SPACE AND ATTENTION IN PARIETAL CORTEX

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ABSTRACT

The space around us is represented not once but many times in parietal cortex. These multiple representations encode locations and objects of interest in several egocentric reference frames. Stimulus representations are transformed from the coordinates of receptor surfaces, such as the retina or the cochlea, into the coordinates of effectors, such as the eye, head, or hand. The transformation is accomplished by dynamic updating of spatial representations in conjunction with voluntary movements. This direct sensory-to-motor coordinate transformation obviates the need for a single representation of space in environmental coordinates. In addition to representing object locations in motoric coordinates, parietal neurons exhibit strong modulation by attention. Both top-down and bottom-up mechanisms of attention contribute to the enhancement of visual responses. The saliance of a stimulus is the primary factor in determining the neural response to it. Although parietal neurons represent objects in motor coordinates, visual responses are independent of the intention to perform specific motor acts.

INTRODUCTION

Space is a supramodal construct not limited to a specific sensation. We can estimate an object's spatial location from many different sensory cues, but only with our own movement can the accuracy of that estimation be determined. Although space must be calculated from sensation and calibrated by movement, it is not necessarily linked to any specific sensation or movement. Thus we can identify a spatial location by sight, sound, or touch, and we can look at it or reach for it with either hand. Even Shakespeare understood this: In *King Lear* Regan invites the newly blinded Gloucester to "smell his way to Dover" (Act III, scene vii). The nature of the brain's spatial representation has been the subject of much debate (see Stein 1992), though the parietal lobe is considered crucial for that representation (Critchley 1953). In this review, we consider how space is represented in the parietal cortex of humans and monkeys, and how that representation is related to the generation of movement and to the more general process of visuospatial attention.

MULTIPLE REPRESENTATIONS OF SPACE IN PARIETAL CORTEX

The traditional view of the representation of space, supported by subjective experience, is that we construct a single spatial map of the world in which objects and actions are represented in a unitary framework. The alternative view holds that the brain constructs multiple spatial representations with each representation linked to a different action or region of space (Arbib 1991, Colby & Duhamel 1991, 1996; Fogassi et al 1996; Graziano et al 1994; Jeannerod et al 1995). While each spatial representation may be related to a specific class of actions, it is not clear whether the parietal lobe actually plans those actions (Snyder et al 1997) or only provides the sensory substrate for them (Goodale & Milner 1992).

Behavioral and neuropsychological studies in humans indicate that multiple spatial reference frames are used to guide behavior and that parietal cortex is central to the construction of these representations. Patients with lesions of the parietal lobe exhibit a variety of spatial deficits. The most striking of these is neglect, the tendency to ignore objects in the half of space opposite the side of the lesion (Bisiach & Vallar 1988, Heilman 1979). 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, including retinocentric, body-centered, and environment-centered. 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 peripersonal space, while responding normally to distant stimuli, or vice versa (Bisiach et al 1986, Cowey et al 1994, Halligan & Marshall 1991). Distance-specific neglect may be apparent only when the subject must produce a motor response to the stimulus, and not when spatial perception alone is tested (Pizzamiglio et al 1989).

The variety of deficits observed following parietal lobe damage suggests that parietal cortex must contain more than one kind of spatial representation. Physiological and anatomical studies in monkeys have provided direct evidence that parietal cortex contains several separate functional areas and multiple representations of space (Andersen et al 1997; Caminiti et al 1996; Colby & Duhamel 1991, 1996; Colby et al 1988; Jeannerod et al 1995; Lacquaniti et al 1995; Rizzolatti et al 1997; Stein 1992) (Figures 1 and 2).

The anatomical connections between parietal areas and their cortical targets provide some insight into the spatial reference frames served. Parietal cortical areas are strongly linked with areas of prefrontal cortex, premotor cortex, and the frontal and supplementary eye fields, which themselves encode object locations in relation to a variety of reference frames (Gentilucci et al 1983; Graziano et al 1994, 1997; Rizzolatti et al 1981b). These spatial reference frames have been
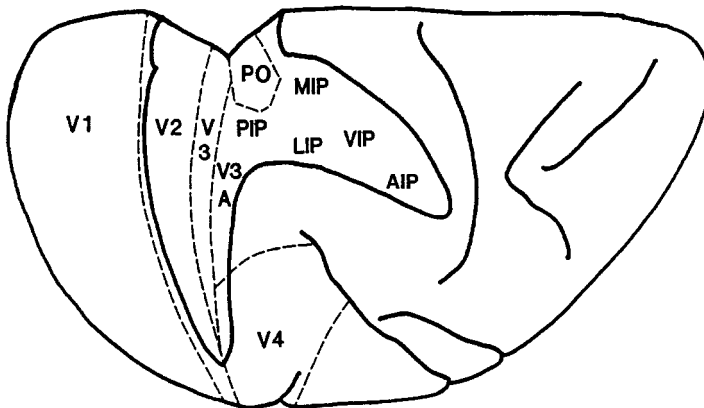

Figure 1 Location of visually responsive areas in macaque cortex. In this dorsal view of the right hemisphere, the lunate and intraparietal sulci are opened up to show the locations of several extrastriate areas and visually responsive areas within the intraparietal sulcus. Visual areas V2, V3, and V3A are shown in the lunate sulcus. PO, the parieto-occipital area; PIP, the posterior intraparietal area; MIP, the medial intraparietal area; LIP, the lateral intraparietal area; VIP, the ventral intraparietal area; and AIP, the anterior intraparietal area. Adapted from Colby et al (1988).
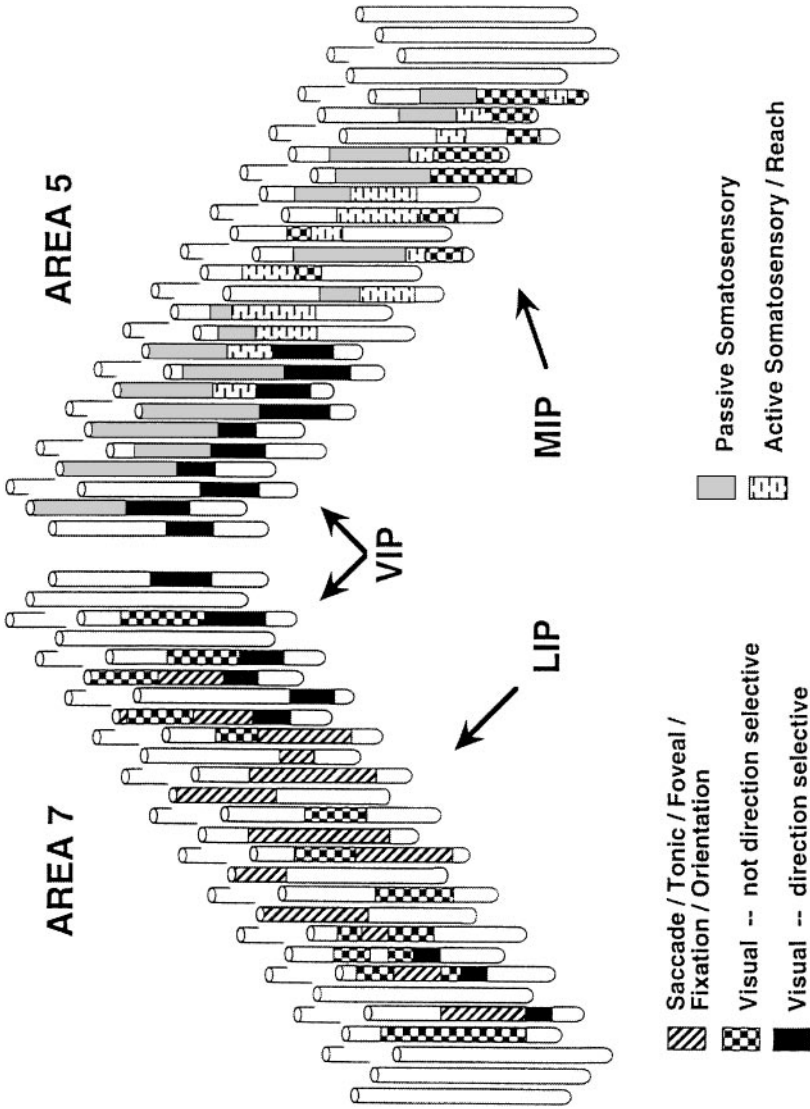
Figure 2 Distribution of neural response properties in the intraparietal sulcus. The anterior part of the sulcus is shown at the *top* of the figure. The posterior part of the sulcus is shown at the *bottom*, where the banks of the sulcus have been separated. Each column depicts responses recorded along a single 10 mm penetration through the lateral or medial bank. Penetrations are spaced 1 mm apart. Adapted from Colby & Duhamel (1991).

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). The following sections describe the evidence for multiple spatial representations in parietal cortex.

VIP REPRESENTS PERIORAL SPACE

Neurons in the ventral intraparietal (VIP) area are strongly visually responsive, yet most can also be excited by tactile stimuli. The tactile receptive fields are generally restricted to the head and face, and the visual and tactile receptive fields match in size and location. In a monkey fixating a central point, a neuron that responds to a visual stimulus in the upper left quadrant also responds to a tactile stimulus applied to the upper left portion of the face. The fovea of the visual representation corresponds to the mouth of the tactile representation. Neurons with visual receptive fields near the fovea have tactile receptive fields close to the mouth, indicating that the maps are aligned with respect to the most sensitive regions of the receptor surfaces. Tactile and visual receptive fields also match with respect to direction preference: A neuron that responds preferentially to a visual stimulus moving in one direction relative to the fovea also responds preferentially to a stimulus moving across the tactile receptive field in the same direction relative to the mouth (Figure 3).

VIP neurons contribute to more than one spatial representation. Visual receptive fields range from purely retinocentric to purely head-centered when studied in a head-fixed monkey (Duhamel et al 1997). In addition, some VIP neurons are sensitive to vestibular stimulation, encoding motion of the head in the world (Bremmer et al 1997). Some bimodal neurons in VIP link gaze-independent visual receptive fields with tactile receptive fields on the face. The neuron illustrated in Figure 4 has a tactile receptive field on the mouth, and responds to visual stimuli moving toward its tactile receptive field. The response is independent of gaze, so that a stimulus with given retinal trajectory only excites the neuron when the object's spatial trajectory approaches the tactile receptive field. This pattern of response indicates that the neuron does not code the stimulus 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 codes information about space in a head-centered frame: It responds to a tactile receptive field or an object in the visual world approaching that receptive field.

One function of the head-centered representation in area VIP may be to specify goals for movements of the head, lips, and tongue and facilitate reaching with the mouth. Further evidence for this view comes from an unusual class of neurons that respond only to visual stimuli presented at very close range, within 5 cm of the face (Colby et al 1993). These ultranear neurons are equally well activated
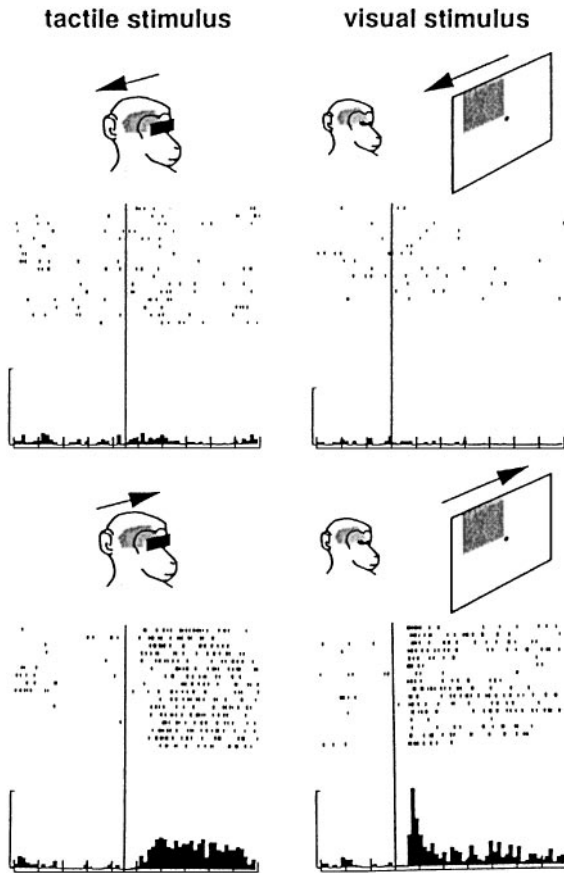
Figure 3   Correspondence of visual and tactile receptive fields in area VIP of the monkey. The rasters in the *left column* show the tactile responses and those in the *right column*, the visual responses of a neuron in VIP. The cartoons show the visual and tactile receptive fields. *Upper row*: nonpreferred direction. *Lower row*: preferred direction. Note the similarity of directional selectivities and the congruence of receptive field location for the two modalities. Reproduced with permission from Duhamel et al (1998).

by monocular or binocular stimulus presentation, and respond to nearby stimuli regardless of the plane of fixation, indicating that their selectivity for nearby stimuli is independent of any given depth cue such as disparity or accommodation. Ultranear neurons in VIP could specify a target for a mouth movement.

VIP projects to F4, a region in premotor cortex that contributes to head and mouth movements. This region contains neurons that resemble those found in VIP: trajectory neurons (Fogassi et al 1992, 1996), bimodal neurons, and

neurons selective for near visual space (Gentilucci et al 1988; Rizzolatti et al 1981a,b). The activity and connections of VIP are consistent with alternative interpretations for the utility of its representation of perioral space. It could have a role in planning action in perioral space. Alternatively, VIP could provide the representation of space that a more sophisticated frontal motor system uses to determine the coordinates for action.

MIP REPRESENTS IMMEDIATE EXTRAPERSONAL SPACE

Neurons in the medial intraparietal (MIP) area are specialized for responding to stimuli within reaching distance and exhibit a range of response properties from purely somatosensory, to bimodal, to purely visual (Colby & Duhamel 1991). These different response types are encountered sequentially as an electrode is moved down the bank of the sulcus toward the fundus (Figure 2). Purely somatosensory neurons usually have receptive fields on the contralateral limbs, most often on the hand. Bimodal neurons respond to both the onset of a stationary visual stimulus and to passive touch. These bimodal neurons are strongly activated when the monkey reaches for a visual target and can be specific both for 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. These cells are reminiscent of the ultranear cells in VIP, but with selectivity for the region of space within reach of the arm.

The change in sensory receptive field properties through the depth of MIP is reflected in the response properties observed in a directional-reaching task. For more dorsal neurons, selectivity for movement direction is prominent around the time of the movement, while more ventral neurons show direction selectivity around the time of stimulus (Johnson et al 1996). Neurons with reaching-related activity have been found to encode stimulus features, such as location and direction of stimulus motion (Eskandar & Assad 1997). Neurons in a medial parietal area maintain the memory of a reach target during the delay period of a memory-guided reach task, but are less active during the delay period of a memory-guided saccade task to the same stimulus (Snyder et al 1997). The presence of visual neurons selective for stimuli within reaching distance suggests that area MIP contributes to the construction of a spatial representation useful for the control of arm movements (Colby & Duhamel 1991). Area MIP may be the source of the spatial information used by premotor cortex for visually guided reaching movements (Caminiti et al 1996).
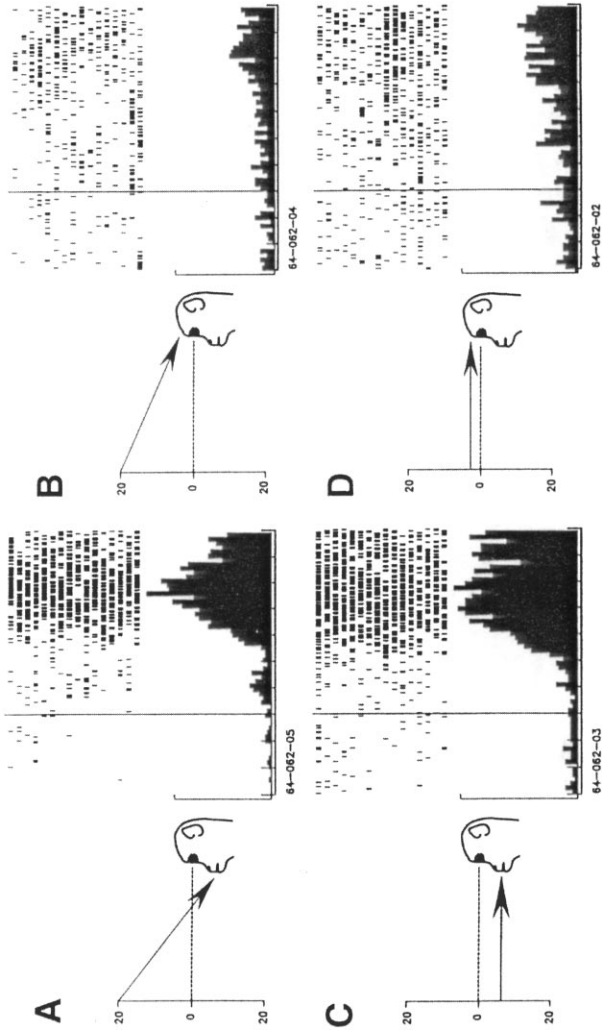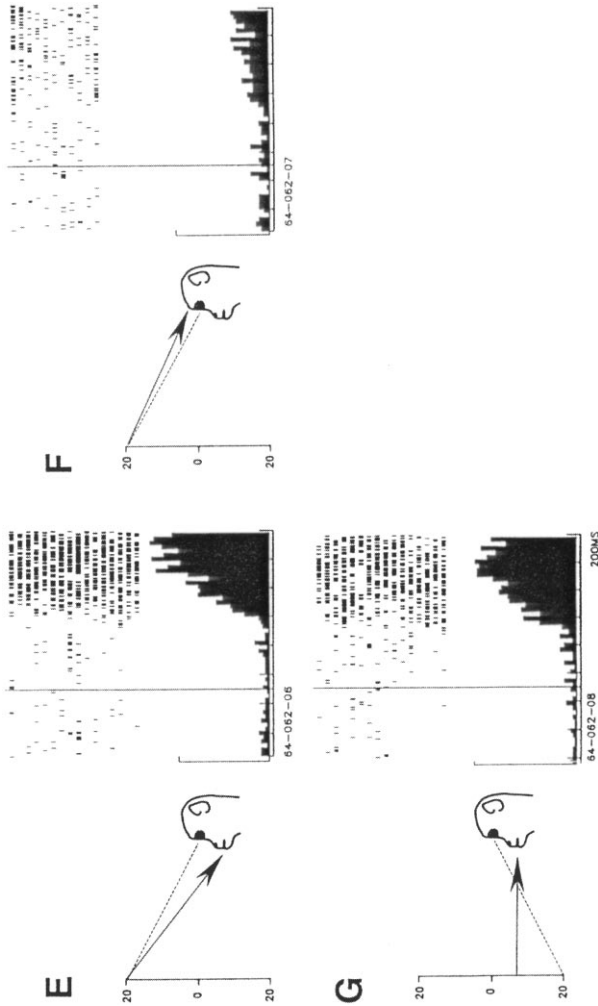
Figure 4   (Continued)

Figure 4   Relationship of a gaze-independent visual receptive field and a tactile receptive field on the face.   This neuron has a tactile receptive field on the muzzle, and responds best to a visual stimulus approaching the mouth from any direction (*A* and *C*) but does not respond to the same visual stimulus on a trajectory toward the brow (*B* and *D*). The neuron responds to visual stimuli moving along a trajectory toward the tactile receptive field regardless of where the monkey is looking when the stimulus starts to move (*E* and *G*). A trajectory similar to the one shown in *E* that approaches the brow is ineffective in driving the neuron (*F*). Adapted from Colby et al (1993).

Receptive fields in area MIP are 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 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). In these experiments, monkeys used a rake to retrieve distant objects, and visual receptive fields were mapped before and immediately after tool use. The visual receptive fields expand when the monkey uses the rake as an extension of its hand, while the somatosensory receptive fields are unchanged. This is interpreted as a change in the body image: The enlargement of the visual receptive field reflects the neural correlate of a hand representation that now incorporates the tool. The visual receptive fields return to their original size within a few minutes after tool use is discontinued. 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 neural connections that allow for the expansion must be in place all along. These MIP neurons, like those in the lateral intraparietal (LIP) area (see below), have access to visual information well beyond the classical receptive field.

AIP CONTRIBUTES TO A GRASP-RELATED SPATIAL REPRESENTATION

Neurons in the anterior intraparietal (AIP) area respond to visual stimuli that the monkey can manipulate. Activity in AIP is different from that described above in that the spatial dimension represented is the desired shape of the hand rather than its position in egocentric space. Visual neurons in both the caudal intra-parietal sulcus and in AIP are sensitive to the shape and orientation of objects (Kusunoki et al 1993, Sakata et al 1995, Shikata et al 1996). Moreover, motor neurons in AIP 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 (Gallese et al 1994). These findings indicate that area AIP has a very specific, action-oriented spatial representation dedicated to the visual guidance of grasping with the hand, and this representation is used by premotor cortex to control hand shape and grip (Gallese et al 1997, Jeannerod et al 1995). In contrast to the object recognition functions of shape-selective neurons in ventral stream visual areas, such as those in inferior temporal cortex, these AIP neurons are involved in constructing an action-relevant representation that translates visual information into a form usable to specify motor action.

LIP REPRESENTS THE SPACE EXPLORED
BY EYE MOVEMENTS

Eye movements are the predominant means by which we explore the world beyond our reach. The contribution of parietal cortex to this exploration has been extensively investigated (Hyvarinen & Poranen 1974, Mountcastle et al 1975). Recent work has focused on neural activity in the lateral intraparietal (LIP) area. In the following sections, we discuss experiments on the significance of neural responses in LIP, and then turn to the spatial representation constructed in LIP.

The Significance of Neural Signals in LIP

LIP neurons respond when a light flashes and a monkey looks at it. This response could represent a visual signal, a motor signal, an attentional signal, or an intentional signal. Introducing a delay between the visual stimulus and the motor response can help to distinguish among these possibilities (Hikosaka & Wurtz 1983). Analysis of neural activity during the distinct time epochs of the delayed saccade task indicates that single neurons carry multiple signals (Barash et al 1991a, Colby et al 1996, Gnadt & Andersen 1988). LIP neurons respond to the appearance of the stimulus, and may maintain activity during the delay and/or discharge around the time of the saccade. For some neurons in LIP, delay period activity increases as a monkey chooses a target for a saccade, and the rate of increase correlates inversely with the difficulty of the decision (Gottlieb et al 1998, Shadlen & Newsome 1996).

Nearly all LIP neurons respond to the appearance of a visual stimulus in the receptive field in a fixation task (Robinson et al 1978). These responses can be behaviorally modulated: About two thirds of the neurons respond at a significantly higher frequency to the appearance of a stimulus that the monkey is going to use for behavior (Figure 5). This increased response to a behaviorally significant stimulus was first observed in the superior colliculus (Goldberg & Wurtz 1972). The enhanced response in LIP is independent of the monkey's intended action: It occurs whether or not the monkey is going to make a saccade to the attended stimulus (Colby et al 1996). The amount of enhancement is similar for either a saccade (the delayed saccade task) or a bar release (the peripheral attention task). This response-independent enhancement is very different from the saccade-specific enhancement found in the frontal eye field (Goldberg & Bushnell 1981) and the superior colliculus (Wurtz & Mohler 1976), where cells give enhanced responses to saccade targets but not to stimuli that signal when the monkey must respond with a hand movement. Because of this dramatic difference between LIP and the more clearly oculomotor frontal eye field and superior colliculus, we have postulated that enhancement in LIP reflects visuospatial attention (Colby et al 1996, Goldberg et al 1990, Kusunoki et al 1997).
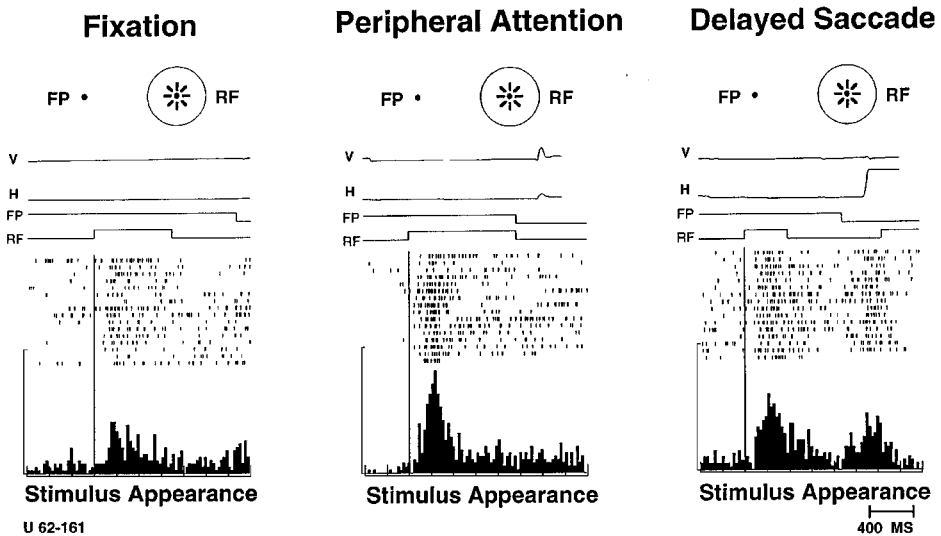
Figure 5   Behavioral enhancement of visual responses in LIP. Each panel shows a cartoon with the locations of the receptive field (RF) and fixation point (FP). Horizontal (H) and vertical (V) eye position traces are shown for a single trial, with the time course of the lights at the fixation point (FP) and the stimulus (RF) shown beneath. The neuron responds when the stimulus appears in its receptive field (*left*, Fixation). The visual response is enhanced when the monkey will respond to the stimulus by making a hand movement when it dims (*center*, Peripheral Attention) or when the monkey will make a saccade to the stimulus (*right*, Delayed Saccade). Note the second burst in the Delayed Saccade Task. This burst was synchronized with saccade onset. This cell also discharged in association with learned saccades in total darkness, when there was no recent stimulus (not shown). Adapted from Goldberg et al (1990).

All of the standard tasks (fixation, delayed saccade, peripheral attention) probe the visual activity of a neuron with the use of a stimulus flashed in the receptive field. There is a systematic confound in the time-honored use of an abruptly appearing stimulus to assess visual responses in awake animals. Psychological analysis indicates that an abrupt onset captures attention (Jonides & Yantis 1988; Yantis & Jonides 1984, 1990, 1996). The appearance of a task-irrelevant stimulus may itself capture attention, regardless of the wishes of the investigator. These results raise the possibility that activity evoked by a suddenly appearing stimulus is primarily an attentional response rather than a purely visual one.

A new task that distinguishes between these alternatives is the stable array task (Gottlieb et al 1998). In this task, the monkey sees a stable array of symbols on a screen in front of him. The symbols do not change at all during the experiment, but remain constantly illuminated and immobile. As the monkey

makes saccades across the stable array, stimuli are brought into and out of receptive fields. Unlike the abruptly appearing stimuli used in most tasks, these stimuli are new only to the receptive field, and not to the visual environment as a whole. When the monkey makes a saccade that brings a stable, non-novel stimulus into the receptive field of a neuron in LIP, the activity evoked by the stimulus is marginal. In contrast, in the fixation task, the same stimulus evokes a strong response when it suddenly appears in the receptive field (Figure 6).
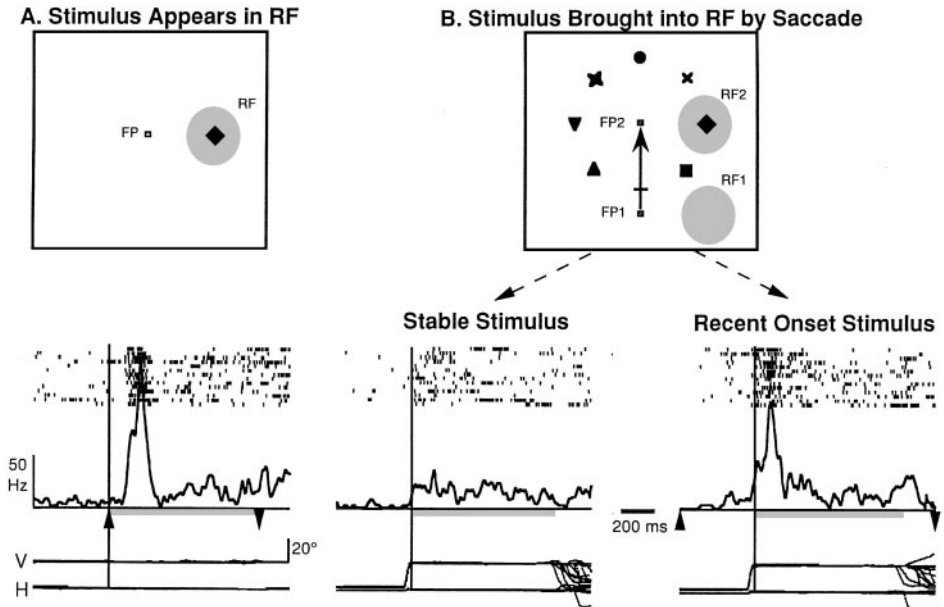
Figure 6 Effect of recent onset on LIP neuronal response. (*A*) Response to the onset of a diamond-shaped stimulus flashed in the receptive field. The cartoon above illustrates the spatial relationship of the fixation point (FP), the stimulus (*diamond*), and an estimate of receptive field (RF). Raster and spike density plots, synchronized on the appearance of the stimulus, are below the cartoon. The eye position traces from each trial illustrated in the raster diagram are superimposed on the vertical (V) and horizontal (H) eye position traces. Stimulus appears at the *up-triangle* and disappears at the *down-triangle*. Note a brisk response roughly 80 ms after the appearance of the stimulus. (*B*) Responses when the stimulus is brought into the receptive field by a saccade. The cartoon above illustrates the array of symbols, which remain stably on the tangent screen in front of the monkey. The trial begins when the monkey fixates FP1. At that time the receptive field lies outside the array. The monkey makes a saccade from FP1 to FP2, which moves the receptive field onto the diamond-shaped stimulus. When the diamond is stable, its arrival in the receptive field is accompanied by a weak response of the neuron that begins at the end of the saccade (Stable Stimulus). When the diamond stimulus flashes immediately before the saccade (Recent Onset Stimulus), the cell discharges almost as intensely as in the flashed stimulus case. Reproduced with permission from Gottlieb et al (1998).

Control tasks indicate that the different responses in these two cases are not due to visual factors, such as the motion of the stimulus across the retina during the saccade or the presence of other stimuli outside the receptive field. In the control task, one member of the array (the one that will be in the receptive field) appears immediately before the saccade. This restores the response to that evoked by the abrupt onset of the stimulus in the receptive field in the fixation task. This result suggests that the on-response to a visual stimulus in the fixation task reflects the attention attracted by the abrupt onset as well as the visual properties of the stimulus. This is in contrast to striate cortex, where neurons respond at high frequencies to stimuli brought into their receptive fields by a saccade (Livingstone et al 1996). The LIP response in the stable array task resembles visual activity in the frontal eye field, where visual neurons respond to a stable stimulus brought into the receptive field only if that stimulus is behaviorally relevant (Burman & Segraves 1994).

The stable array experiment shows that previous LIP studies significantly underestimate the amount of enhancement. If we consider the baseline visual response of neurons to be that elicited when a saccade brings a stable target into the receptive field, then three quarters of LIP neurons exhibit enhancement, and the average increase in activity is more than double. It is also apparent from these experiments that the lesser on-response seen in earlier experiments, in which attention had previously been shifted to the spatial location of the stimulus, should not be considered a true suppression of response, but instead a diminution of enhancement (Robinson et al 1995, Steinmetz et al 1994). The visual response to the appearance of a new stimulus in an already attended spatial location is still greater than the response one would expect when a saccade brings a stable stimulus into the receptive field. One cannot, therefore, consider this diminished on-response as an argument against the role of LIP in the generation of attention (Andersen et al 1997).

Although stable objects in the environment are irrelevant to behavior most of the time, they can be rendered relevant by the demands of a task. You can direct your attention to the clock on the wall when you want to know what the time is, even though it is not a new object. Attention can be directed to a stable object by requiring the monkey to use that object for some sort of behavior. The stable target task (Figure 7) accomplishes this by cueing the monkey to make a saccade to a stable target that itself never changes during the experiment. The monkey first fixates at a location such that the receptive field is outside the array. A cue that matches a member of the array appears briefly. The monkey then makes a saccade to the center of the array, which brings one member of the array into the receptive field. The monkey then makes a second saccade to the stable symbol that matched the cue. Trials in which the cue matches each of the eight symbols are randomly intermixed. When the cue matches the symbol
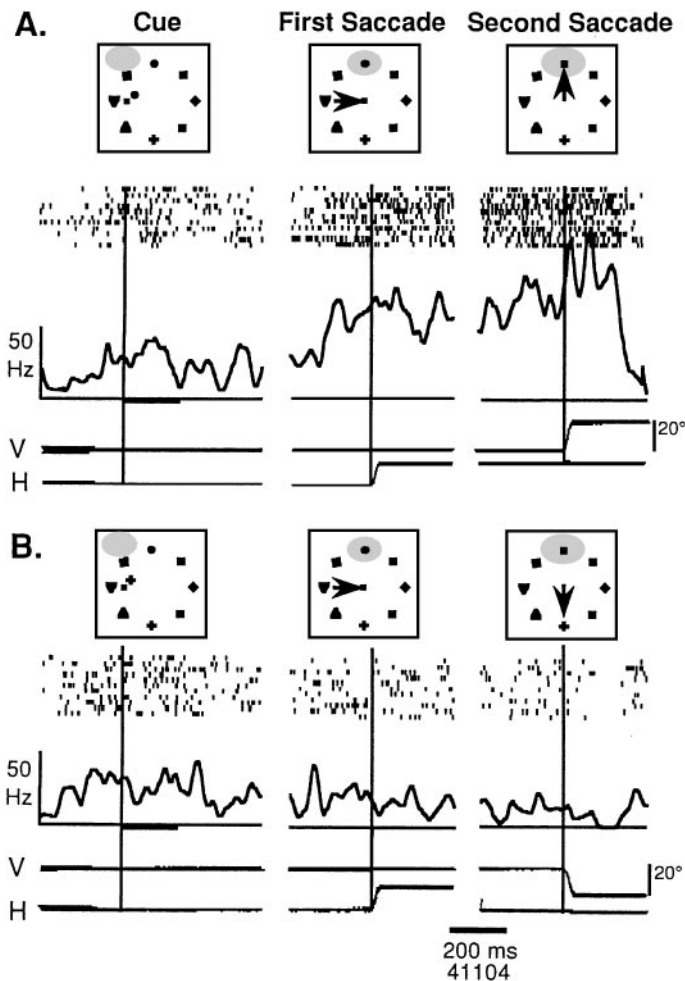
Figure 7 Responses of an LIP neuron during the stable target task. The cartoon above each diagram illustrates the task. The monkey fixates the *small square* which is located so that the receptive field is outside the array. A cue that matches a member of the array (the *circle*) briefly appears near the fixation point. The fixation point steps to the center of the array and the monkey makes a saccade to it. The fixation point then disappears and the monkey makes a second saccade to the member of the array that matches the cue. (*A*) The cue matches the stimulus in the receptive field and the monkey makes a saccade to the stable stimulus in the receptive field. (*B*) The cue matches a stimulus outside the receptive field and the monkey makes a saccade to a stimulus not in the receptive field. The first saccade brings the stimulus into the receptive field in both *A* and *B*. There is no response at the time of cue appearance (*left column*). The neuron does respond around the time of the first saccade when that saccade brings a salient stimulus into the receptive field (*A*) but does not respond when the stimulus is not salient (*B, middle column*). The response to one salient stimulus continues until after the second saccade (*right column*). Adapted from Gottlieb et al (1998).

in the receptive field, the cell begins to discharge around the time of the first saccade. When the cue does not match the symbol in the receptive field, the cell does not discharge. The simplest interpretation of these data is that the stimulus in the receptive field has become salient by virtue of the match, and the neural response reflects the representation of a salient stimulus. Making the stimulus behaviorally relevant has enhanced the response, just as its sudden appearance enhanced the response.

An alternate interpretation is that this activity is related specifically to planning the second saccade. It is well established that LIP neurons exhibit presaccadic activity in delayed saccade tasks, and it is clear that some of this activity is independent of visual stimulation (Colby et al 1996). Some LIP neurons discharge before saccades even in the context of a learned saccade made without any recent visual stimulation, as do movement neurons in the frontal eye field (Bruce & Goldberg 1985). Across the population, the amplitude of presaccadic activity in LIP is less than that of the visual response in the peripheral attention task. This is markedly different from the frontal eye field (FEF), where an entire class of neurons, the movement neurons, exhibit little or no visual activity. These movement neurons provide the bulk of the projection from the FEF to the superior colliculus (Segraves & Goldberg 1987) and pons (Segraves 1992). The purely visual cells in the FEF do not project to the superior colliculus or pons at all. In contrast, a large majority of collicular projection neurons in LIP have significant visual responses (Paré & Wurtz 1997). These observations suggest that the FEF has neurons appropriate for generating motor commands or intentions, while LIP does not.

In order to test whether activity in LIP is better characterized as attentional or intentional, a learned-saccade variant of the stable target task was performed (Figure 8). This task dissociates activity evoked by a saccade target from activity reflecting a planned saccade. In this version of the task, the symbols remain on the screen as in the stable target task. The monkey fixates in the center of the array, the cue appears outside the receptive field, and the monkey makes a saccade to the stimulus in the receptive field when the fixation point disappears. After a block of trials that symbol is removed and the monkey makes the saccade to the spatial location of the now-vanished symbol. For most neurons the activity falls significantly even though the monkey plans and executes the same saccade. Clearly, activity in the stable target task cannot be attributed to the monkey's intention to make the saccade. Maximal activity in the majority of LIP neurons requires a stimulus. That stimulus need not be new, but it must be salient.

Further evidence that activity in LIP reflects salience comes from experiments in which the stimulus evoking the response cannot be construed as a saccade target. In the stable target task described above, the cue that dictated the saccade
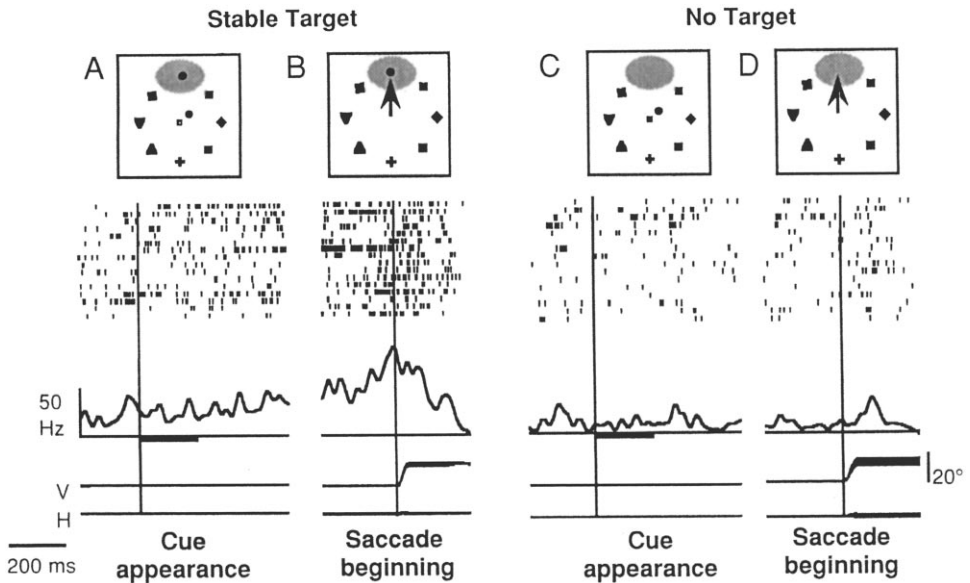
Figure 8   Dependence of activity on the presence of a saccade target (same neuron as in Figure 7.)
(*A* and *B*) The monkey fixates in the center of the array, and a cue appears near the fixation point
matching the stimulus in the receptive field. When the fixation point disappears, the monkey makes a
saccade to the target. Unlike the previous experiment, where saccade direction is randomized, in this
experiment the saccade direction is always into the receptive field. Rasters are shown synchronized
on the cue appearance (*A*) and the beginning of the saccade to the target (*B*). Note that although
there is no response to the cue, the cell becomes active well before the saccade. (*C* and *D*) In the next
block of trials, the symbol in the receptive field is removed from the array and the monkey makes a
saccade to the empty spatial location in the receptive field. Rasters are again shown synchronized
on the cue appearance (*C*) and the beginning of the saccade (*D*). Without a target, the response is
significantly smaller. Reproduced with permission from Gottlieb et al (1998).

was outside the receptive field. It is also possible to place the cue in the receptive
field. In this case, the neuron responds to the cue regardless of the saccade that
the monkey will make. In other words, paying attention to information in the
receptive field drives the neuron no matter what direction of saccade the monkey
is planning.

The results described so far indicate that LIP neurons have sensory responses
that are strongly modulated by the salience of the stimulus regardless of the
particular behavioral response required. The issue of whether LIP neuron ac-
tivity reflects attention to a stimulus or the intention to make a saccade to that
stimulus has also been addressed in two previous studies using the delayed sac-
cade task. In the first, a monkey learned to use a peripheral cue as the signal to

initiate the saccade in a memory-guided delayed saccade task (Platt & Glimcher 1997). When the saccade target was in the receptive field, delay period activity was greater than when the cue was in the receptive field, although the responses to the appearance of either stimulus in the receptive field were equivalent. In the second study, monkeys were trained to make memory-guided reaches or saccades (Snyder et al 1997). In many cells the delay period activity was greater when the monkey had to make a saccade to the target than when it had to reach to it. When the monkey had to make a saccade and reach simultaneously to different targets, delay period activity was often greater when the saccade target was in the receptive field. The authors of both studies conclude that LIP is primarily devoted to saccade generation, and that any response in LIP not related to an overt saccade is in fact related to an intended saccade that was canceled.

There are several problems with this interpretation. The first is that the neurons described in both studies gave vigorous on-responses to stimuli that would never be the targets of saccades. Since any on-response attests to the salience of a target, the on-responses in these tasks must signify some more general property of salience or attention. The second problem is that no experiments have yet established the allocation of attention during a delay. Both groups assert that because the monkey responds to the cue [in the Platt & Glimcher (1997) experiment] or the reach target [in the Snyder et al (1997) experiment], the monkey attends to its spatial location throughout the delay period. However, attention ordinarily moves to the spatial location of a saccade target (Deubel & Schneider 1996, Kowler et al 1995). Furthermore, psychophysical experiments suggest that humans cannot pay attention to two separate spatial locations simultaneously (Joseph & Optican 1996). Therefore, diminished activity when a monkey simultaneously prepares a saccade and a reach in opposite directions does not establish that the neurons are dedicated exclusively to the generation of saccades. Such activity could also arise by default if the monkey attended to the saccade target rather than the reach target when neither target is difficult to localize. Further, as described above, LIP neurons do not predict when or if a saccade will occur. Finally, LIP neurons respond to stimuli that could never be saccade targets, and are often silent before purposive saccades made without a target, in contrast to frontal neurons which are active before learned saccades in total darkness (Bruce & Goldberg 1985). For all these reasons it is difficult to assert that LIP neurons plan saccades. Rather, one could say that their activity selects targets from the environment for possible but easily cancelable saccades. The latter statement is a good definition of visual attention in the primate.

LIP has connections that are suitable for transmitting information about stimulus salience to the oculomotor and visual systems. It has projections to and

from the frontal eye field, and to the intermediate layers of the superior colliculus (Andersen et al 1985, Lynch et al 1985, Schall et al 1995, Stanton et al 1995). These connections are appropriate for transmitting spatial information to the oculomotor system. LIP also has projections to visual areas such as V4, TE, and TEO (Baizer et al 1991, Webster et al 1994) which are known to have activity dependent upon spatial attention (Moran & Desimone 1985), but are not known to be involved in the generation of saccadic eye movements. It also projects to the parahippocampal gyrus (Suzuki & Amaral 1994), which is critical in spatial memory. A signal that is related to the general aspects of visuospatial attention is useful for all of the projection targets of LIP.

We conclude that the function of LIP is the representation of attended or salient spatial locations. The hallmark of neuronal activity in LIP is that, like spatial perception itself, it is not tied to any particular modality. Neurons in LIP respond to salient visual stimuli, but they provide more than an exclusively visual representation because they also respond to attended auditory stimuli (Stricanne et al 1996), respond weakly before saccades without visual targets, and respond even in anticipation of the appearance of a salient target (Colby et al 1996). For the reasons outlined above, neurons in LIP cannot be linked to the planning of any particular movement. This combination of activity suggests that LIP represents the space that we explore best with our eyes—space not constrained to the immediate grasp of our arms or mouth. This representation is limited to attended objects and their locations, and damage to it may cause the neglect described in patients and monkeys with parietal lesions (Critchley 1953, Duhamel et al 1992b, Lynch & McLaren 1989). The next critical problem is to understand the reference frame in which LIP represents attended space.

Spatial Representation in LIP

Neurons in LIP have retinotopic receptive fields. These neurons carry visual, memory, and saccade-related signals that describe stimuli in terms of the distance and direction of the stimulus or saccade location relative to the center of gaze. This retinotopic organization presents a paradox: How can accurate spatial information be derived from retinotopic input? 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 and move accurately in it. 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 an internal image of it. The brain must construct a representation that can compensate for changes in eye position.
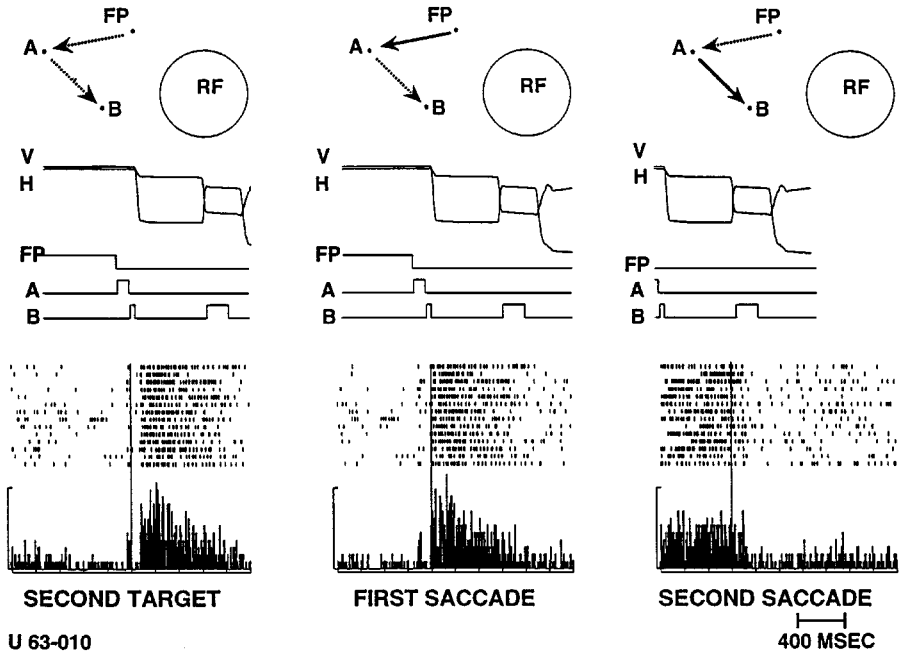
Figure 9   Activity of an LIP neuron in the double-step task. The cartoon shows the geometric arrangement of receptive field, fixation point, and saccade targets. The receptive field is shown relative to the fixation point. The stimuli flash at A and B. Neither is in the receptive field of the neuron. When the monkey is looking at A, the spatial location of B is in the receptive field of the neuron. (*Left*) raster synchronized on the appearance of the B target. (*Middle*) raster synchronized on the first saccade to target A. (*Right*) raster synchronized on the second saccade to target B. The cell discharges after the first saccade and until the second, during the time the receptive field encompasses the spatial location at which the target appeared. This neuron had no presaccadic activity. Adapted from Goldberg et al (1990).

The problem of how neurons maintain an accurate representation of space across eye movements has been studied using the double step task. In this task, two targets are presented sequentially and the subject's task is simply to look at the targets in order (Figure 9). Because the targets are illuminated very briefly (about 100 ms), they are no longer present at the time the eye movements are performed. Programming the first saccade is easy because 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 dimensions of the first saccade, and adjust the direction and amplitude of the second saccade accordingly. Both humans and monkeys can perform this task (Hallett & Lightstone 1976, Mays & Sparks 1980a).

Accurate spatial performance in the double-step task has been used to suggest that the saccadic system has access to the position of the target in head-centered coordinates (Mays & Sparks 1980b, Zee et al 1976). However, no one has yet observed an explicit head-centered signal in the oculomotor system. Instead, all of the higher centers that contribute to target selection and the generation of saccades exhibit a signal that specifies the vanished saccade target in the coordinates of the new fixation [for example, the intermediate layers of the superior colliculus (Mays & Sparks 1980a), the frontal eye field (Goldberg & Bruce 1990), and LIP (Barash et al 1991a,b; Gnadt & Andersen 1988; Goldberg et al 1990)]. Rather than using a head-centered coordinate system, these areas transform visual information about the second target location from retinal coordinates into the motor coordinates appropriate for generating a saccade toward it. In LIP and the frontal eye field, even cells that have only visual activity accomplish this coordinate transformation (Goldberg & Bruce 1990, Goldberg et al 1990). This shows that the transformation from retinal to oculomotor coordinates takes place at the level of the visual signal.

This transformation depends more upon the behavioral context than the actual performance of the movement. Because the double-step task is difficult to perform, monkeys sometimes make mistakes. Analysis of error trials, in which the monkey made a saccade directly to the second target and then to the first target, shows that the neuron responded as though the monkey had acquired the targets in the proper order (Goldberg et al 1990). This result demonstrates that the coordinate transformation depends on a corollary discharge of the intended motor action rather than on an efference copy of the actual signal at the motor neurons.

The coordinate transformation first observed in the double-step experiment is not limited to that rather artificial task. Every time a monkey makes a saccade, the representation of the salient visual world in LIP shifts into a new coordinate system whose origin is the postsaccadic center of gaze (Duhamel et al 1992a). The effect of saccades on the representation of remembered objects demonstrates this most dramatically. The experiment illustrated in Figure 10 shows that the memory trace of a previous stimulus is updated when the eyes move. The activity of a single LIP 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 recent visual stimulus. The unexpected result is shown in the right panel. Here the
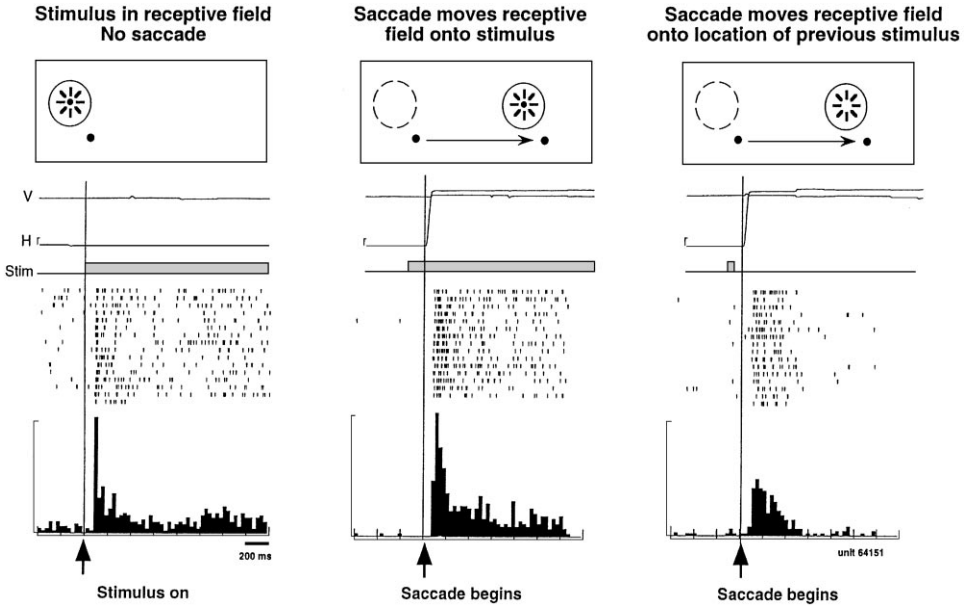
Figure 10 Remapping of visual activity in area LIP. Diagrams show the arrangement of the fixation point, receptive field, stimulus location, and saccade. (*Left*) In the fixation task, the neuron responds to the onset of a stimulus in the receptive field. (*Middle*) The same neuron responds when a saccade moves the receptive field onto the location of a recent stimulus. (*Right*) Response after a saccade moves the receptive field onto a previously stimulated location. The stimulus is flashed on for only 50 ms and is extinguished before the saccade begins. The neuron is responding to the remapped memory trace of the previous stimulus. Control experiments (not shown) indicate that neither the stimulus alone nor the saccade alone can drive the neuron. Adapted from Duhamel et al (1992a).

monkey makes the same saccade but the stimulus appeared for only 50 ms so that it was already extinguished before the saccade began. This means that no stimulus was ever physically present in the receptive field (as determined in a fixation task), yet the cell responds.

We interpret this result as indicating that the representation of the stimulus has been remapped from a coordinate system whose origin is the initial fixation point, to one whose origin is the new fixation point. At the time of stimulus onset, while the monkey is looking at the initial fixation point, the stimulus activates a set of neurons whose receptive fields encompass the stimulated location. Some of these neurons will continue to fire after stimulus disappearance, encoding a memory trace of the location at which the stimulus occurred (Gnadt & Andersen 1988). At the time of the eye movement, the activity evoked by the now-vanished stimulus is passed from the original neurons to a new set of neurons whose receptive fields now encompass the stimulated location.

The neural mechanism underlying this transfer of activity 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 LIP neurons have access to visual information from the entire visual field and not just from the classically defined receptive field. LIP neurons must already have in place the connections that provide input from distant regions of the visual field.

This remapping takes place gradually in the epoch around the saccade. Some neurons actually begin to respond before the saccade to stimuli that will enter the receptive field after the saccade (Duhamel et al 1992a). Such predictive shifts are not unique to LIP. They also occur in the frontal eye field (Umeno & Goldberg 1997) and the intermediate layers of the superior colliculus (Walker et al 1995).

Remapping updates the internal representation of space in conjunction with eye movements so that it always matches the current eye position. Visual information is thereby maintained in eye-centered coordinates. Such a representation is necessary for the guidance of oculomotor responses directed toward the stimulated location. An eye-centered representation has the advantage, compared to a head-centered or world-centered representation, 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 the kind of representation needed for acquiring visual targets.

Recent psychophysical evidence suggests that not only eye movements, but arm movements also utilize an eye-centered reference frame. The performance of humans reaching to remembered targets is more consistent with an eye-centered than a body- or arm-centered reference frame (Henriques et al 1998). Ultimately, however, the visual representation in the premotor system shifts from an eye-centered frame to a head-centered (Boussaoud 1995) or an arm-centered frame in the premotor cortex (Graziano et al 1994). How this shift occurs is currently not well understood.

The remapping process requires a sophisticated calculation to effect a shift of excitation from the original coordinate frame to the postsaccadic coordinate frame. Two different mechanisms have been proposed to account for this process. The first takes advantage of the orbital position modulation of the visual responses observed in many visual areas including LIP, 7a (Andersen et al 1990), V3A (Galletti & Battaglini 1989), V1 (Weyand & Malpeli 1993), and even the lateral geniculate nucleus (Lal et al 1990). In these areas the visual response of many neurons is modulated by the position of the eye in the orbit ("planar gain fields"), although their receptive fields remain retinotopic. A neural network can use eye position and retinotopic information to calculate absolute position in space (Zipser & Andersen 1988). Units with planar gain fields can be found in the hidden layer of such a network. The necessary postsaccadic retinal receptive field can then be calculated from the absolute target position implicit in the network. A second mechanism postulates a dynamic calculation using eye movement information. This mechanism would subtract a vector of the preceding or impending eye movement from the retinal location where the stimulus appeared. The result of this subtraction is the vector from the center of gaze to the spatial location of the stimulus. This mechanism does not ever require an absolute position signal (Goldberg & Bruce 1990).

Clinical evidence favors the latter hypothesis (Duhamel et al 1992b). If remapping underlies spatially accurate behavior, then a lesion in the cortical areas responsible for remapping should manifest itself not as an absolute spatial deficit but as a difficulty in compensating for a previous saccade. This prediction was verified in a case study of a patient who sustained a hemorrhage into the right frontoparietal cortex. The patient had a mild left hemiparesis, mild left visual and somatosensory neglect and a left inferior quadrantanopsia that spared the central $6°$ of the visual field. With the head in a fixed position, she had a directional deficit for saccades between targets presented $5°$ to the left and to the right in a random walk: Leftward saccades were hypometric and had a longer latency than rightward ones. These deficits did not vary with the starting position of the eye: The same spatial location acquired by an accurate rightward saccade would only be approached by a hypometric leftward saccade.

Saccadic accuracy was measured in two versions of the double step task. First, in the slow version of the double step task, the patient was instructed to make sequential saccades to the two targets in the order in which they appeared (Figure 11, *top*). Each target stayed on for 500 msec, so both saccades were visually guided—no memory trace was needed to perform the task accurately. The order of the targets was likewise unimportant. Leftward saccades followed by rightward saccades were just as accurate as the reverse order, although all leftward saccades were somewhat inaccurate.

In the second version, the targets were flashed so briefly that both were gone before any eye movement took place. In this condition, the first saccade was still a visually guided saccade and the patient's performance was accurate for first targets in either the affected field or the good field (Figure 11, *bottom*). The interesting case is performance of the second saccade. To make the correct saccade, the subject must know where the second target appeared relative to the new eye position. This requires taking into account the change in eye position resulting from the first saccade. The patient did this correctly when the first saccade was into the good field: An initial saccade to the right was followed by a reasonably accurate saccade to the left (bottom left panel). The deficit appeared only when the patient made the first saccade into the affected field. An initial saccade to the left reached the first target location but the patient was then completely unable to generate a saccade to the location of the second target (bottom right panel).

This finding is somewhat counterintuitive: The patient failed on saccades in the good direction, to targets that appeared in the good field. Nevertheless, she clearly did not have a general spatial deficit for either field. On trials in which she neglected the first target (in the affected field) and went directly to the second target (in the good field) performance was accurate. Her specific deficit was an inability to calculate the change in target position relative to eye position. She could not compensate for the first saccade when it was in the direction of the affected field. We conclude that she failed to update an internal representation of the stimulus: The memory trace was not remapped following leftward saccades. Although this was only a single case report, the phenomenon has been replicated in a large number of patients and was exhibited only by patients whose lesion included the right posterior parietal cortex and not patients with damage limited to frontal cortex (Heide et al 1995).

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
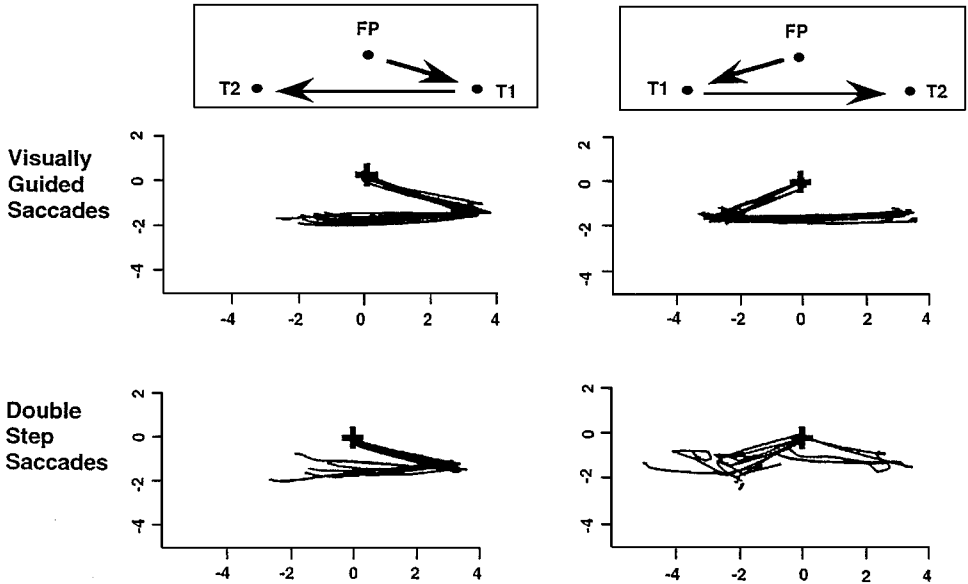
Figure 11   Sequential saccades in a patient with a right frontoparietal lesion. The cartoons (*top row*) show the arrangement of stimuli and saccade directions for the experiments in the columns beneath. The *middle* and *bottom rows* show eye position plotted in horizontal and vertical coordinates. This reproduces the spatial pattern of the eye movements. The subject begins by looking at the fixation point (FP), and makes saccades to T1 and T2 in response to sequential flashes. In the *left column* the stimulus flashes first in the ipsilesional, normal left visual field, and then in the contralateral, affected visual field. In the *right column* the stimulus flashes first in the contralesional, affected visual field and then in the ipsilesional, normal visual field. The *middle row* shows eye movements in the visually guided task, in which the stimuli remain illuminated long enough (500 ms each) for each sequential saccade to be visually guided. The saccades into the normal field are accurate and those into the contralateral field are hypometric, regardless of which direction comes first. The *bottom row* shows eye movement in the true double-step condition, with the T1 flashing for 100 ms and T2 for 80 ms. When the stimulus flashes first in the normal field, the patient makes accurate saccades into the normal field and hypometric saccades into the affected field (*left column*). When the stimulus flashes first in the affected field and then in the normal field, two alternative eye movement patterns occur: Either the patient makes a direct saccade to the second stimulus, neglecting the stimulus flashed in the affected field, or the patient makes a saccade to the stimulus in the contralesional field and then fails to make the saccade into the normal field. Adapted from Duhamel et al (1992b).

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 field and the discovery of remapped visual responses in the frontal eye field (Goldberg & Bruce 1990, Umeno & 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 a saccade (Andersen et al 1997, Brotchie et al 1995, Krauzlis et al 1997).

SUMMARY

Parietal cortex has multiple representations of space. These representations are linked to spheres of action, and their outputs may be used by the frontal cortex for the planning and generation of movement. It is important to emphasize that parietal activity specifies neither whether nor when a movement will occur. Instead, at least for the lateral intraparietal area, neural activity signifies the salience of a stimulus at a given spatial location. This representation of salience may contribute to the selection of a target for a saccade, but it also contributes to the processes of spatial attention and spatial memory, for which only salient objects are effective stimuli.

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