

From Thought to Action: The Parietal Cortex as a Bridge between Perception, Action, and Cognition

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The lateral intraparietal area (LIP) is a subdivision of the inferior parietal lobe that has been implicated in the guidance of spatial attention. In a variety of tasks, LIP provides a “salience representation” of the external world—a topographic visual representation that encodes the locations of salient or behaviorally relevant objects. Recent neurophysiological experiments show that this salience representation incorporates information about multiple behavioral variables—such as a specific motor response, reward, or category membership—associated with the task-relevant object. This integration occurs in a wide variety of tasks, including those requiring eye or limb movements or goal-directed or nontargeting operant responses. Thus, LIP acts as a multifaceted behavioral integrator that *binds* visuospatial, motor, and cognitive information into a topographically organized signal of behavioral salience. By specifying attentional priority as a synthesis of multiple task demands, LIP operates at the interface of perception, action, and cognition.

Introduction

Consider an attentionally demanding activity such as driving a car on a busy road. To be successful at this task, the brain must constantly monitor the external world: it must survey the visual environment, singling out significant objects such as nearby cars, pedestrians, or traffic lights; and it must physically orient and reorient the eyes to any new or significant object in the scene. In cognitive neuroscience, the process of rapid, online visual selection is referred to as “attention” (or “selective attention”), and the eye movements used to scan the environment are known as saccades, or rapid eye movements.

The control of spatial orienting through either attention or saccades depends on a network of dorsal stream areas that includes the lateral intraparietal area (LIP), the frontal eye field (FEF), and the superior colliculus (SC) (Bisley and Goldberg, 2003b; Goldberg et al., 2002; Snyder et al., 2000). All three areas contain neurons that have spatially restricted visual receptive fields and respond selectively to conspicuous or behaviorally relevant objects. These areas are thought to provide topographic representations of the environment, which encode the salience of different objects and directly specify the attentional weight, or priority, associated with these objects (Gottlieb et al., 1998; Thompson and Bichot, 2005).

Converging evidence suggests that salience representations in these areas are constructed dynamically, continuously incorporating information about behavioral variables relevant for allocating attention. Spatially selective activity in the LIP and FEF is modulated by various behavioral factors, including behavioral context and goals, memory for past events, and the expectation of reward (Thompson and Bichot, 2005). More surprisingly, two recent experiments show that in area LIP this integration

of visuospatial and behavioral information also occurs during tasks that do not require goal-directed movements but, rather, nontargeting manual responses guided by abstract rules—for instance, pressing a bar to report the shape or category of a visual cue (Freedman and Assad, 2006; Oristaglio et al., 2006). This implies that such rule-based behaviors also have specific attentional demands, prompting us to consider the broader role of attention in linking relevant sensory information with behavior not only for motor orienting but also for higher-order, rule-based actions. Here I review our current knowledge of the cellular mechanisms by which LIP neurons link visuospatial input with behavior for covert attention, eye movements, and rule-based actions.

LIP Provides a Topographic Salience Representation that Guides Covert (Perceptual) Attention

Psychophysical studies traditionally define “spatial attention” through its effect on visual perception: attention is the transient focusing of the sensory/perceptual apparatus on a small portion of the external world and is measured behaviorally as improvement in the ability to detect or discriminate the selected object, often with a concomitant worsening in the perception of nonattended objects (Reynolds and Chelazzi, 2004). Attention is therefore a mechanism for rapid, dynamic extraction of information about objects of immediate importance. As I discuss below, attentional selection is sometimes accompanied by an overt orienting movement (usually an eye movement) toward the attended object. However, this is not necessarily the case, and much attentive visual analysis proceeds covertly, through internal selection without overt motor orienting.

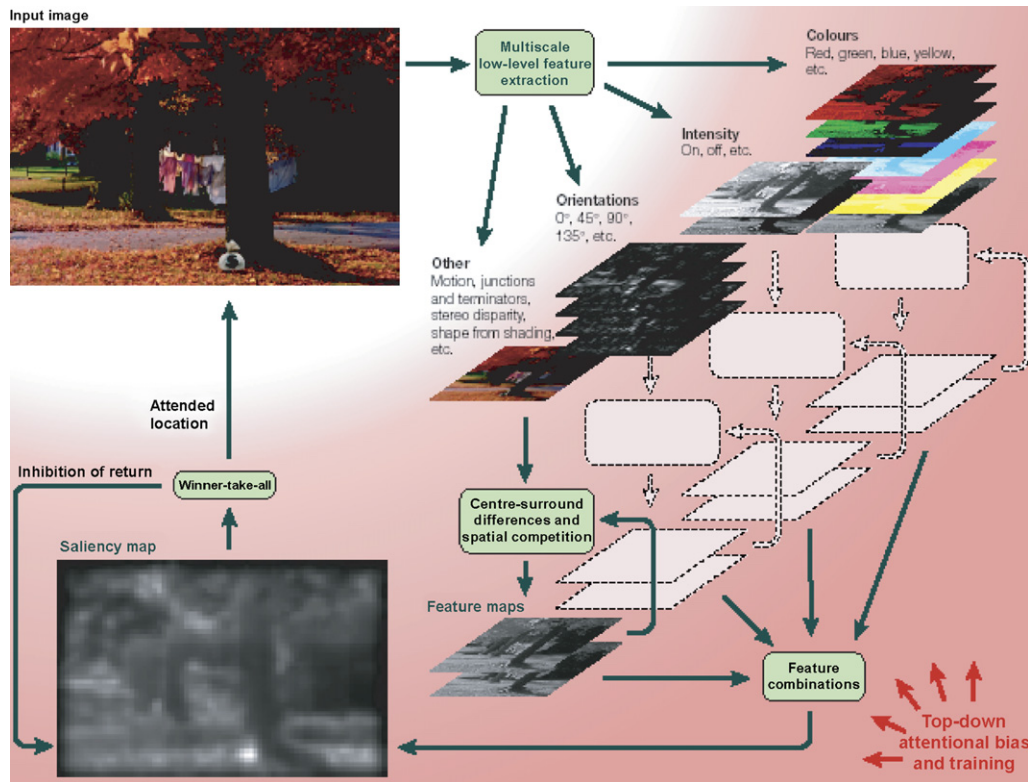


Figure 1. Theoretical Concept of a Saliency Map

Saliency maps are topographic maps of the environment that encode the conspicuity of visual stimuli. The model depicted here concentrates on links between the saliency map and the visual system. However, as discussed here, top-down factors are also integrated within the saliency map. See text for further details. Reproduced with permission from Itti and Koch, 2001 (reprinted by permission from Macmillan Publishers Ltd: Nature Reviews Neuroscience, copyright 2001).

Several studies have suggested that the LIP (like the FEF) provides a “saliency representation” of the world that specifies the momentary locus of attention. The term “saliency representation” refers to a theoretical entity originally proposed in computational studies of attention (Itti and Koch, 2001; Navalpakkam and Itti, 2005). As illustrated in Figure 1, a saliency representation is an intermediate, topographic visual representation that encodes not the mere presence or physical properties of external objects but rather the saliency (conspicuity) of these objects. The saliency map is presumed to receive converging information from feature-selective visual areas and in turn to send topographically organized attentional feedback to the visual system. This results in the transient, selective modulation of perceptual quality that is operationally defined as attention (Reynolds and Chelazzi, 2004).

Consistent with the theoretical saliency map, LIP has strong anatomical connections with both dorsal and ventral extrastriate visual areas and contains a large population of neurons with well-defined retinotopic receptive fields (Lewis and Van Essen, 2000). Like units in the theoretical saliency map, LIP neurons are not strongly feature selective and do not respond automatically to inconspicuous objects entering their receptive field. Instead, neurons

respond selectively to objects that are rendered salient even if these are not relevant to the monkey’s task (Figure 2A) or for objects that are rendered task-relevant by being designated the target for an eye movement or to a perceptual discrimination (Balan and Gottlieb, 2006; Gottlieb et al., 1998; Oristaglio et al., 2006). Neural responses correlate with behaviorally measured shifts of attention to salient or task-relevant objects (Balan and Gottlieb, 2006; Bisley and Goldberg, 2003a; Oristaglio et al., 2006), and experimental *inactivation* of LIP using local injections of the GABA agonist muscimol causes deficits in finding and discriminating visual targets in the hemifield contralateral to the inactivated site (Wardak et al., 2002, 2004).

These experiments suggest that LIP indeed functions similarly to the theoretical saliency map: it provides a priority map of various objects and locations that is functionally related to the dynamic changes in perceptual quality due to attention.

LIP Simultaneously Guides Covert Attention and Specifies Potential Saccade Targets

In its original conception, a saliency representation is thought of as modulating visual (sensory) areas with little influence on motor output (Figure 1). However, in addition

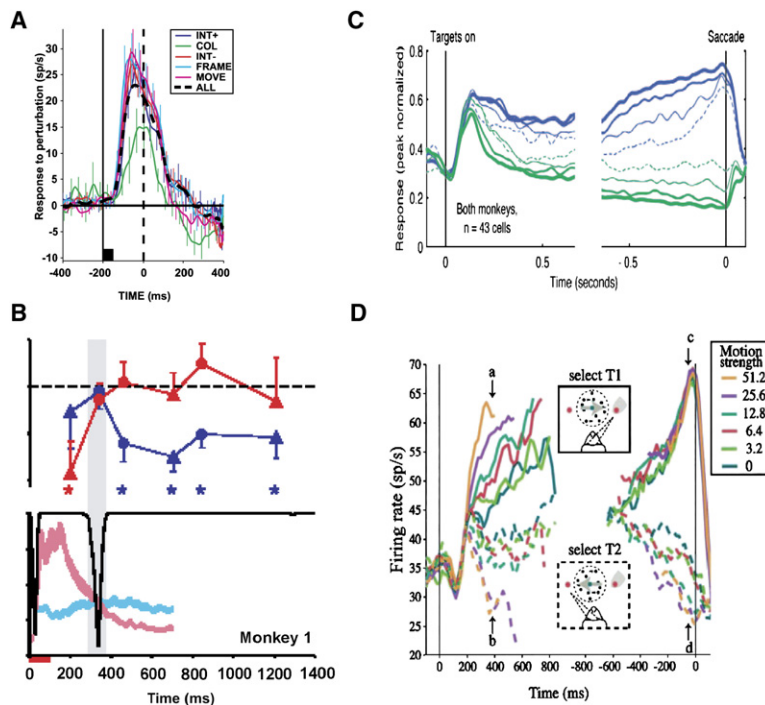


Figure 2. Multiple Bottom-Up and Top-Down Influences in Area LIP

(A) LIP neurons respond to distracting visual transients with different physical properties. A visual perturbation consisting of the appearance of a new object (FRAME), increase or decrease in luminance (INT+ and INT–), or change in position (MOVE) or color (COL) was presented during performance of a covert search task. The perturbation was shown for 50 ms and was followed 200 ms later by appearance of the search array (time 0, dashed vertical line). Traces represent the difference in population firing rates on trials in which a perturbation did and did not appear in the receptive field. Reproduced with permission from Balan and Gottlieb, 2006 (copyright 2006 by the Society for Neuroscience).

(B) Convergence of responses to saccade targets and bottom-up salience in LIP and behavior in one monkey. Bottom panels show population activity in LIP evoked by a saccade target (cyan) or a distractor (pink) in the receptive field and the p value from a running Wilcoxon test comparing the two responses (black). The top panels show normalized contrast thresholds at the location of the target (blue) or of the distractor (red). The locus of lowered contrast threshold (values below 1, dashed line) switched from the distractor at the earliest time point to the target at later time points. The time of this switch coincides with the time when the balance of LIP activity

switches from greater responses to the distractor to greater responses to the target. Reproduced with permission from AAAS from Bisley and Goldberg, 2003a.

(C) LIP responses are modulated by reward probability. Monkeys performed a dynamic foraging task in which they tracked the changing reward values of each of two saccade targets. Traces represent population responses (peak normalized) for neurons with significant effects of reward probability. Blue traces represent saccades toward the receptive field, and green traces represent saccades opposite the receptive field. Traces are further subdivided according to local fractional income (reward probability during the past few trials): solid thick lines, 0.75–1.0; solid medium lines, 0.5–0.75; solid thin line, 0.25–0.5; dotted thin lines, 0–0.25. Activity for saccades toward the receptive field increased, and that for saccades away decreased as function of local fractional income, resulting in more reliable spatial selectivity (difference between the two saccade directions) with increasing reward probability. Reproduced with permission from AAAS from Sugrue et al., 2004.

(D) LIP responses reflect the accumulation of information in a perceptual discrimination task. The monkey viewed a random-dot display containing a variable motion signal and made a saccade to one of two targets to indicate their perception of motion direction. When monkeys made saccades toward the receptive field (solid traces, T1), LIP activity increased faster for increasing motion strength (percent of coherently moving dots). When the saccade choice was opposite the receptive field (dashed traces, T2), LIP responses declined more sharply for higher motion strength. Thus, the depth of spatial selectivity in LIP reflected the strength on the perceptual evidence on which the decision was based. Reproduced with permission from Roitman and Shadlen, 2002 (copyright 2002 by the Society for Neuroscience).

to its responses during covert attention, LIP (like the FEF and SC) also reliably responds in relation to saccadic eye movements. LIP neurons encode the selection and memory for upcoming saccade targets (Gottlieb et al., 1998; Ipata et al., 2006; Powell and Goldberg, 2000), and pharmacological inactivation of this area impairs saccade target selection during visual search (Wardak et al., 2002). Thus, in parallel with its role in covert attention, LIP is also important for selecting targets for saccadic eye movements.

This dual recruitment in relation to attention and saccade planning raises the question of how neural substrates mediating covert attention relate to those driving overt action. Psychophysical studies reveal that this relation is complex, reflecting both interdependence and independence of the two functions. On one hand, as discussed above, attention can be shifted covertly, without necessarily triggering an eye movement, illustrating the independence of attention and saccades. On the other

hand, if a saccade is planned, the preparation of the movement automatically draws attention to the saccade goal, showing a degree of overlap between neural substrates of attention and saccades (Bisley and Goldberg, 2003a; Kowler et al., 1995). Thus, mechanisms of attention are dissociable, but only partly so, from those driving eye movements.

Consistent with these behavioral observations, single neuron recordings show that LIP neurons have complex mixtures of attentional and saccade-related responses. However, even though LIP neurons have saccade-related activity, their activity more closely reflects covert attention than saccade motor output. A good illustration of this point is in the findings of Bisley and Goldberg, who directly measured the locus of covert attention during a task involving both saccade planning and a salient distractor (Bisley and Goldberg, 2003a). Monkeys were briefly shown a saccade target and were required to remember the location of this target across a delay interval

(Figure 2B). On some trials, a salient distractor, which attracted attention but was never a saccade goal, was flashed at a location separate from the saccade goal. Bisley and Goldberg found that during the delay period the locus of attention (the locus of lowered contrast thresholds on a concurrent shape discrimination task) was by default pinned at the goal of the planned saccade and shifted toward the distractor transiently, shortly after distractor onset. In other words, monkeys, like humans (Kowler et al., 1995), by default allocate perceptual resources to a physically conspicuous objects *and* to the goal of an upcoming saccade. Consistent with this, LIP neurons responded both to the saccade target and to the distractor, and critically, the momentary locus of attention was predicted by the balance of these two responses (Figure 2B): the attentional advantage was at the distractor location for as long as the population response to the distractor was higher than that to the saccade target and shifted to the saccade goal when the balance of activity in LIP reversed.

These findings show that LIP neurons reliably specify the locus of covert attention and, because they also have saccade-related activity, may be instrumental in producing the tendency to align attention with eye movements in natural behavior. However, if attention must be dissociated from saccade planning, the LIP response is not sufficient to specify the final motor decision. For example, in the experiment of Bisley and Goldberg, the biggest LIP response was elicited by the distractor, which was never a saccade target. Similarly, in an earlier experiment using “antisaccades” (saccades directed *opposite* a visual cue), LIP neurons reliably encoded the location of the cue in their initial visual response but did not encode the motor decision, even as monkeys were executing the movement itself (Gottlieb and Goldberg, 1999). This implies that motor decision mechanisms operating downstream from LIP can supplement and contravene the salience response from LIP if so required by the behavioral context. This motor decision stage appears to be represented in a class of neurons that are found in the FEF and SC but have not been reported in LIP—the movement neurons, which respond solely in relation to overt saccades but have no visual or attentional response (Bruce and Goldberg, 1985; Hanes and Schall, 1996; Krauzlis et al., 2004). In sum, the salience map in LIP may be instrumental in the selection of attention-worthy objects, which often also constitute *potential*, or *desirable*, targets for eye movements. However, final motor decisions are taken by downstream, independent mechanisms, thus adding an important level of flexibility in the link between covert selection and overt action.

Accumulation of Information toward a Decision

The selection of an attention-worthy object—or the setting of attentional priority—is a complex decision, which, to be useful for behavior, must take into account multiple sources of information regarding the current behavioral context and goals. For example, a moving car is worthy of

attention if one is driving or crossing the road, but much less so if one is trying to read the morning news in a sidewalk cafe. Therefore, the mechanisms that control attention might be expected to integrate information about multiple behavioral demands, and this sort of behavioral integration, or synthesis, may indeed be a key function of LIP.

In a well-known “decision-making” paradigm, monkeys are trained to choose between two possible saccade targets based on the direction of motion in a random-dot motion display presented at the center of gaze (Figure 2D). As expected, LIP neurons encode the direction of the upcoming saccade. Most importantly, the vigor and rate of rise of their saccade-related activity depends on the strength of the evidence instructing the choice: responses grow slowly if the motion signal is weak (low fraction of coherently moving dots) but rise progressively faster at higher motion strength, consistent with the idea that LIP represents a decision variable—a quantity that reflects the accumulation of evidence in favor of a specific choice (Figure 2D) (Huk and Shadlen, 2005; Mazurek et al., 2003; Roitman and Shadlen, 2002). In other decision-making paradigms, saccade-related activity increases as a function of the difference in the amount or probability of reward for the two choices, a quantity that can likewise be interpreted as the evidence in favor of one or the other saccade choice (Figure 2C) (Platt and Glimcher, 1999; Sugrue et al., 2004). These findings are consistent with the idea that LIP reflects the accumulation of information regarding a spatial choice.

A number of other factors have been shown to modulate spatially selective responses in LIP, and although not explicitly studied in the context of decision making, may also represent cues that guide spatial choice. LIP neurons show anticipatory responses for the expected location of a visual discriminandum as well as correlates of a form of spatial memory known as inhibition of return (Assad and Maunsell, 1995; Balan and Gottlieb, 2006; Colby et al., 1996; Robinson et al., 1995). Just as they predict spatial locations, neurons have activity predicting the *time* of occurrence of a saccade go-signal and estimating the duration of visual stimuli (Janssen and Shadlen, 2005; Leon and Shadlen, 2003). Finally, neurons encode the context of a specific trial as defined by the consistent spatial relationship between a salient distractor and a task-relevant target, and this contextual information is translated into a stronger response to the distractor in a context in which it is more likely to convey task-relevant information (Balan and Gottlieb, 2006).

Like motion coherence and reward, these behavioral factors do not independently activate LIP neurons but rather modulate their spatially selective activity. The most straightforward interpretation is therefore that these influences reflect continuous interactions between the salience map in LIP and a number of behavioral systems that convey information relevant for spatial choices. For example, LIP sensitivity to reward probability (Figure 2C) may represent interactions between LIP and reward systems and mediate “incentive salience”—the stronger

drive to orient toward the site of higher expected reward (Genovesio et al., 2006; Sugrue et al., 2004; Watanabe et al., 2001). Similarly, influences related to spatial memory and time prediction may underlie the ability to bias attention and action predictively in response to dynamic environments and recent experience (Ciaramitaro et al., 2001; Janssen and Shadlen, 2005). Finally, contextual effects may reflect global behavioral or attentional strategies applied in circumstances in which lower-level variables such as location and timing are not predictable (Balan and Gottlieb, 2006). Thus, a general function of LIP may be to translate cognitive and behavioral information into a spatially coded signal appropriate for allocating attention. In this signal, the locus of attention is coded through the identity (receptive field) of the active neurons, while the value, or priority, of the attended location is coded through the firing rates of those neurons.

Nonspatial Behaviors

The experiments reviewed above examine the role of LIP in spatial orienting, be it by means of covert attention or rapid eye movements. However, two recent experiments show that the spatial representation in LIP is also recruited during tasks requiring nontargeting behavioral responses, which are guided by visual cues but are not spatially related to those cues (Wise and Murray, 2000). These tasks fall into the general class of “rule-guided” behaviors, which are arguably critical components of higher-order intelligence, including language and social communication (Wise and Murray, 2000). While intuitively we might agree that such acts are attentionally demanding, their specific links with systems of *spatial* attention have remained, until recently, unexplored.

In one experiment, Oristaglio et al. trained monkeys to report orientation of a peripheral visual cue using a nontargeting manual response—by releasing a bar grasped with the right or left hand (Figure 3A) (Oristaglio et al., 2006). The large majority of LIP neurons selectively responded to the cue relative to a distractor in their receptive field, thus providing the expected salience response encoding the location of the task-relevant instruction cue. Unexpectedly, however, this visuospatial response was modulated by the monkey’s choice of limb for the behavioral report: some neurons responded more strongly to the cue if the monkey released the right bar while others showed preference for left-bar release (Figure 3A). Control experiments showed that limb effects represented the active effector itself—the right or left limb—independently of cue orientation or the side of space where the limb was located. As shown in Figure 3A, neurons were not activated by the grasp release in and of itself, but showed limb selectivity only if the monkey attended to the object in the receptive field, that is, only as a modulation of the attentional response. In other words, neurons represented the location of the cue together with the associated motor report, even though this report was a mere nontargeting release of a bar and did not, in and of itself, require selection of a motor goal.

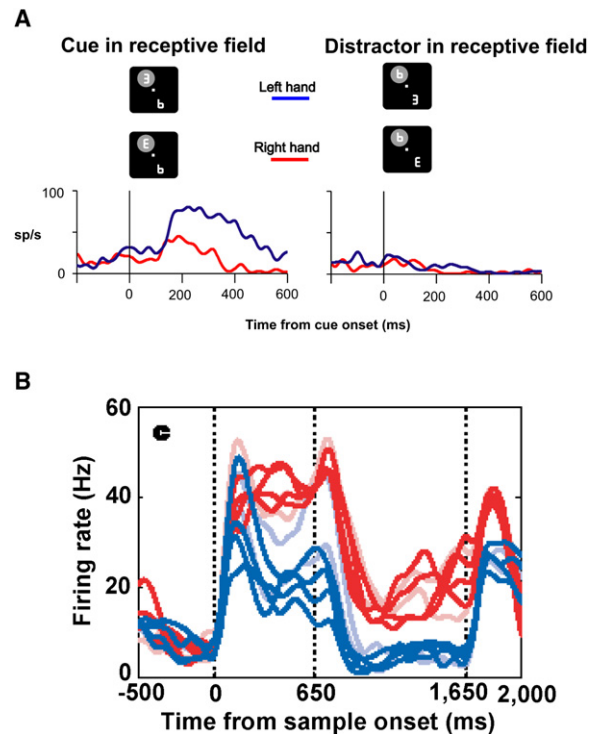


Figure 3. LIP Neurons Responsive for Remote Visuomotor Associations and Categorization

(A) LIP neurons are modulated by limb motor planning. Monkeys viewed a display containing a cue (a letter “E”) and several distractors. Without moving gaze from straight ahead, they reported the orientation of the cue by releasing one of two bars grasped with their hands. The neuron illustrated here responded much more strongly when the cue than when a distractor appeared in its receptive field (left versus right panels). This cue-related response was modulated by the manual release: the neuron responded much more when the monkey released the left than when she released the right bar (blue versus red traces). Limb modulations were much stronger when the cue than when a distractor was in the receptive field. Bar-release latencies were on the order of 400–500 ms. Reproduced with permission from Oristaglio et al., 2006 (copyright 2006 by the Society for Neuroscience).

(B) Responses of a representative neuron during a categorization task. Local motion samples were presented in the neuron’s receptive field. Samples could have one of 12 different directions (individual traces), which were arbitrarily assigned to two categories (red versus blue). After a delay interval (650–1650 ms), a series of test stimuli appeared, and monkeys were rewarded for releasing a response bar for the first stimulus that matched the sample. The neuron conveyed significant information about the category of the sample stimulus during the sample, delay, and test intervals (dashed lines). Reproduced with permission from Freedman and Assad, 2006 (reprinted by permission from Macmillan Publishers Ltd: Nature, copyright 2006).

In a second study, Freedman and Assad showed that the spatial map in LIP can be modulated by an even more abstract stimulus property—the category to which a stimulus is arbitrarily assigned—independently of specific sensory or motor associations (Freedman and Assad, 2006). Monkeys first viewed a sample stimulus that contained motion in one of 12 possible directions arbitrarily assigned to two categories (Figure 3B). Following the sample, several successive test stimuli appeared, and monkeys released a bar for the test stimulus that fell into

the same category as the sample. In this task, therefore, the motor response was constant (release of a bar), and only its timing varied, so that there was no fixed association between a stimulus category and a motor response. LIP neurons responded to the sample stimuli when these appeared in their receptive field and in addition also encoded the category of this stimulus. Thus, the spatial map in LIP was modulated by an abstract concept of category membership even when category was defined without reference to a specific sensory or motor association.

Traditionally, behaviors such as the arbitrary stimulus-response association studied by Oristaglio et al. and the categorization studied by Freedman and Assad have not been thought to depend on attention-related areas. Arbitrary sensorimotor associations are thought to be acquired through direct links between feature-selective visual areas and hand-related premotor areas, and also to rely on the prefrontal cortex, basal ganglia, and hippocampus, structures important for rule-based behaviors and associative memory (Wise and Murray, 2000). Similarly, the ability for abstract categorization is thought to depend primarily on the prefrontal cortex (Miller et al., 2002). The findings of Oristaglio et al. and Freedman and Assad therefore raise the question of the functional significance of the recruitment of attention-related areas in such tasks.

While the answer to this question must await further studies, it is important to note that the findings of Oristaglio et al. and Freedman and Assad are similar to those from experiments using eye movements in one important respect. As in oculomotor tasks, during rule-based behaviors the primary response in LIP encodes the locus of attention, and this response is continuously modified by information about task-relevant variables—the active limb in the experiment of Oristaglio et al. and stimulus category in the experiment of Freedman and Assad. This suggests that the integration of visuospatial and behavioral information is a constant property of the attention-related network, which applies generally whether the required behavior is an eye or a limb movement or a goal-directed or a nontargeting movement.

The findings of Oristaglio et al. show that the integration of visuospatial and behavioral information may give rise to unexpected interactions between spatial orienting and cognitive task demands. Oristaglio et al. reported that LIP neurons tended to prefer the limb contralateral to the recording hemisphere. Since neurons also had predominantly contralateral visual receptive fields, their strongest responses were on trials in which both the cue and the active limb were contralateral to the recording site, that is, when they were congruent with each other. The overall bias for the contralateral limb in LIP in an individual monkey correlated with the manual congruence effect shown by that monkey—the monkey's automatic bias to respond with the hand congruent with the cue's location regardless of the orientation of the cue. In other words, the juxtaposition of visuospatial and effector information in attention-related areas in this case produced an involuntary ten-

dency to align the loci of attentional and motor selection even during a nontargeting, symbolically cued movement. These findings suggest that the modification of spatial maps by behavioral variables (whether for spatial or nonspatially defined acts) is a general mechanism by which attentional resources are allocated to simultaneous task demands, in this case, to processes of visuospatial selection and stimulus-response mapping.

Overview and Perspective

Neuropsychological studies in humans have long suggested that attention is a gateway between perceptual selection and behavior in the widest sense of the word (Mesulam, 1999). In its broadest definition, attention is a mechanism, or a family of mechanisms, by which multiple behavioral demands are synthesized and brought to bear onto covert perceptual analysis and overt action. Neurophysiological experiments such as those reviewed here reveal the cellular mechanisms of this operation. In a wide range of behavioral tasks—involving ocular or manual, goal-directed, or rule-based operant responses—LIP encodes a topographically organized salience representation of the external world, which binds task-relevant information from the sensory, motor, cognitive, and motivational domains. A key function of such representations appears to be to guide spatial orienting, whether covert (through attention) or overt (through eye movements), according to immediate behavioral needs.

This view implies that LIP, along with other attention-related areas, may mediate interactions between spatial orienting and higher-level, more abstract, cognitive functions. This possibility resonates with evidence from studies implicating the human parietal lobe in visuomotor as well as cognitive tasks (Culham and Kanwisher, 2001) as well as with the emerging idea of “embodied cognition” that holds that abstract cognitive functions, rather than being performed by centralized computational devices, tap into and interact with substrates of sensorimotor processing (Wilson, 2002). The challenge for further research is to provide specific evidence of such interactions. For example, how does attention influence, and how is it influenced by, decision making? How is attentional selection impacted, and how is it influenced, by the category of visual stimuli?

A second significant challenge is to determine to what extent the view of LIP as bridging attention, action, and cognition applies more broadly to other sensorimotor association areas. Two other attention-related areas, the frontal eye field and the superior colliculus, also respond selectively to physically conspicuous or behaviorally relevant objects and are sensitive to motor and cognitive variables (Krauzlis et al., 2004; Thompson and Bichot, 2005). Similarly, parietal and premotor areas traditionally associated with limb motor planning are now thought to have complex perceptual and cognitive contributions for nonspatial sensorimotor associations (Gail and Andersen, 2006; Wise and Murray, 2000) and possibly for social cognition and self-awareness (Ehrsson et al., 2005;

Gallese et al., 2004; Nelissen et al., 2005; Rizzolatti et al., 2006; Rizzolatti and Wolpert, 2005). An exciting prospect of future work is to elucidate the similarities and differences between the contributions of LIP and other association areas in bridging perception, action, and cognition.

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