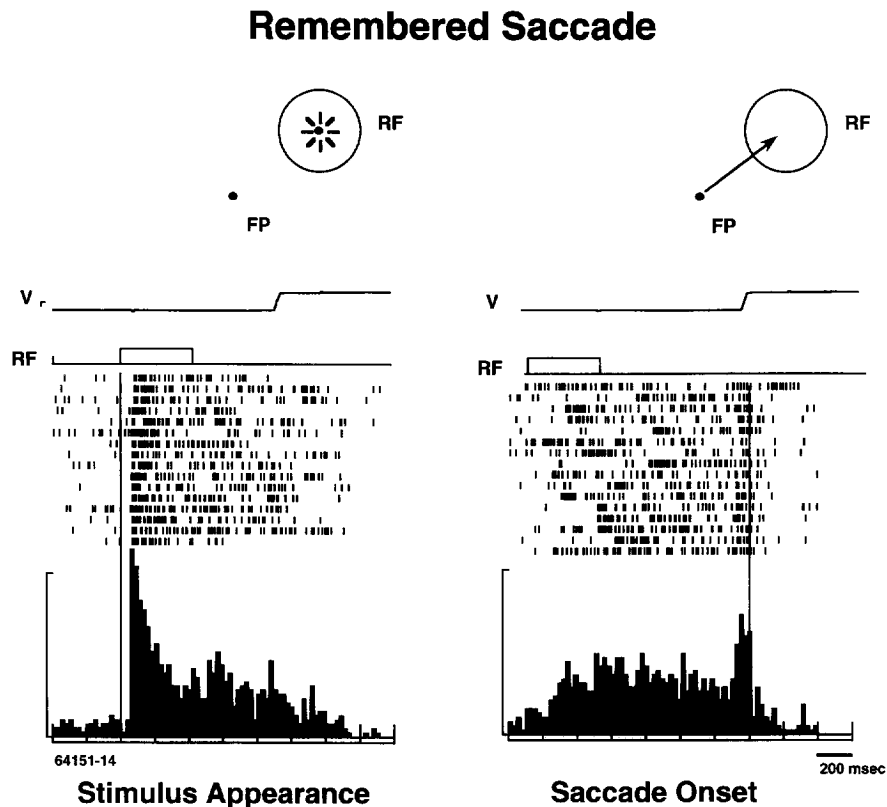


Fig. 2. Response of an LIP neuron in a remembered saccade task. The cartoon above each diagram shows the relative locations of the fixation point (FP) and the receptive field (RF). The time lines show vertical eye position ( $V$ ) and the onset and offset of a stimulus in the RF. Each tick mark in the raster diagram signifies a single action potential. Successive trials are shown on successive lines, synchronized (vertical line) on the event indicated below the histogram. The calibration bar at left signifies a response rate of 100 spikes/s. In this task, the monkey must fixate while a stimulus is briefly presented in the RF. After a variable delay, the fixation point is extinguished and the monkey saccades to the location where the stimulus appeared. Separate visual and motor bursts are seen in each trial, as well as tonic activity during the memory period.

receptive field location (i.e., in head-centered coordinates), it would remain silent after the saccade because there was never any stimulus at that location. Likewise, if the neuron had access only to retinal information (retinal coordinates) it would also remain silent, since no stimulus appeared in its retinal receptive field. The results show instead that LIP

neurons do respond when the receptive field is brought to land on a previously stimulated location (Fig. 3B). There is no stimulus present on the screen, so the neuron can only be responding to a memory trace of the stimulus. Control experiments confirm that neither the stimulus alone (Fig. 3C) nor the saccade alone (Fig. 3D) can drive the neuron.

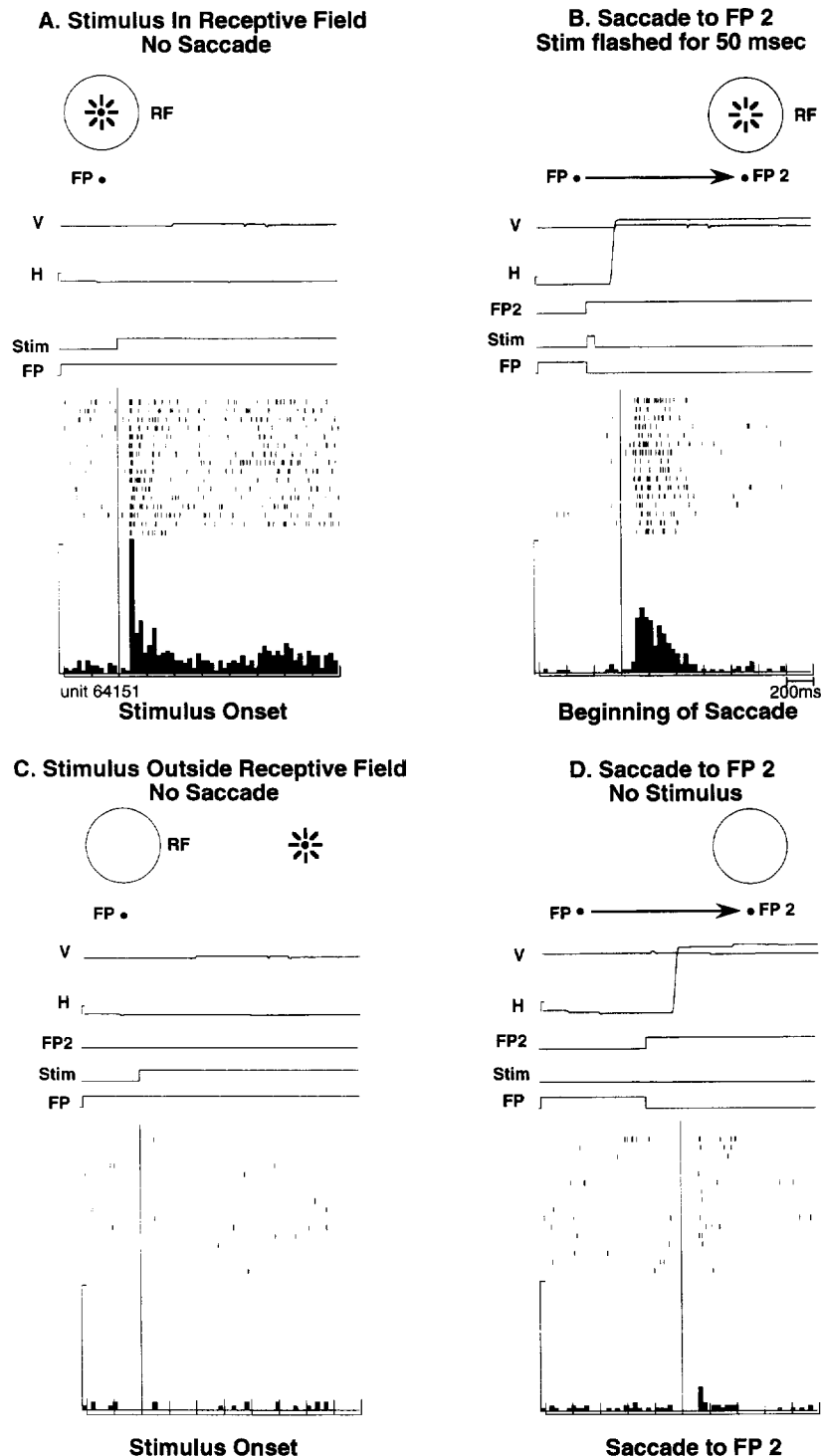


Fig. 3. LIP neuron response to the memory trace of a stimulus. A: fixation condition – neuron responds to a stimulus in the RF. B: memory trace condition – the stimulus is flashed outside the RF and is gone before the saccade to FP2 begins. C: stimulus control condition – a stimulus presented outside the RF does not drive the cell in the absence of a saccade. D: saccade control condition – the saccade alone does not drive the cell in the absence of a stimulus.

We conclude that the neuron is responding to a remapped memory trace of the stimulus which is encoded in oculo-centric coordinates.

The specific spatial problem which LIP must solve is how to signal a spatial location with reference to the current position of the fovea. By remapping memory traces,

parietal cortex constructs a spatial representation that encodes stimulus location in terms of distance and direction from the current center of gaze. While neurons in LIP have retinotopic receptive fields, visual information in LIP is dynamically updated in conjunction with eye movements to produce an oculocentric representation: stimuli are coded

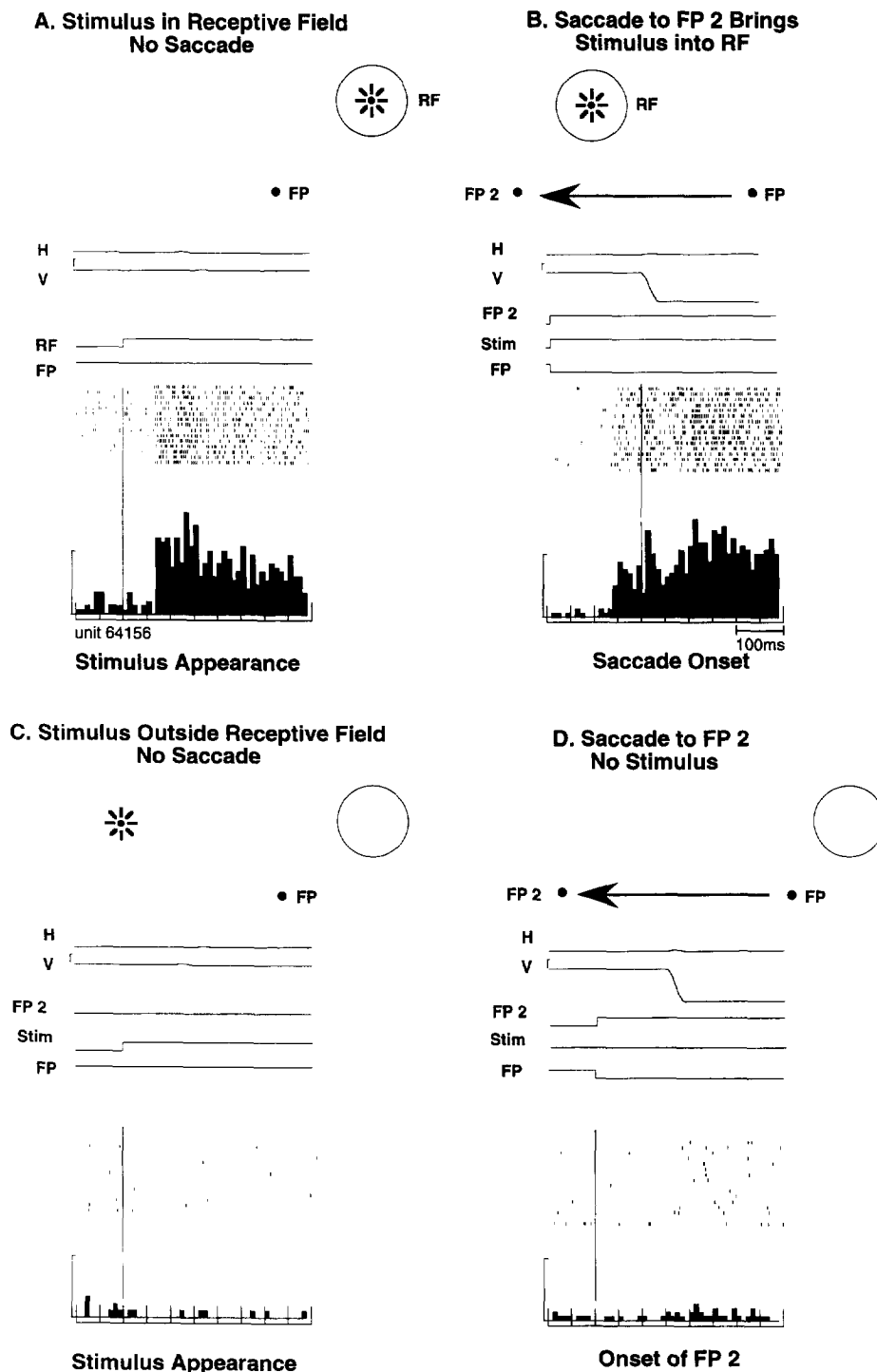


Fig. 4. Predictive remapping. A: fixation condition – LIP neuron responds to a stimulus in the RF. B: saccadic remapping condition – while the monkey fixates, a stimulus appears outside the RF as well as a new fixation point (FP2) to which the monkey must saccade. The neuron responds to the stimulus even before the saccade begins. C: stimulus control condition – a stimulus presented outside the RF does not drive the neuron. D: saccade control condition – the saccade alone does not drive the neuron.

in terms of their distance and direction from the fovea. LIP neurons maintain an oculocentric representation of target position by using a corollary discharge from the eye movement command to update retinotopic visual information. This remapping of stimulus location serves to maintain an alignment between the external world and the internal representation of it.

Psychophysical evidence for remapping has been presented by Hikosaka et al. [24,25]. They have shown that the locus of attention can remain stationary with respect to the environment even when the eyes move. In their paradigm, a light flash draws attention to a single location. When a stationary bar is subsequently presented on one side of the cued location, the observer sees a line moving out from the spot. This illusory motion is unchanged by an intervening saccade, indicating that attention remains at the original spatial location. Remapping of a memory trace could be the mechanism underlying this illusion: the cue is perceived as remaining at the same location despite the saccade because the memory trace of the flashed cue is remapped. These psychophysical results suggest that remapping has perceptual consequences as well as contributing to the specific spatial representation used for oculomotor behavior. With regard to spatial representation for action, remapping provides the oculomotor system with continuously accurate information about the vector of the

saccadic eye movement necessary to acquire the stimulated location. Remapping is the means by which a coordinate transformation is effected from retinotopic to oculocentric coordinates.

In a further set of experiments, we found that the intention to make a saccade is itself sufficient to shift the receptive field of an LIP neuron, that is, LIP neurons can predict the sensory consequences of an impending saccade. They respond to a stimulus that will be brought into the receptive field as if the stimulus were already present in it. This remapping occurs with every saccade, whether or not the stimulus will be the target of a later saccade. An example of this phenomenon is shown in Fig. 4. In the fixation task (Fig. 4A) this LIP neuron responds to the appearance of stimulus in its receptive field with a latency of 70 ms. When the stimulus is presented outside the receptive field, and the monkey is required to make the specific saccade that will bring the stimulus into the receptive field, the neuron begins to respond even before the saccade is initiated (Fig. 4B). Control experiments confirm that this activity is a predictive visual response. The first control condition shows that the stimulus is in fact outside the receptive field when the monkey looks at the original fixation point (Fig. 4C). The second control condition shows that the saccade to the new fixation point is not associated with neural activity by itself (Fig. 4D).

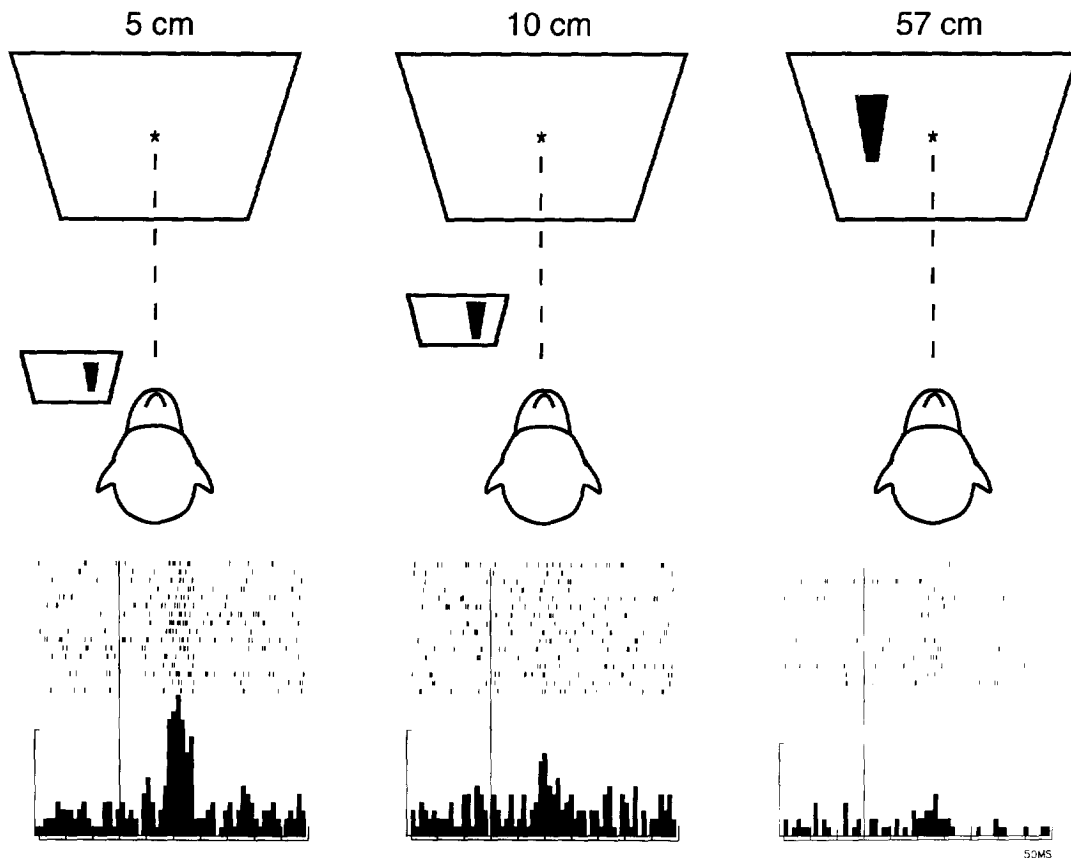


Fig. 5. Distance selectivity in a VIP neuron. Each panel shows the response to a stimulus presented at a different distance from the monkey. Stimuli were equated for size and luminance. In all conditions the monkey had to maintain fixation on a point on the tangent screen at 57 cm.

Many LIP neurons with predictive responses, like the one illustrated here, have visual responses but no saccade related activity in the remembered saccade task, indicating that the predictive response must be visual and not related to motor planning. In predictive remapping, the area of retina that is capable of stimulating the cell transiently shifts, so that the cell responds to stimuli that will be in its receptive field after the saccade. This phenomenon enables accurate localization of visual objects without the processing delay inherent in relying on reafferent information following a saccade.

In summary, neurons in LIP encode events at specific spatial locations. Their activity is not uniquely related to either sensory or motor events. Rather, they signal the location at which an event occurred. The spatial coordinate frame used by LIP neurons is oculocentric: locations are specified in terms of their distance and direction from the fovea. This representation is of prime usefulness for the oculomotor system which must program movements not to

a target in absolute space but relative to the current center of gaze.

#### 4. Spatial representation in area VIP

The ventral intraparietal area is located in the fundus of the intraparietal sulcus and has been defined on the basis of its distinctive visual response properties [9]. Cortex dorsal to VIP in the anterior portion of the medial bank is purely somatosensory with an emphasis on hand representation (Fig. 1). Near the fundus of the sulcus, there is a sudden transition to a region of strong visual responsiveness. This visual area extends from the medial bank across the fundus to the lateral bank. VIP neurons are well driven by moving visual stimuli and most are selective for direction of stimulus motion. Other properties similar to those found in areas MT and MST, such as speed tuning and responsiveness to whole-field motion, are also observed,

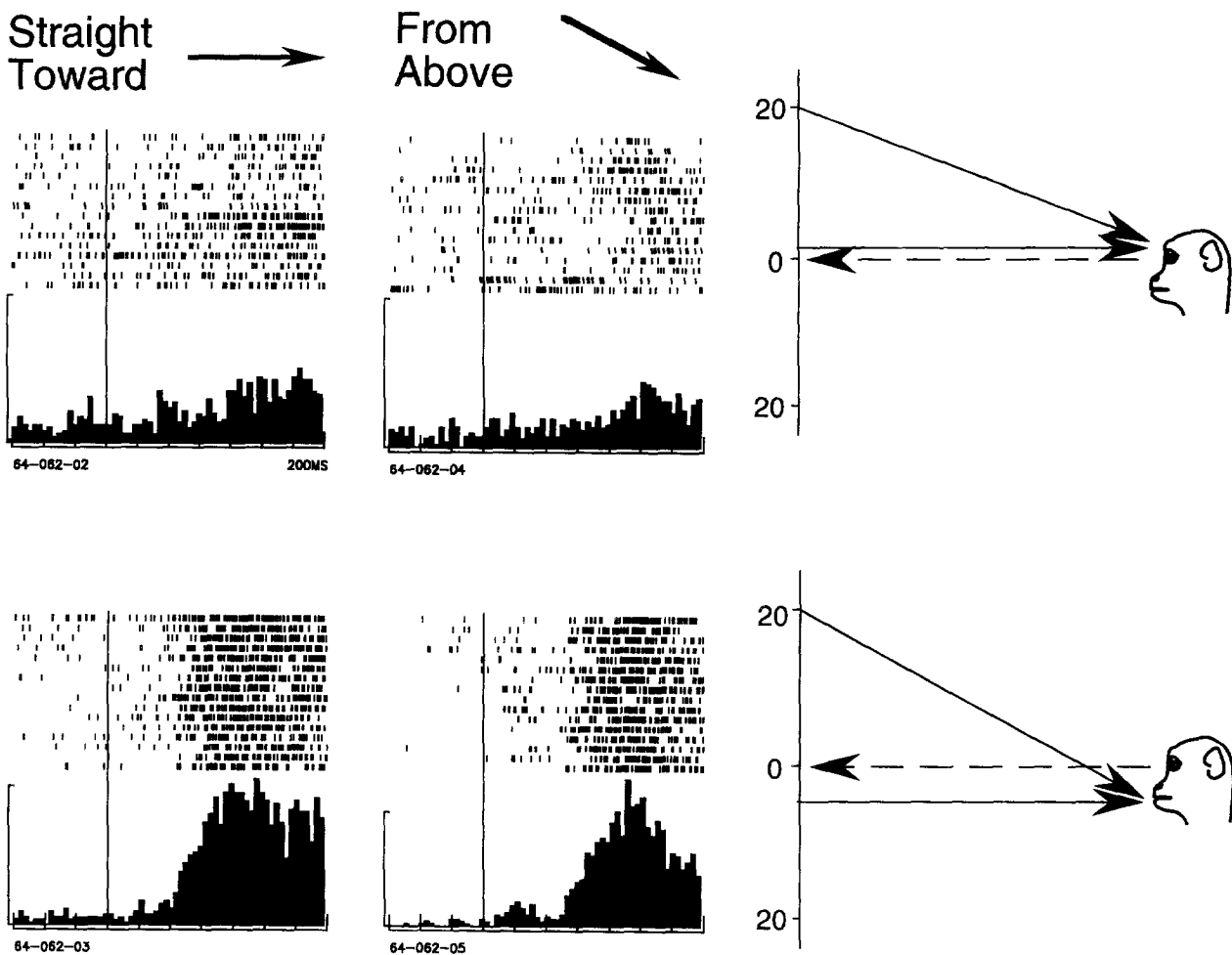


Fig. 6. Trajectory selectivity in a VIP neuron. Top row: stimuli are moved toward the monkey's brow while the monkey fixates a central FP on the tangent screen. Bottom row: the same stimuli are moved toward the monkey's chin, evoking a much larger response. The projected point of contact of the stimulus is more strongly related to response rate than either the absolute direction of motion (straight toward vs. down and toward) or the portion of the visual field stimulated (upper vs. lower).

consistent with its inputs from these areas [3,34]. These visual response properties set VIP apart from the surrounding cortex.

Two special types of VIP neurons are of interest with regard to spatial representation. The first is the ultraneur cells. These visual neurons respond only to stimuli presented very close to the animal, within a few centimeters of the face (Fig. 5). These neurons may signal the presence of a stimulus that can be acquired by reaching with the mouth. The second special type is trajectory neurons. These cells respond selectively to a stimulus moving towards or away from the animal. For these neurons, the absolute direction of stimulus motion is less important than the anticipated point of contact of the stimulus. In the example shown, a stimulus moved toward the chin elicited a much stronger response than the same stimulus moved toward the brow (Fig. 6). This result suggests that something other than a simple retinal coordinate frame is used to represent space in VIP. This suggestion was confirmed by having the monkey change its gaze direction (Fig. 7). The neuron continued to respond best to a stimulus moving towards the chin regardless of eye position. This

insensitivity to eye position indicates that the stimulus is encoded in head-centered coordinates and not retinal coordinates.

A surprising feature of VIP is that most neurons can be independently driven by somatosensory stimulation [12,13]. The somatosensory receptive fields are found primarily on the face and head. The visual and somatosensory receptive fields correspond to one another in location, in size and in directional selectivity, as illustrated in Fig. 8. This neuron responds both to a peripheral visual stimulus moved toward the fovea and to a cutaneous stimulus moved across the face toward the mouth. VIP neurons with visual receptive fields in the upper hemifield have somatosensory receptive fields on the upper part of the face and brow, while neurons with lower field visual receptive fields have somatosensory receptive fields on the lower part of the face. Strikingly, VIP neurons with foveal visual receptive fields have somatosensory receptive fields around the mouth, as though the mouth were the 'fovea' of the facial somatosensory system. For bimodal trajectory sensitive neurons, the visual response is tied to the location of the somatosensory receptive field. Finally, some VIP neurons with very large visual receptive fields have somatosensory receptive fields that include the hand and arm as well as the head.

These findings on VIP response properties are consistent with a spatial representation in head-centered coordinates. Both the ultraneur and the trajectory sensitive neurons appear to encode stimulus location in a head-centered coordinate frame. The bimodal neurons may have a special role in hand, eye and mouth coordination. Overall, visual targets may be coded in VIP in terms of how they can be acquired by reaching with the head and mouth.

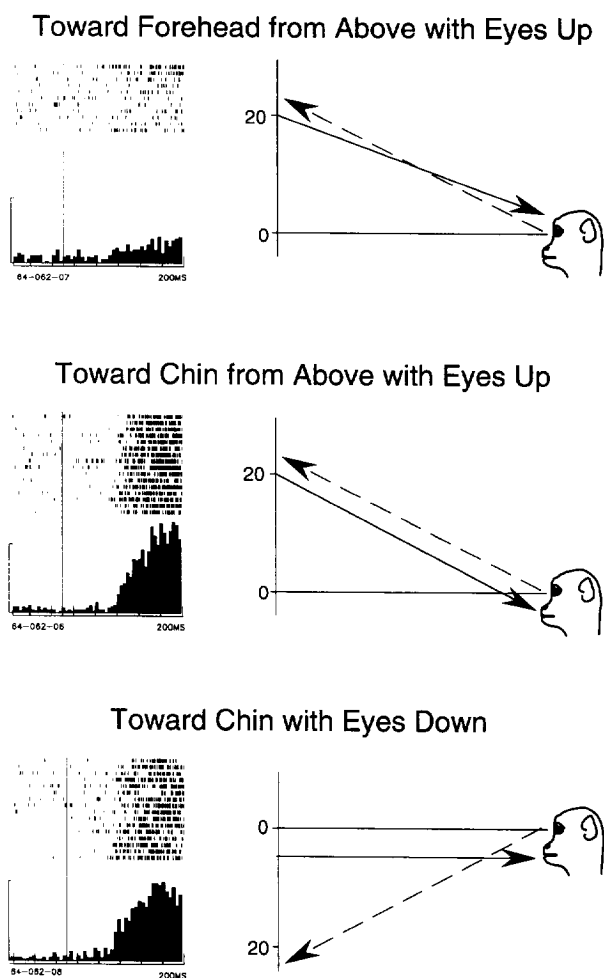


Fig. 7. Head-centered spatial coordinates in VIP. Changes in eye position do not change selectivity for stimuli moving towards the chin.

## 5. Spatial representation in area MIP

The medial intraparietal area (MIP) is located in the posterior portion of the medial bank. As shown in Fig. 1, a regular sequence of different cell types is encountered in penetrations parallel to the cortical surface. Near the shoulder of the sulcus, adjacent to convexity cortex, neurons respond well to passive somatosensory stimulation. Receptive fields are generally found on the limbs and are commonly restricted to the contralateral hand. Slightly deeper in the sulcus, cells are most active during reaching movements. These cells may still be purely somatosensory: the monkey may provide himself with somatosensory stimulation during active reach that we are unable to duplicate during passive stimulation. Midway down the sulcus, cells with bimodal responses become common. These neurons respond both to somatosensory and to visual stimuli presented while the monkey is maintaining fixation. Most of these cells can be driven independently by either stimulus alone, as is also the case for bimodal neurons in area 7

[33]. Some of these bimodal cells exhibit additivity in their responsiveness: simultaneous visual and somatosensory stimulation evokes a stronger response than either stimulus alone. Others of these bimodal neurons are responsive only during active reaching and looking. The neuron illustrated in Fig. 9 has virtually no response when the monkey saccades to a visual target and has only a moderate response when the monkey reaches towards the target in the dark but fires strongly during the same eye and hand movement when performed in the light.

Deep in the posterior portion of the medial bank is a purely visual region. Cells here respond well to visual stimuli, especially those presented in the peripheral contralateral visual field and are not responsive to somatosensory stimulation. A minority of these visual cells are selective for the distance at which a visual stimulus appears: stimuli within reaching distance elicit stronger responses than those presented on the standard tangent screen at 57 cm from the animal. The observation of visual responsiveness in these medial bank neurons is surprising given the traditional assignment of this cortex to area 5, somatosensory association cortex, but is in accord with both the anatomical demonstration of connections with visual area PO [10] and previous physiological results indicating visual activity in this region [28]. This visual area corresponds in location to the medial intraparietal area (MIP), a region connected with visual area PO. There is a

gradual shift from purely somatosensory to bimodal to purely visual responsiveness in this posterior part of the medial bank and it is not clear whether MIP has sharp borders like VIP. Such borders may yet be revealed by use of particular stimuli or particular behavioral conditions.

The existence of visual neurons in MIP selective for stimuli within reaching distance suggests that area MIP may have yet another kind of spatial representation, one designed to contribute to the control of arm movements. This region of the medial bank projects selectively to the arm region of premotor cortex [27] where neurons encode targets in arm-centered coordinates [5]. Area MIP may be the source of the visual information which guides arm movements.

## 6. Summary

Parietal cortex contains multiple representations of visual space. Single neurons in area LIP encode attended locations relative to the fovea, while some VIP neurons encode stimulus location relative to the head and some MIP neurons may encode location relative to the arm. These multiple representations are tailored to guide specific kinds of actions: eye movements, head movements and arm movements, respectively. The function of parietal cortex is to signal the location of attended objects relative to the observer. It does so in order to allow the organism to

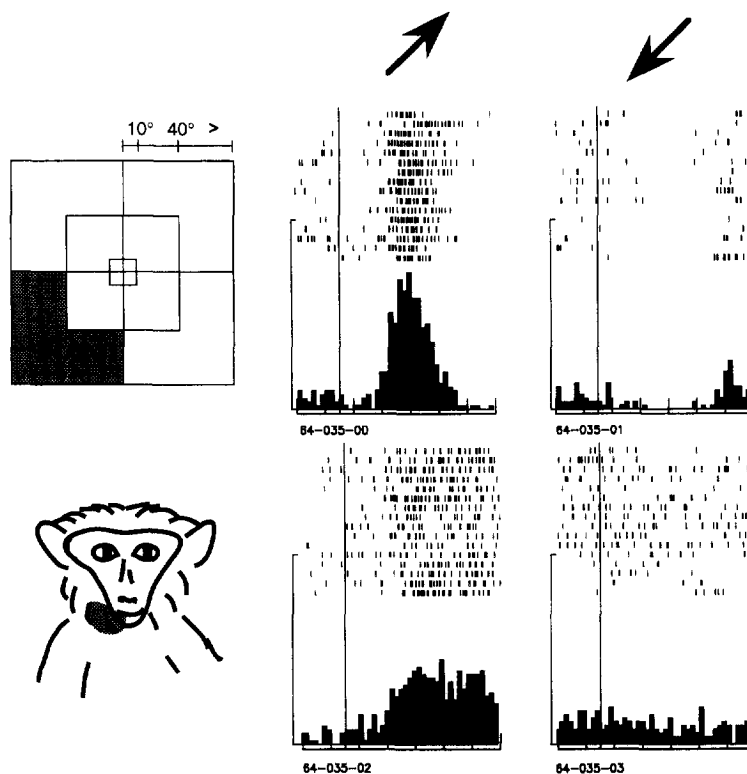


Fig. 8. Bimodal sensory responsiveness in a VIP neuron. Top panel shows the location of the visual RF and a directionally selective response to a stimulus moved through the RF. Bottom panel shows the location of the somatosensory RF for the same single neuron and a directionally selective response to a somatosensory stimulus moved across the RF (tested with eyes closed).

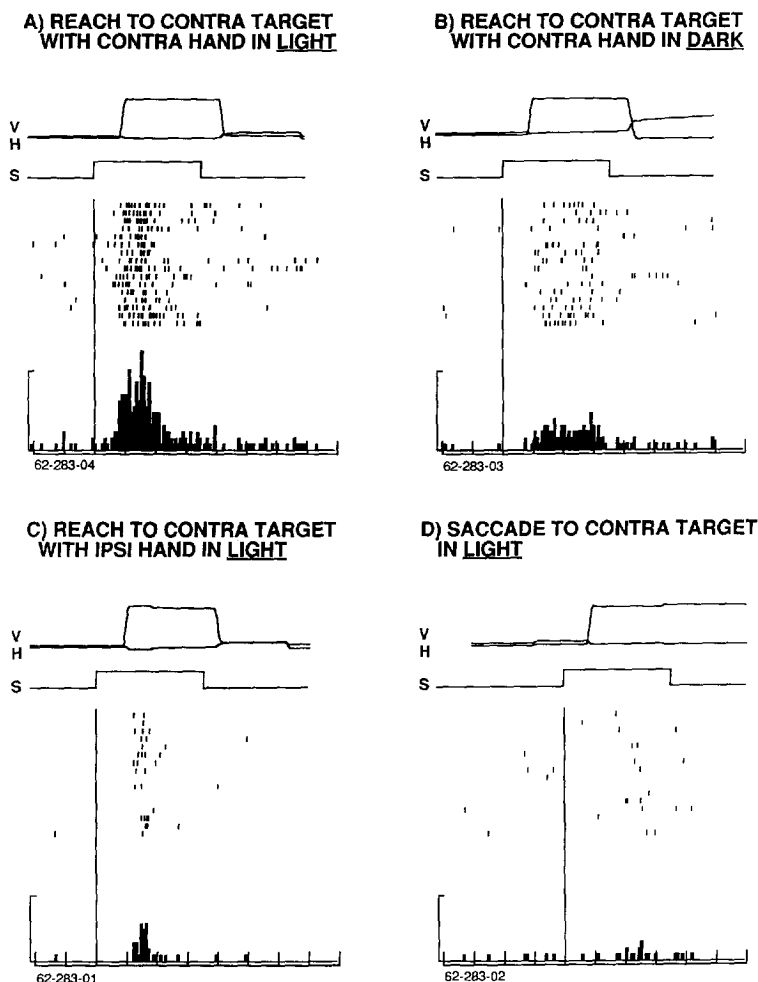


Fig. 9. Visual and somatosensory activity in an MIP neuron. In each panel, time lines show the onset and offset of a visual stimulus presented on a reach panel. A: reaching with the contralateral hand under visual guidance produces consistent and strong activation. B: the same hand and eye movements produce less activation when done in the dark. C: reaching with the ipsilateral hand produces little activation. D: the saccade alone does not activate the neuron.

act on its environment. The many different kinds of actions that can be performed are likely to be supported by these very different kinds of spatial representations.

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### References

- [1] Andersen, R.A., Asanuma, C. and Cowan, M., Callosal and prefrontal associational projecting cell populations in area 7a of the macaque monkey: a study using retrogradely transported fluorescent dyes, *J. Comp. Neurol.*, 232 (1985) 443–455.
- [2] Andersen, R.A., Asanuma, C., Essick, G. and Siegel, R.M., Cortico-cortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule, *J. Comp. Neurol.*, 296 (1990) 65–113.
- [3] Boussaoud, D., Ungerleider, L.G. and Desimone, R., Pathways for motion analysis: Cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque, *J. Comp. Neurol.*, 296 (1990) 462–495.
- [4] Bushnell, M.C., Goldberg, M.E. and Robinson, D.L., Behavioral enhancement of visual responses in monkey cerebral cortex: I. Modulation in posterior parietal cortex related to selective visual attention, *J. Neurophysiol.*, 46 (1981) 755–772.
- [5] Caminiti, R., Johnson, P.B., Galli, C., Ferraina, S. and Burnod, Y., Making arm movements in different parts of space: the premotor and motor cortical representation of a coordinate system for reaching to visual targets, *J. Neurosci.*, 11 (1991) 1182–1197.
- [6] Colby, C.L., The neuroanatomy and neurophysiology of attention, *J. Child Neurol.*, 6 (1991) S88–118.
- [7] Colby, C.L. and Duhamel, J.-R., Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey, *Neuropsychologia*, 29 (1991) 517–537.
- [8] Colby, C.L., Duhamel, J.-R. and Goldberg, M.E., The analysis of visual space by the lateral intraparietal area of the monkey: the role of extraretinal signals. In T.P. Hicks, S. Molotchnikoff and T. Ono (Eds.), *Progress in Brain Research*, Vol. 95, Elsevier, 1993, pp. 307–316.
- [9] Colby, C.L., Duhamel, J.-R. and Goldberg, M.E., Ventral intraparietal area of the macaque: Anatomic location and visual response properties, *J. Neurophysiol.*, 69 (1993) 902–914.

- [10] Colby, C.L., Gattass, R., Olson, C.R. and Gross, C.G., Topographic organization of cortical afferents to extrastriate visual area PO in the macaque: a dual tracer study, *J. Comp. Neurol.*, 269 (1988) 392–413.
- [11] Crist, C.F., Yamasaki, D.S.G., Komatsu, H. and Wurtz, R.H., A grid system and a microsyringe for single cell recording, *J. Neurosci. Methods*, 26 (1988) 117–122.
- [12] Duhamel, J.-R., Colby, C.L. and Goldberg, M.E., Congruent visual and somatosensory response properties of neurons in the ventral intraparietal area (VIP) in the alert monkey, *Soc. Neurosci. Abstr.*, 15 (1989) 162.
- [13] Duhamel, J.-R., Colby, C.L. and Goldberg, M.E., Congruent representations of visual and somatosensory space in single neurons of monkey ventral intraparietal cortex (area VIP). In J. Paillard (Ed.), *Brain and Space*, Oxford University Press, Oxford, 1991, pp. 223–236.
- [14] Duhamel, J.-R., Colby, C.L. and Goldberg, M.E., The updating of the representation of visual space in parietal cortex by intended eye movements, *Science*, 255 (1992) 90–92.
- [15] Fogassi, L., Gallese, V., Pellegrino, G. di, Fadiga, L., Gentilucci, M., Luppino, G., Matelli, M., Pedotti, A. and Rizzolatti, G., Space coding by premotor cortex, *Exp. Brain Res.*, 89 (1992) 686–690.
- [16] Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., Camarda, R. and Rizzolatti, G., Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements, *Exp. Brain Res.*, 71 (1988) 475–490.
- [17] Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., Camarda, R. and Rizzolatti, G., Somatotopic representation in inferior area 6 of the macaque monkey, *Brain Behav. Evol.*, 33 (1989) 118–121.
- [18] Gentilucci, M., Scandolara, C., Pigarev, I.N. and Rizzolatti, G., Visual responses in the postarcuate cortex (area 6) of the monkey that are independent of eye position, *Exp. Brain Res.*, 50 (1983) 464–468.
- [19] Gnadt, J.W. and Andersen, R.A., Memory related motor planning activity in posterior parietal cortex of macaque, *Exp. Brain Res.*, 70 (1988) 216–220.
- [20] Goldberg, M.E. and Bruce, C.J., Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal, *J. Neurophysiol.*, 64 (1990) 489–508.
- [21] Goldberg, M.E., Colby, C.L. and Duhamel, J.-R., The representation of visuomotor space in the parietal lobe of the monkey, *Cold Spring Harbor Symp. Quant. Biol.*, 55 (1990) 729–739.
- [22] Graziano, M.S., Yap, G.S. and Gross, C.G., Coding of visual space by premotor areas, *Science*, 266 (1994) 1054–1057.
- [23] Gross, C.G. and Graziano, M.S.A., Multiple representations of space in the brain, *Neuroscientist*, 1 (1995) 43–50.
- [24] Hikosaka, O., Miyauchi, S. and Shimojo, S., Visual attention revealed by an illusion of motion, *Neurosci. Res.*, 18 (1993) 11–18.
- [25] Hikosaka, O., Miyauchi, S. and Shimojo, S., Voluntary and stimulus-induced attention detected as motion sensation, *Perception*, 22 (1993) 517–526.
- [26] Hyvarinen, J., Regional distribution of functions in parietal association area 7 of the monkey, *Brain Res.*, 206 (1981) 287–303.
- [27] Johnson, P.B., Ferraina, S. and Caminiti, R., Cortical networks for visual reaching, *Exp. Brain Res.*, 17 (1993) 361–365.
- [28] Macko, K.A. and Mishkin, M., Metabolic mapping of higher-order visual areas in the monkey. In L. Sokoloff (Ed.), *Brain Imaging and Brain Function*, Raven Press, New York, 1985.
- [29] Maunsell, J.H.R. and Van Essen, D.C., The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey, *J. Neurosci.*, 3 (1983) 2563–2586.
- [30] Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H. and Acuna, C., Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space, *J. Neurophysiol.*, 38 (1975) 871–908.
- [31] Rizzolatti, G., Gentilucci, M., Luppino, L., Matelli, M. and Ponzoni-Maggi, S., Neurons related to goal-directed motor acts in inferior area 6 of the macaque monkey, *Exp. Brain Res.*, 67 (1987) 220–224.
- [32] Rizzolatti, G., Scandolara, C., Matelli, M. and Gentilucci, M., Afferent properties of periarculate neurons in macaque monkeys: I. Somato-sensory responses, *Behav. Brain Res.*, 2 (1981) 125–146.
- [33] Robinson, D.L., Goldberg, M.E. and Stanton, G.B., Parietal association cortex in the primate: Sensory mechanisms and behavioral modulations, *J. Neurophysiol.*, 41 (1978) 910–932.
- [34] Ungerleider, L.G. and Desimone, R., Cortical connections of visual area MT in the macaque, *J. Comp. Neurol.*, 248 (1986) 190–222.