

# Action-Oriented Spatial Reference Frames in Cortex

## Review

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Where are you? To answer the question you have to know what kind of information is being requested. Does “where” mean where relative to the room, to the building, or to New York? The spatial reference frame that you use determines the answer, and you can imagine an endless variety of such reference frames. What reference frame does the brain use? The traditional view, strongly supported by subjective experience, is that the brain constructs a single map of the world in which the self, objects, and actions are all represented in a unitary framework. The reference frame for this map is usually thought to be in “real world” coordinates, as though we had access to some kind of absolute spatial representation. To create and use such a representation, the brain would have to transform sensory information from the coordinates of several receptor surfaces (e.g., retina, cochlea, or skin surface) into this ultimate spatial representation and later read the information back out into the motor coordinates needed for each effector system (e.g., eye, head, limb, trunk). It has proven difficult to understand how the brain combines the spatial information contained in topographic maps within each sensory system into a single, coherent representation of space, much less how this spatial information could be used to guide motor action (see Stein, 1992, for discussion).

A new view holds that the brain constructs multiple spatial representations (Arbib, 1991; Colby and Duhamel, 1991, 1996; Rizzolatti et al., 1994, 1997; Gross and Graziano, 1995). Starting from the topographic maps in primary sensory cortices, higher order cortical areas create a series of maps in a variety of reference frames. These can be described in terms of two broad classes: egocentric representations, in which objects and locations are represented relative to the observer; and allocentric representations, in which locations are represented in reference frames extrinsic to the observer. Examples of egocentric reference frames are those in eye-centered, head-centered, and arm-centered coordinates. Allocentric representations include those in environmental (room-centered) coordinates and those centered on an object of interest (object-centered coordinates). The full range of reference frames used in cortex is just beginning to be explored physiologically. Progress in understanding spatial representation has come from the insight that we construct these multiple representations in order to act on the world around us. Specific representations are created to guide particular actions, especially those that allow us to acquire or avoid an object (Colby and Duhamel, 1996). The following sections describe the behavioral evidence for multiple representations in humans and summarize the neurophysiological evidence from animal studies.

Neuropsychological studies support the view that the brain makes use of multiple spatial reference frames and indicate that parietal cortex is central to the construction of these representations. Damage to parietal cortex produces dramatic impairments of spatial perception and action. The most striking of these deficits is neglect, the tendency to ignore objects in the half of space opposite to the side of the lesion (Heilman et al., 1985; Bisiach and Vallar, 1988). A patient with a right parietal lobe lesion may fail to notice or respond to objects on the left, including food on the left side of a plate or words on the left side of a page. Neglect occurs in all sensory modalities and can be expressed relative to any of several spatial reference frames. A patient with right parietal damage is typically unaware of objects on the left, but “left” may be defined with respect to a variety of axes. Patients may neglect objects on the left with respect to the body, with respect to the line of sight, or with respect to the object to which they are attending (Gazzaniga and Ladavas, 1987; Farah et al., 1990; Driver and Halligan, 1991; Karnath et al., 1991; Moscovitch and Behrmann, 1994). For example, a neglect patient may shave only one half of his face (head-centered frame) or dress only one side of her body (body-centered frame).

Neglect can also be expressed relative to spatial reference frames that are extrinsic to the observer. A particularly striking example of a deficit expressed in an allocentric spatial reference frame has been described by Moscovitch and Behrmann (1994). They showed that patients neglected a somatosensory stimulus on the left side of the wrist (toward the thumb) when the right hand was palm down. When the hand was turned over so that the palm faced up, the neglected region shifted to the other side (toward the little finger). This demonstrates that the impairment is not of a somatosensory map of the skin surface but rather of an abstract representation of somatosensory space. The dynamic nature of the impairment, changing from moment to moment as a function of body posture, indicates that this representation is constantly being updated. Impairments in different kinds of representations can coexist, and individual patients exhibit different impairments under different behavioral demands (Behrmann and Moscovitch, 1994). Multiple frames of reference may even be used simultaneously (Behrmann and Tipper, 1994; Tipper and Behrmann, 1996). In sum, neuropsychological and behavioral studies support the view that multiple spatial representations are called into play according to the specific demands of the task (Tipper et al., 1992; Sirigu et al., 1996).

These deficits in spatial perception are matched by corresponding deficits in the generation of spatially directed actions. For example, neglect can be specific for stimuli presented at particular distances. Some patients tend to ignore stimuli presented near the body, in personal space, while responding normally to distant stimuli, or vice versa (Bisiach et al., 1986; Duhamel and Brouchon, 1990; Halligan and Marshall, 1991; Cowey et al., 1994). Interestingly, this form of neglect is apparent only when the subject must produce a motor response

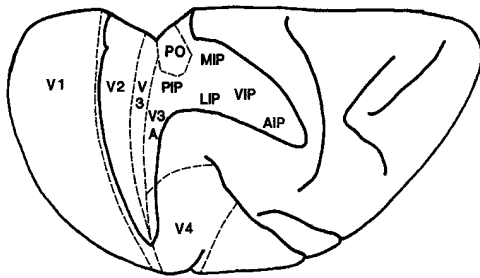


Figure 1. Intraparietal Areas in the Macaque  
Dorsal view of macaque right hemisphere with lunate and intraparietal sulci opened to show the location of functionally defined areas. Adapted from Colby et al., 1988.

to the stimulus and not when spatial perception alone is tested (Pizzamiglio et al., 1989). This dependence on action indicates that spatial representations in parietal cortex incorporate both sensory information about distance and information about intended actions. Milner and Goodale (1995) have emphasized the role of parietal cortex in generating spatial representations for the guidance of action.

The variety of deficits observed following parietal lobe damage suggests that parietal cortex contains more than one kind of spatial representation. To understand more precisely how parietal cortex contributes to spatial perception and action, several groups of investigators have carried out recordings from single neurons in alert monkeys trained to perform spatial tasks. Since the pioneering studies in the 1970s of Hyvarinen, Sakata, Mountcastle, Goldberg, and Robinson, physiologists have sought to specify the sensory and motor conditions under which parietal neurons are activated, using tasks that typically require a hand or an eye movement toward a visual target. This work in monkeys has provided direct evidence that parietal cortex contains several distinct functional areas (Figures 1 and 2) and multiple representations of space (Colby et al., 1988; Colby and Duhamel,

1991, 1996; Stein, 1992; Jeannerod et al., 1995; Lacquaniti et al., 1995; Caminiti et al., 1996; Andersen et al., 1997; Rizzolatti et al., 1997). Parietal cortical areas are strongly linked with areas of frontal cortex (premotor cortex and the frontal and supplementary eye fields), which themselves encode object locations relative to a variety of reference frames (Rizzolatti et al., 1981a, 1981b, 1994; Gentilucci et al., 1983; Goldberg and Bruce, 1990; Graziano et al., 1994, 1997; Gross and Graziano, 1995; Olson and Gettner, 1995). The spatial reference frames used in parietal and frontal cortex have been described either in terms of the body parts to which they are anchored (eye, head, limb) or in terms of the actions to which they contribute (looking, reaching, grasping). Beyond these egocentric representations, recent work has demonstrated the existence at the single unit level of more abstract, allocentric representations that encode stimulus locations and actions in coordinates that are independent of the observer (Olson and Gettner, 1995, 1996). The following sections describe evidence for five distinct spatial reference frames used in parietal and frontal cortex: eye-centered, head-centered, reaching-related, grasp-related, and object-centered.

### Eye-Centered Spatial Representation

At first glance, the map of space in the lateral intraparietal area (LIP) seems simple. Neurons in area LIP have receptive fields at locations defined relative to the retina. These neurons carry visual, memory, and saccade-related signals that can be modulated by orbital position (Bushnell et al., 1981; Gnadt and Andersen, 1988; Andersen et al., 1990; Goldberg et al., 1990). These apparently heterogeneous signals can all be understood as reflecting the degree to which spatial attention has been allocated to the location of the receptive field (Colby et al., 1995, 1996). The spatial representation is not simply retinotopic, however. Rather, neurons combine visual and eye movement information to construct a stable, eye-centered representation of space (Goldberg et al.,

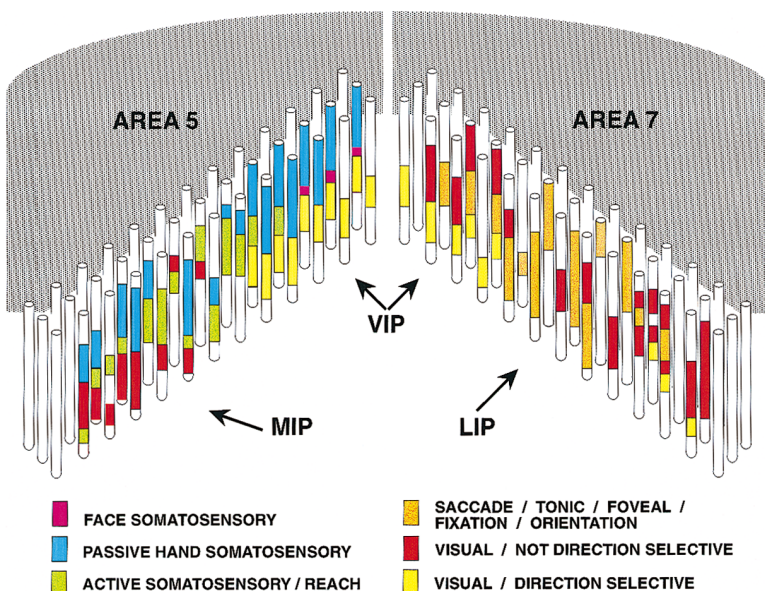


Figure 2. Functional Mapping of Intraparietal Sulcus

Distribution of neuronal response properties in the middle third of the intraparietal sulcus in one monkey. Each column represents results from a single 10 mm electrode penetration through the medial or lateral bank. Penetrations are spaced 1 mm apart. The banks of the sulcus have been separated at the posterior end of the sulcus (bottom of figure). Somatosensory activity predominates on the medial bank, with a visual region near the posterior portion of the fundus (area MIP). Visual and oculomotor activity predominate on the lateral bank (area LIP). Bimodal visual and somatosensory neurons with strong direction selectivity are found in the fundus (area VIP). Adapted from Colby and Duhamel, 1991.

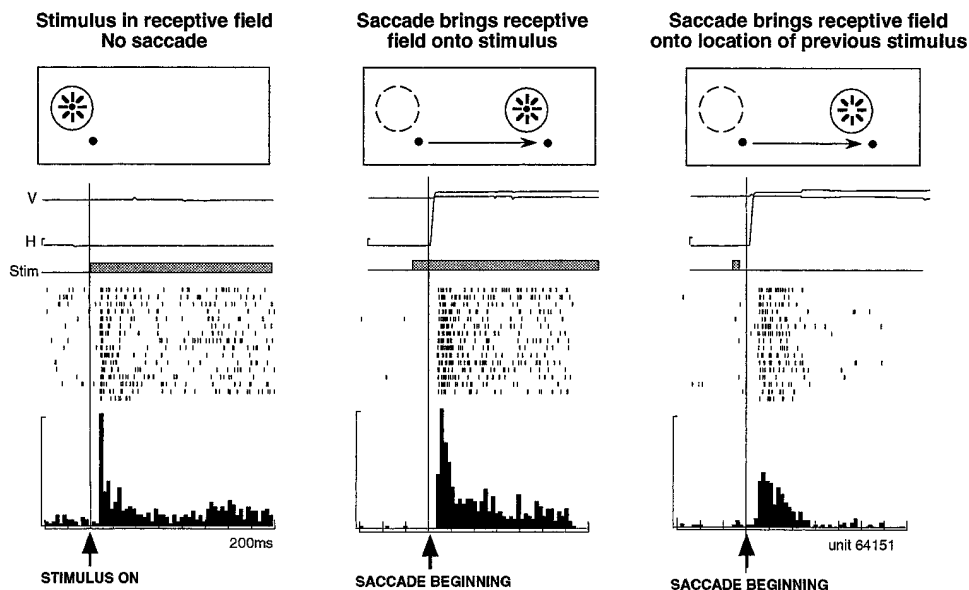


Figure 3. Remapping of Memory Trace Activity in Area LIP

Responses of one LIP neuron in three conditions. Left panel: during fixation, the neuron responds to the onset of a stimulus in the receptive field. Center: response following a saccade that moves the receptive field onto a stimulus. Right: response following a saccade that moves the receptive field onto a previously stimulated location. The stimulus is presented for only 50 ms and is extinguished before the saccade begins. The response is to a memory trace that has been remapped from the coordinates of the initial eye position to those of the final eye position. Adapted from Duhamel et al., 1992a.

1990; Duhamel et al., 1992a; Colby et al., 1993a). This combination is essential because neural representations of space are maintained over time, and the brain must solve the problem of updating them when a receptor surface is moved. Every time we move our eyes, each object in our surroundings activates a new set of retinal neurons. Despite these changes, we experience the world as stable.

More than a century ago, Helmholtz (1866) proposed that the reason the world stays still when we move our eyes is that the “effort of will” involved in making an eye movement simultaneously adjusts our perception to take that eye movement into account. He suggested that when a motor command is issued to shift the eyes in a given direction, a copy of that command, a corollary discharge, is sent to brain areas responsible for generating our internal image of the world. This image is itself shifted so as to stay in alignment with the new visual information that will arrive following the eye movement. A simple experiment convinces most observers that Helmholtz’ account must be essentially true. When you displace your retina by pressing on the eye, the world does seem to move. In contrast, we are generally oblivious to the changes in the retinal image that occur with each eye movement. This perceptual stability has long been understood to reflect the fact that what we “see” is not a direct impression of the external world but a construction or internal representation of it. It is this internal representation that is updated in conjunction with eye movements.

Neurons in area LIP contribute to updating the internal image (Duhamel et al., 1992a; Colby et al., 1993a). The experiment illustrated in Figure 3 shows that the memory trace of a previous stimulus is updated when the eyes

move. The activity of a single neuron is shown in three conditions. In a standard fixation task (left panel), the neuron responds to the onset of a stimulus in the receptive field. In a saccade task (center), the neuron responds when an eye movement brings the receptive field onto a location containing a visual stimulus. The unexpected result is shown in the right panel. Here the monkey made the same saccade, but the stimulus was flashed on for only 50 ms so that the stimulus was already extinguished before the saccade began. This means that no stimulus was ever physically present in the receptive field. So why does the neuron fire? We infer that an updated memory trace of the stimulus is driving the cell. At the time of stimulus onset, while the monkey is looking at the initial fixation point, the stimulus activates neurons whose receptive fields encompass the stimulated location. Some of these neurons will continue to fire after stimulus offset, encoding the location at which the stimulus occurred (Gnadt and Andersen, 1988). At the time of the eye movement, information about the stimulus is passed from these neurons to a new set of neurons whose receptive fields now encompass the stimulated location.

The neural mechanism underlying this information transfer must depend on a corollary discharge of the eye movement command: knowledge about the eye movement causes the memory trace of the stimulus to be updated, or remapped, from the coordinates of the initial fixation point to the coordinates of the new fixation point. Nearly all neurons in area LIP exhibit this kind of remapping of stimulus memory traces. An important implication of this finding is that neurons have access to visual information from the entire visual field, not just from the classically defined receptive field. These

neurons must already have in place the connections that provide input from distant regions of the visual field.

Remapping updates the internal representation of space in conjunction with eye movements so that the internal image always matches the current eye position. Visual information is thereby maintained in eye-centered coordinates. This representation is essential for the guidance of oculomotor responses directed toward the stimulated location. Compared to a head-centered or world-centered representation, an eye-centered representation has the advantage that it is already in the coordinates of the effector system that will be used to acquire the target. Neurons in area LIP accomplish the sensory to motor coordinate transformation and generate an action-oriented spatial representation for the guidance of eye movements.

Studies of patients indicate that remapping and the construction of an eye-centered representation are impaired as a result of parietal lobe damage. This has been demonstrated using an eye movement task in which two targets are presented sequentially. The subjects' task is simply to look at the targets in order. Because the targets are very brief (on the order of 100 ms), they are no longer present at the time the eye movements are performed. Programming the first saccade is easy. The size and direction of the required saccade exactly match the retinal position of the first target. Programming the second saccade presents a problem. The second target was seen from one location, but the saccade toward it will start from a different location. In order to program this second saccade, the system must take into account the difference between the initial eye position and the new eye position. Remapping the memory trace of the second target from the coordinates of the initial eye position to the coordinates of the new eye position accomplishes the necessary transformation. If remapping underlies spatially accurate behavior, then a lesion in the cortical areas responsible for remapping should manifest itself as a difficulty in compensating for a previous saccade.

This prediction was verified in two studies of patients with unilateral parietal lobe damage (Duhamel et al., 1992b; Heide et al., 1995). These patients made both saccades accurately when the first saccade was directed into the good (ipsilesional) hemifield. They failed only when the first saccade was directed into the contralesional field, exhibiting an inability to remap the second target. This is not a memory deficit. Patients occasionally saccade directly to the second target location, indicating that they both saw and remembered its location. Rather, they failed because they could not calculate the change in target location relative to eye position. Patients with damage limited to frontal cortex do not show this pattern of results (Heide et al., 1995), which suggests that the capacity to use the metrics of a saccade to update the visual representation is a unique property of parietal cortex.

Two conclusions can be drawn from these experiments. First, these patients do not have a simple spatial deficit—they can make visually guided eye movements to all the targets perfectly well. Instead, they have a deficit that affects updating a spatial representation for use by a particular motor system. Second, updating

depends on parietal cortex. The remapping of memory traces, demonstrated in single neurons in area LIP, presumably provides the substrate for the capacity to update an eye-centered spatial representation. Both the physiological and the neuropsychological results indicate that parietal cortex uses information about motor commands to transform visual input from retinal coordinates into an eye-centered representation suitable for the guidance of eye movements. The strong connections between area LIP and the frontal eye fields (Schall et al., 1995; Stanton et al., 1995) and the discovery of remapped visual responses in the frontal eye fields (Goldberg and Bruce, 1990; Umeno and Goldberg, 1997) suggest that these areas work together to construct an eye-centered representation of oculomotor space. Many questions remain as to how this representation is coordinated with the head, body, or world-centered reference frames that are called into play when the goal of foveating a target requires more than an eye movement (Brotchie et al., 1995; Andersen et al., 1997; Krauzlis et al., 1997).

#### Head-Centered Spatial Representation

A head-centered representation is one in which visual receptive fields are tied to the skin surface of the head. As long as the head is stationary, the visual receptive field covers the same part of space, regardless of the position of the eyes or the rest of the body. Some neurons in the ventral intraparietal area (area VIP) represent locations in a head-centered reference frame. Neurons in area VIP are strongly responsive to visual stimuli, yet they can also be driven well by somatosensory stimuli (Colby and Duhamel, 1991; Duhamel et al., 1991, 1998). For most neurons, the somatosensory receptive fields are restricted to the head and face. These tactile receptive fields correspond to the visual receptive fields in three ways. First, they match in location when the monkey looks at a central fixation point: a neuron that responds to a visual stimulus in the upper left visual field also responds when the left side of the brow is touched. The dividing line between somatosensory receptive fields linked to the upper and lower visual fields is not at the level of the eyes, as might be expected for a matched representation, but at the level of the mouth. Neurons with foveal visual receptive fields have somatosensory receptive fields on and around the muzzle, as though the mouth were the fovea of the facial somatosensory system. Second, visual and somatosensory receptive fields match in size. Neurons with small visual receptive fields tend to have restricted somatosensory receptive fields at a matching location, whereas those with large, peripheral visual receptive fields have larger somatosensory receptive fields that may include the side of the head. Third, neurons have matched preferences for the direction in which a stimulus is moved. A neuron that responds to a visual stimulus moving toward the right, but not to one moving left, also responds when a small probe is brushed lightly across the monkey's face in a rightward but not a leftward direction.

The correspondence between visual and tactile receptive field locations immediately raises the question of what happens to the relative locations of these fields

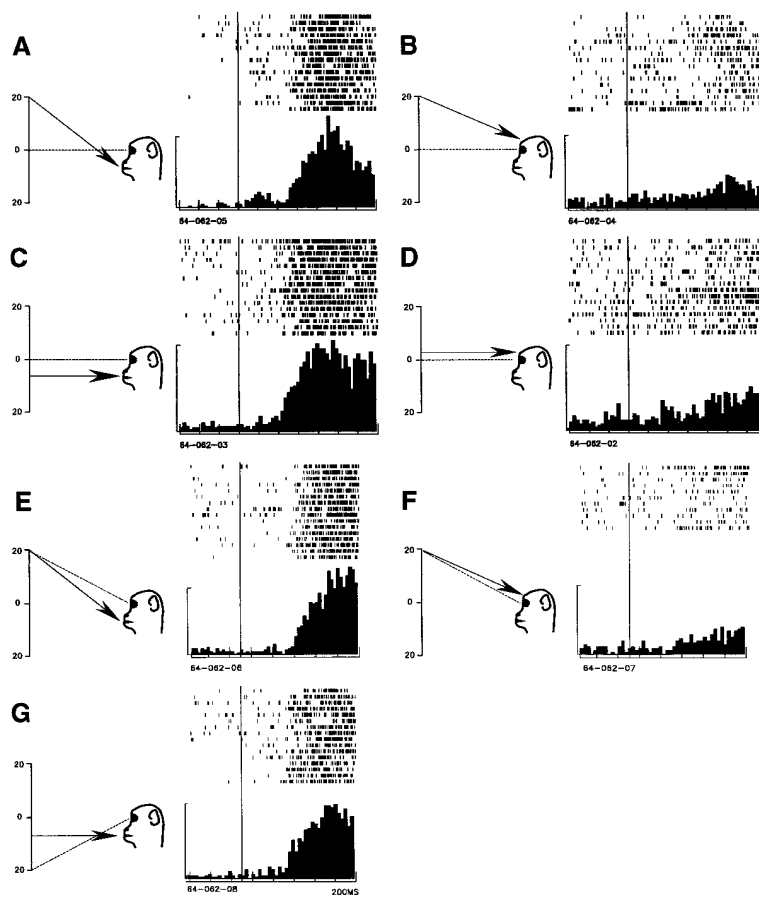


Figure 4. Trajectory Selectivity in Area VIP  
Responses of one VIP visual neuron to stimuli moved toward the mouth (left column) or toward the brow (right column). The response rate (A–D) is more strongly related to the projected point of contact than to either the absolute direction of motion (straight toward versus down and toward) or the portion of the visual field stimulated (upper versus lower). Changes in eye position (E–G) do not affect trajectory selectivity, indicating that stimuli are coded in a head-centered spatial reference frame. Adapted from Colby et al., 1993b.

in a single cell when either receptor surface moves. If the visual receptive field were simply retinotopic, it would occupy the same portion of the retina regardless of eye position, and if the tactile receptive field were purely somatotopic, it would be unchanged by eye position. There could not be a consistent match in location if both receptive fields were defined solely with respect to their receptor surfaces. The answer is that visual receptive fields move across the retina so as to maintain spatial correspondence with somatosensory receptive fields; that is, visual receptive fields are head-centered. An example is shown in Figure 4. This neuron responds best to a visual stimulus approaching the mouth from any direction (left column, Figures 4A and 4C) and does not respond to the same visual stimulus on a trajectory toward the brow (right column, Figures 4B and 4D). This pattern of response indicates that the stimulus is not being encoded in a simple retinotopic coordinate frame: stimuli moving through the same portion of visual space evoke quite different responses depending on the projected point of contact. Rather, this neuron is encoding visual information in a head-centered coordinate frame. This was confirmed by having the monkey shift its gaze to different locations (Figures 4E–4G). Regardless of where the monkey looked, the cell continued to respond best to visual stimuli on any trajectory heading toward the mouth and failed to respond to stimuli moving along similar trajectories but directed toward other points on the face. This neuron has a head-centered receptive

field: it responds to a certain portion of the skin surface and to the visual stimulus aligned with it, no matter what part of the retina is activated. Similar trajectory selective neurons have been described by Rizzolatti and coworkers (Fogassi et al., 1992, 1996) in regions of premotor cortex that receive input from area VIP. Recent work shows that head-centered visual receptive fields are not limited to trajectory-selective neurons: a quantitative study of VIP neuron responses to fronto-parallel motion indicates that many neurons have head-centered receptive fields (Bremmer et al., 1997; Duhamel et al., 1997).

The presumed function of the head-centered representation in area VIP is to guide movements of the head, especially reaching with the mouth. This was suggested by the observation of an unusual class of neurons that respond selectively to visual stimuli presented at very close range, within 5 cm of the face (Colby et al., 1993b). These “ultranear” neurons are equally well activated by monocular or binocular stimulus presentation, which indicates that their distance tuning depends on cues other than disparity. Ultraneur neurons could signal the presence of a stimulus that can be acquired by reaching with the mouth. This idea about the function of the head-centered representation in area VIP fits with the results of anatomical studies showing that area VIP projects to the specific region of premotor cortex involved in the control of head and mouth movements (Matelli et al., 1994, *Soc. Neurosci.*, abstract; Lewis and Van Essen,

1996, Soc. Neurosci., abstract). Neurons in this premotor region, known as area F4, also have bimodal receptive fields, many of which respond best to visual stimuli presented within a few centimeters of the skin surface (Rizzolatti et al., 1981a, 1981b; Gentilucci et al., 1988). Like the trajectory-selective neurons in area VIP, these premotor neurons also maintain visual responsiveness to stimuli approaching the tactile receptive field, regardless of the direction in which the monkey is looking (Fogassi et al., 1992, 1996). In both areas VIP and F4, locations are represented in terms appropriate for a specific kind of action, namely moving the head.

Multiple spatial representations appear to coexist in area VIP. The response properties of many neurons are consistent with a spatial representation in head-centered coordinates: both the ultraneur and the trajectory-selective neurons encode stimulus location relative to the head, as do many bimodal neurons. Results from electrical stimulation support the idea that some neurons contribute to a head-centered representation. Microstimulation in this region can evoke saccades into a restricted zone in head-centered space, independent of the starting position of the eye (Thier and Andersen, 1996). On the other hand, some neurons have purely retinotopic receptive fields and presumably operate in retina-centered coordinates (Duhamel et al., 1997). Finally, some neurons are sensitive to vestibular stimuli, which raises the possibility that they encode motion of the head relative to an inertial, or world-based, reference frame (Bremmer et al., 1997). Taken together, these findings raise the interesting possibility that neurons in a single cortical area contribute to multiple representations of space and the guidance of multiple kinds of action.

### **Arm-Centered and Reaching-Related Spatial Representations**

An arm-centered spatial representation is one in which the visual receptive field is anchored to the skin surface of the limb: when the arm is moved, the visual receptive field moves with it. The most direct evidence for such a representation comes from experiments in which visual receptive fields are mapped with the arm in different positions. Neurons in premotor cortex have receptive fields that move with the arm (Graziano et al., 1994) and encode targets in arm-centered coordinates (Caminiti et al., 1991). The arm region of premotor cortex receives input from a specific portion of parietal cortex (Johnson et al., 1993) where spatial representation is thought to be arm-centered as well. Neurons in the medial intraparietal area (area MIP) are specialized for responding to stimuli within reaching distance and for acting on them by reaching (Colby and Duhamel, 1991). A range of response properties is found in area MIP, from purely somatosensory, to bimodal, to purely visual. These response types are encountered sequentially as an electrode is moved from the lip of the sulcus toward the fundus (Figure 2). Purely somatosensory neurons typically have receptive fields on the contralateral limbs, most often on the hand. Bimodal neurons have visual responses to the onset of a stationary visual stimulus as well as somatosensory responses to passive touch.

These bimodal neurons are strongly activated when the monkey reaches for a visual target and are specific for both the location of the target and for the arm that is used to reach toward it. Below these bimodal neurons is a purely visual region with an unusual property: some neurons here give visual responses that become stronger when the target is moved to within reaching distance. These "near" cells presumably signal the presence of a target that can be acquired by reaching with the arm.

The progression in sensory receptive field properties through the depth of MIP is mirrored in the response properties observed in a directional reaching task. Selectivity for movement direction was prominent around the time of the movement for more dorsal neurons, whereas more ventral neurons showed direction selectivity around the time of stimulus presentation (Johnson et al., 1996). Neurons with reaching-related activity have been found to encode both stimulus features, such as location and direction of stimulus motion (Eskander and Assad, 1997, Soc. Neurosci., abstract) and motor parameters (Andersen et al., 1997). The existence of visual neurons selective for stimuli within reaching distance suggests that area MIP contributes to the construction of a spatial representation designed to control arm movements (Colby and Duhamel, 1991). Area MIP may be the source of the spatial information used by frontal cortex to guide reaching movements.

The spatial reference frame in area MIP is dynamic, reflecting the fact that reaching-related representations must be plastic enough to accommodate expansions of reach space. A tennis player experiences the racquet as an extension of his or her arm, and some intriguing recent experiments suggest that bimodal neurons likewise extend their visual receptive fields when the monkey uses a tool. Iriki et al. (1996) trained monkeys to use a rake to retrieve distant objects and mapped visual receptive fields before and immediately after tool use. While the somatosensory receptive fields were unchanged, the visual receptive fields expanded when the monkey used the rake as an extension of its hand. The authors interpret this as a change in the body image, or schema: the enlargement of the visual receptive field reflects the neural correlate of a representation of the hand that now incorporates the tool. The visual receptive fields return to their original size within a few minutes after tool use is discontinued, and they do not expand at all if the monkey simply holds the rake without intending to use it. These rapid changes in visual receptive field size indicate that the connections that support the expansion must be in place all along. These MIP neurons, like those in area LIP, have access to visual information well beyond the immediately apparent receptive field.

Intended motor actions have an impact on receptive fields and spatial representation in both areas MIP and LIP. These results underscore the importance of looking at the influence of behavior on sensory representations. In both cases, the changes in spatial representation presumably reflect the impact of feedback projections from frontal to parietal cortex (Johnson et al., 1996). We usually think of perception as leading to action. Visual signals arriving in cortex are analyzed and processed



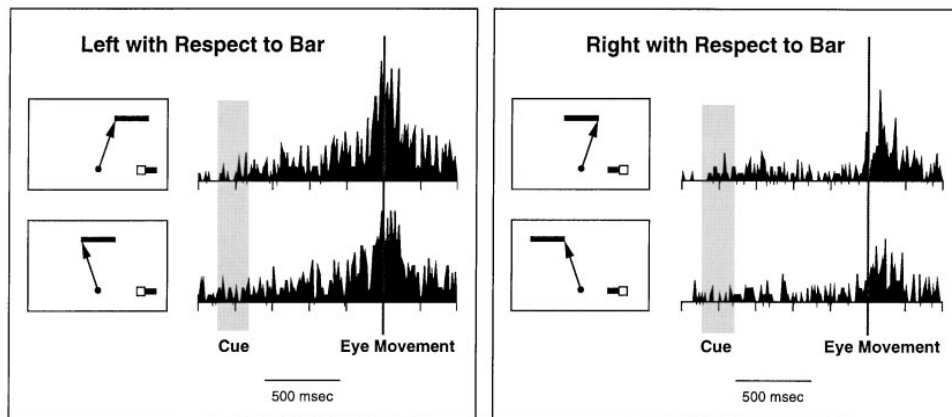


Figure 5. Object-Centered Direction Selectivity in SEF

Responses of one SEF neuron in four conditions. In each condition, the monkey is instructed by a cue (small bar with white dot at one end) to saccade to the left or right end of a target bar. The cue appears briefly (onset indicated by vertical shaded bar) and is followed by a variable delay period during which the monkey maintains central fixation. At the end of the delay, a target bar appears at one of three locations above the fixation point and the monkey saccades to one end of it. Histograms are aligned on the onset of the saccade. The two panels on the left show strong activity during the delay period and the saccade to the left end of the bar, regardless of whether this required a leftward or a rightward eye movement. The two panels on the right show that much less activity was evoked when the monkey made identical eye movements directed toward the right end of the target bar. The firing rate depended on the object-centered direction of the response. Adapted from Olson and Gettner, 1995.

through multiple stages, objects are recognized and locations identified, a decision of some kind is made, and an action is generated. This process is generally conceived of as information moving forward through a system whose output, a motor act, represents the end of the process. Equally important, however, may be the reverse process by which the output is fed back to earlier stages, allowing action to influence perception.

#### Grasp-Related Spatial Representation

The evidence for a grasp-related representation comes from two newly identified regions in the intraparietal sulcus. This representation is different from those described above in that the spatial dimension being represented is the desired shape of the hand rather than its position in egocentric space. Visual neurons in the caudal intraparietal sulcus (Kusunoki et al., 1993, *Soc. Neurosci.*, abstract; Shikata et al., 1996) and in the anterior intraparietal area (area AIP) (Sakata et al., 1995) are sensitive to the shape and orientation of objects, while motor neurons are activated in conjunction with specific hand movements. In a memory-guided reaching task, these neurons are most strongly activated when the monkey is remembering an object with the neuron's preferred object shape (Murata et al., 1996). Reversible inactivation of area AIP interferes with the monkey's ability to shape its hand appropriately for grasping an object but does not produce a deficit in reaching per se (Gallese et al., 1994). In summary, this area has a very specific, action-oriented spatial representation dedicated to the visual guidance of grasping with the hand. This representation is used by premotor cortex to control hand shape and grip (Jeannerod et al., 1995; Gallese et al., 1997). In contrast to the object recognition functions of neurons in ventral stream visual areas such as inferotemporal cortex, these AIP neurons are involved

in constructing an action-oriented representation that translates visual information into motor action.

#### Object-Centered Spatial Representation

Actions are directed toward objects in the environment and toward specific locations on an object. Picking up your coffee cup requires that you locate both the cup in egocentric space and the handle in relation to the cup. The spatial reference frame that guides such movements is not limited to the egocentric representations described above. Evidence from frontal cortex demonstrates that single neurons can encode movement direction relative to the object itself (Olson and Gettner, 1995). The supplementary eye field neuron illustrated in Figure 5 is selective for the object-centered direction of an eye movement: the neuron is strongly active for eye movements directed to the left end of a bar but much less active for eye movements directed to the right end of a bar. This is true even though the physical direction of the eye movement is held constant. This surprising result indicates that neurons can make use of quite abstract spatial reference frames. Object-centered spatial information could potentially guide arm movements as well as eye movements. Additionally, neuropsychological evidence indicates that an object-centered reference frame is used to direct attention: some patients exhibit object-centered neglect after parietal lobe damage (Behrmann and Moscovitch, 1994; Behrmann and Tipper, 1994; Tipper and Behrmann, 1996).

#### Conclusions

The primary insight gained from physiological studies is that our unitary experience of space emerges from a diversity of spatial representations. Objects and locations are represented relative to multiple reference frames. The existence of several independent spatial

representations seems counterintuitive, but the paradox is no deeper than it is for the visual system, where separate populations of neurons encode the color, shape, and motion of a single object. The binding problem—how perceptual unity is achieved from neural multiplicity—has yet to be solved for either vision or spatial awareness.

Why should different populations of neurons encode different aspects of space? The essential answer is that parietal and frontal cortex construct multiple, action-oriented spatial representations in order to serve distinct attentional and sensorimotor goals. Several of these representations transform sensory information from the coordinates of specific receptor surfaces to the coordinates of particular motor effectors: the eye, head, arm, or hand. Neurons within a single cortical area may participate in multiple spatial representations. Neurons in area VIP, for example, contribute to both eye-centered and head-centered representations, in a manner analogous to the participation of hippocampal place field neurons in multiple spatial maps.

Egocentric spatial representations are dynamically updated in conjunction with self-generated movements, including eye movements (area LIP) and even tool use (area MIP). The mechanisms that underlie updating of spatial representations presumably reflect the influence of feedback from frontal cortex to parietal cortex. Effector-centered representations can also incorporate information about object shape and orientation (area AIP), properties normally associated with ventral stream processing, so as to guide actions in space precisely.

Finally, cortical representations of space are not limited to egocentric reference frames. Neurons in frontal cortex construct an allocentric spatial representation in which locations are coded relative to an object of interest. Object-centered representations are potentially useful for acting on, paying attention to, or remembering particular locations as defined with respect to a salient object.

Neuropsychological studies tell us that we use multiple spatial reference frames to perceive and act on the world around us. Physiological studies of parietal and frontal cortex are beginning to show us how these representations are constructed.

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#### References

Andersen, R.A., Bracewell, R.M., Barash, S., Gnadt, J.W., and Fogassi, L. (1990). Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *J. Neurosci.* *10*, 1176–1196.

Andersen, R.A., Snyder, L.H., Bradley, D.C., and Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annu. Rev. Neurosci.* *20*, 303–330.

Arbib, M.A. (1991). Interaction of multiple representations of space in the brain. In *Brain and Space*, J. Paillard, ed. (Oxford: Oxford University Press), pp. 379–403.

Barash, S., Bracewell, R.M., Fogassi, L., Gnadt, J.W., and Andersen, R.A. (1991). Saccade-related activity in the lateral intraparietal area. I. Temporal properties. *J. Neurophysiol.* *66*, 1095–1108.

Behrmann, M., and Moscovitch, M. (1994). Object-centered neglect in patients with unilateral neglect: effects of left-right coordinates of objects. *J. Cog. Neurosci.* *6*, 1–16.

Behrmann, M., and Tipper, S.P. (1994). Object-based attentional mechanisms: evidence from patients with unilateral neglect. In *Attention and Performance*, Vol. 15, C. Umiltà and M. Moscovitch, eds. (Cambridge, MA: MIT Press), pp. 351–375.

Bisiach, E., and Vallar, G. (1988). Hemineglect in humans. In *Handbook of Neuropsychology*, Vol. 1, F. Boller and J. Grafman, eds. (Amsterdam: Elsevier), pp. 195–222.

Bisiach, E., Perani, D., Vallar, G., and Berti, A. (1986). Unilateral neglect: personal and extra-personal. *Neuropsychologia* *24*, 759–767.

Bremmer, F., Duhamel, J.-R., Ben Hamed, S., and Graf, W. (1997). The representation of movement in near extra-personal space in the macaque ventral intraparietal area (VIP). In *Parietal Lobe Contributions to Orientation in 3 D Space*, P. Thier and H.-O. Karnath, eds. (Heidelberg: Springer-Verlag), pp. 619–631.

Brotchie, P.R., Andersen, R.A., Snyder, L.H., and Goodman, S.J. (1995). Head position signals used by parietal neurons to encode locations of visual stimuli. *Nature* *375*, 232–235.

Bushnell, M.C., Goldberg, M.E., and Robinson, D.L. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. *J. Neurophysiol.* *46*, 755–772.

Caminiti, R., Johnson, P.B., Galli, C., Ferraina, S., and Burnod, Y. (1991). Making arm movements within different parts of space: the premotor and motor cortical representations of a coordinate system for reaching to visual targets. *J. Neurosci.* *11*, 1182–1197.

Caminiti, R., Ferraina, S., and Johnson, P.B. (1996). The sources of visual information to the primate frontal lobe: a novel role for the superior parietal lobule. *Cereb. Cortex* *6*, 319–328.

Colby, C.L., and Duhamel, J.-R. (1991). Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. *Neuropsychologia* *29*, 517–537.

Colby, C.L., and Duhamel, J.-R. (1996). Spatial representations for action in parietal cortex. *Cog. Brain Res.* *5*, 105–115.

Colby, C.L., Gattass, R., Olson, C.R., and Gross, C.G. (1988). Topographic organization of cortical afferents to extrastriate visual area PO in the macaque: a dual tracer study. *J. Comp. Neurol.* *269*, 392–413.

Colby, C.L., Duhamel, J.-R., and Goldberg, M.E. (1993a). The analysis of visual space by the lateral intraparietal area of the monkey: the role of extraretinal signals. In *Progress in Brain Research*, Vol. 95, T.P. Hicks, S. Molotchnikoff, and T. Ono, eds. (Amsterdam: Elsevier), pp. 307–316.

Colby, C.L., Duhamel, J.-R., and Goldberg, M.E. (1993b). Ventral intraparietal area of the macaque: anatomic location and visual response properties. *J. Neurophysiol.* *69*, 902–914.

Colby, C.L., Duhamel, J.-R., and Goldberg, M.E. (1995). Oculocentric spatial representation in parietal cortex. *Cereb. Cortex* *5*, 470–481.

Colby, C.L., Duhamel, J.-R., and Goldberg, M.E. (1996). Visual, presaccadic and cognitive activation of single neurons in monkey lateral intraparietal area. *J. Neurophysiol.* *76*, 2841–2852.

Cowey, A., Small, M., and Ellis, S. (1994). Left visuo-spatial neglect can be worse in far than near space. *Neuropsychologia* *32*, 1059–1066.

Driver, J., and Halligan, P.W. (1991). Can visual neglect operate in object-centered coordinates? An affirmative single case study. *Cog. Neuropsychol.* *8*, 475–496.

Duhamel, J.-R., and Brouchon, M. (1990). Sensorimotor aspects of unilateral neglect: a single case analysis. *Cog. Neuropsychol.* *7*, 57–74.

Duhamel, J.-R., Colby, C.L., and Goldberg, M.E. (1991). Congruent representation of visual and somatosensory space in single neurons of monkey ventral intraparietal cortex area (area VIP). In *Brain and*



- Space, J. Paillard, ed. (Oxford: Oxford University Press), pp. 223–236.
- Duhamel, J.-R., Colby, C.L., and Goldberg, M.E. (1992a). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255, 90–92.
- Duhamel, J.-R., Goldberg, M.E., FitzGibbon, E.J., Sirigu, A., and Grafman, J. (1992b). Saccadic dysmetria in a patient with a right frontoparietal lesion: the importance of corollary discharge for accurate spatial behavior. *Brain* 115, 1387–1402.
- Duhamel, J.-R., Bremmer, F., BenHamed, S., and Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389, 845–848.
- Duhamel, J.-R., Colby, C.L., and Goldberg, M.E. (1998). Ventral intraparietal area of the macaque: convergent visual and somatic response properties. *J. Neurophysiol.* 79, 126–136.
- Farah, M.J., Brunn, J.L., Wong, A.B., Wallace, M.A., and Carpenter, P.A. (1990). Frames of reference for allocating attention to space. *Cog. Neuropsychol.* 28, 335–347.
- Fogassi, L., Gallese, V., di Pellegrino, G., Fadiga, L., Gentilucci, M., Luppino, G., Matelli, M., Pedotti, A., and Rizzolatti, G. (1992). Space coding by premotor cortex. *Exp. Brain Res.* 89, 686–690.
- 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.
- Gallese, V., Murata, A., Kaseda, M., Niki, N., and Sakata, H. (1994). Deficit of hand preshaping after muscimol injection in monkey parietal cortex. *Neuroreport* 5, 1525–1529.
- Gallese, V., Fadiga, L., Fogassi, L., Luppino, G., and Murata, A. (1997). A parieto-frontal circuit for hand grasping movements in the monkey: evidence from reversible inactivation experiments. In *Parietal Lobe Contributions to Orientation in 3 D Space*, P. Thier and H.-O. Karnath, eds. (Heidelberg: Springer-Verlag), pp. 619–631.
- Galletti, C., Fattori, P., Kutz, D.F., and Battaglini, P.P. (1997). Arm movement-related neurons in the visual area V6A of the macaque superior parietal lobule. *Eur. J. Neurosci.* 9, 410–413.
- Gazzaniga, M., and Ladavas, E. (1987). Disturbances in spatial attention following lesion or disconnection of the right parietal lobe. In *Neurophysiological and Neuropsychological Aspects of Spatial Neglect*, M. Jeannerod, ed. (Amsterdam: Elsevier), pp. 203–213.
- Gentilucci, M., Scandolara, C., Pigarev, I.N., and Rizzolatti, G. (1983). Visual responses in the postarcuate cortex (area 6) of the monkey that are independent of eye position. *Exp. Brain Res.* 50, 464–468.
- 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.
- Gnadt, J.W., and Andersen, R.A. (1988). Memory related motor planning activity in posterior parietal cortex of macaque. *Exp. Brain Res.* 70, 216–220.
- Goldberg, M.E., and Bruce, C.J. (1990). Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *J. Neurophysiol.* 64, 489–508.
- Goldberg, M.E., Colby, C.L., and Duhamel, J.-R. (1990). The representation of visuomotor space in the parietal lobe of the monkey. *Cold Spring Harbor Symp. Quant. Biol.* 60, 729–739.
- Graziano, M.S.A., Yap, G.S., and Gross, C.G. (1994). Coding of visual space by premotor neurons. *Science* 266, 1054–1056.
- Graziano, M.S., Hu, X.T., and Gross, C.G. (1997). Visuospatial properties of ventral premotor cortex. *J. Neurophysiol.* 77, 2268–2292.
- Gross, C.G., and Graziano, M.S.A. (1995). Multiple representations of space in the brain. *Neuroscientist* 1, 43–50.
- Halligan, P.W., and Marshall, J.C. (1991). Left neglect for near but not far space in man. *Nature* 350, 498–500.
- Heide, W., Blankenburg, M., Zimmermann, E., and Kompf, D. (1995). Cortical control of double-step saccades: implications for spatial orientation. *Ann. Neurol.* 38, 739–748.
- Heilman, K.M., Watson, R.T., and Valenstein, E. (1985). Neglect and related disorders. In *Clinical Neuropsychology*, K.M. Heilman and E. Valenstein, eds. (Oxford: Oxford University Press), pp. 131–150.
- Helmholtz, H. (1924/1866). *Treatise on Physiological Optics*. (New York: Dover).
- Iriki, A., Tanaka, M., and Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* 7, 2325–2330.
- Jeannerod, M., Arbib, M.A., Rizzolatti, G., and Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci.* 18, 314–320.
- Johnson, P.B., Ferraina, S., and Caminiti, R. (1993). Cortical networks for visual reaching. *Exp. Brain Res.* 97, 361–365.
- Johnson, P.B., Ferraina, S., Bianchi, L., and Caminiti, R. (1996). Cortical networks for visual reaching: physiological and anatomical organization of frontal and parietal lobe arm regions. *Cereb. Cortex* 6, 102–119.
- Karnath, H.O., Schenkel, P., and Fischer, B. (1991). Trunk orientation as the determining factor of the ‘contralateral’ deficit in the neglect syndrome and as the physical anchor of the internal representation of body orientation in space. *Brain* 114, 1997–2014.
- Krauzlis, R.J., Basso, M.A., and Wurtz, R.H. (1997). Shared motor error for multiple movements. *Science* 276, 1693–1695.
- Lacquaniti, F., Guigon, E., Bianchi, L., Ferraina, S., and Caminiti, R. (1995). Representing spatial information for limb movement: role of area 5 in the monkey. *Cereb. Cortex* 5, 391–409.
- Milner, A.D., and Goodale, M.A. (1995). *The Visual Brain in Action*. (Oxford: Oxford University Press).
- Moscovitch, M., and Behrmann, M. (1994). Coding of spatial information in the somatosensory system: evidence from patients with neglect following parietal lobe damage. *J. Cog. Neurosci.* 6, 151–155.
- Murata, A., Gallese, V., Kaseda, M., and Sakata, H. (1996). Parietal neurons related to memory-guided hand manipulation. *J. Neurophysiol.* 75, 2180–2186.
- Olson, C.R., and Gettner, S.N. (1995). Object-centered direction selectivity in the macaque supplementary eye field. *Science* 269, 985–988.
- Olson, C.R., and Gettner, S.N. (1996). Representation of object-centered space in the primate frontal lobe. *Cog. Brain Res.* 5, 147–156.
- Pizzamiglio, L., Cappa, S., Vallar, G., Zoccolotti, P., Bottini, G., Ciurli, P., Guargua, C., and Antonucci, G. (1989). Visual neglect for far and near extra-personal space in humans. *Cortex* 25, 471–477.
- Rizzolatti, G., Scandolara, C., Matelli, M., and Gentilucci, M. (1981a). Afferent properties of periarculate neurons in macaque monkeys. I. Somato-sensory responses. *Behav. Brain Res.* 2, 125–146.
- Rizzolatti, G., Scandolara, C., Matelli, M., and Gentilucci, M. (1981b). Afferent properties of periarculate neurons in macaque monkeys. II. Visual responses. *Behav. Brain Res.* 2, 147–163.
- Rizzolatti, G., Riggio, L., and Sheliga, B.M. (1994). Space and selective attention. In *Attention and Performance*, Vol. 15, C. Umiltà and M. Moscovitch, eds. (Cambridge, MA: MIT Press), pp. 231–265.
- Rizzolatti, G., Fogassi, L., and Gallese, V. (1997). Parietal cortex: from sight to action. *Curr. Opin. Neurobiol.* 7, 562–567.
- Robinson, D.L., Goldberg, M.E., and Stanton, G.B. (1978). Parietal association cortex in the primate: sensory mechanisms and behavioral modulation. *J. Neurophysiol.* 41, 910–932.
- Sakata, H., Taira, M., Murata, A., and Mine, S. (1995). Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cereb. Cortex* 5, 429–438.
- 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.
- Shikata, E., Tanaka, Y., Nakamura, H., Taira, M., and Sakata, H. (1996). Selectivity of the parietal visual neurons in 3D orientation of surface of stereoscopic stimuli. *Neuroreport* 7, 2389–2394.
- Sirigu, A., Duhamel, J.R., Cohen, L., Pillon, B., Dubois, B., and Agid, Y. (1996). The mental representation of hand movements after parietal cortex damage. *Science* 273, 1564–1568.
- Stanton, G.B., Bruce, C.J., and Goldberg, M.E. (1995). Topography of projections to posterior cortical areas from the macaque frontal eye fields. *J. Comp. Neurol.* 353, 291–305.

Stein, J.F. (1992). The representation of egocentric space in the posterior parietal cortex. *Behav. Brain Sci.* 15, 691–700.

Thier, P., and Andersen, R.A. (1996). Electrical stimulation suggest two different forms of representation of head-centered space in the intraparietal sulcus of rhesus monkeys. *Proc. Natl. Acad. Sci. USA* 93, 4962–4967.

Tipper, S.P., and Behrmann, M. (1996). Object-centered not scene-based visual neglect. *J. Exp. Psychol. [Hum. Percept.]* 22, 1261–1278.

Tipper, S.P., Lortie, C., and Baylis, G.C. (1992). Selective reaching: evidence for action-centered attention. *J. Exp. Psychol. [Hum. Percept.]* 18, 891–905.

Umeno, M.M., and Goldberg, M.E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *J. Neurophysiol.* 78, 1373–1383.