

Parietal mechanisms of target representation

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Recent single-neuron recordings show that representation of the external environment in the parietal lobe is highly selective for objects that are immediately relevant to behavior. Parietal neurons change their selectivity in accordance to immediate behavioral needs, integrate evidence about behavioral relevance from multiple sources, and appear to actively participate in the selection of potential behavioral targets. The selective parietal representations may represent a general-purpose attentional mechanism that can simultaneously specify targets for exploratory movements and for perception.

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Abbreviations

AIP	anterior intraparietal area
CIP	caudal intraparietal area
IPL	inferior parietal lobule
LIP	lateral intraparietal area
MIP	medial intraparietal area
SPL	superior parietal lobule
VIP	ventral intraparietal area

Introduction

The parietal cortex is important for the analysis of space and, in the monkey, parietal neurons are sensitive to spatial variables such as object location, motion and shape. Recent experiments show that neurons in a subdivision of parietal cortex, the inferior parietal lobule (IPL, Figure 1), form highly selective ‘salience representations’ of the environment, in which only objects that are immediately relevant to behavior are strongly represented. Much debate has revolved around the functional significance of these representations. One hypothesis suggests that this parietal activity is dedicated to the representation of targets for exploratory movements of the eye, arm or hand. An alternative hypothesis states that parietal activity specifies targets for spatial attention — the selective allocation of perceptual resources independently of overt movement. Although these two functions are often treated as separate entities, psychophysical experiments suggest that they are, in fact, very closely related. In particular, the selection of targets for movement appears to rely on the same attentional mechanisms that modify perception. Here, I review evidence suggesting that parietal neurons form part of target selection mechanisms that are common for movement and perception. With strong connections to motor and premotor systems, as well as to extrastriate visual areas, the parietal lobe is in a good position to guide coordinated

motor and perceptual orienting toward common targets (see also [1,2]).

Selectivity of the spatial representations in the inferior parietal lobule

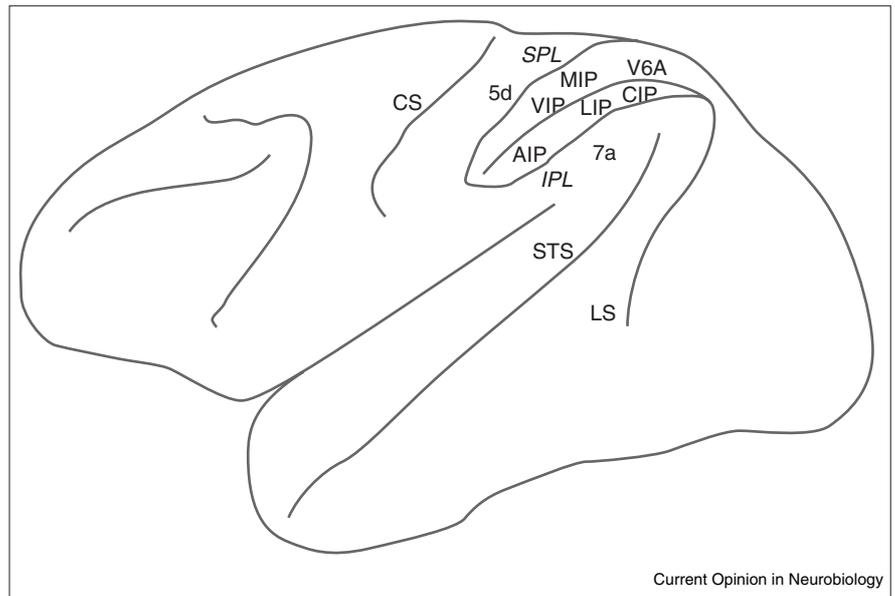
It has been known for several decades that the visually evoked responses of neurons in areas 7a and the lateral intraparietal area (LIP, Figure 1) are by no means ‘passive sensory’, but are influenced in complex ways by behavioral context and by the motivational state of the animal [3]. In the most general terms, the sensory evoked activity in the IPL can be characterized as reflecting the relevance, or potential relevance, of a given object to the animal’s behavior.

IPL neurons actively integrate evidence for behavioral relevance from multiple sources, including physical conspicuity, the selection of targets for movement, the expectation of reward, and long-term, learned associations. Figure 2 illustrates a neuron in area 7a that responds selectively to a visual stimulus, only when that stimulus is physically salient — for example, when it appears in isolation, or when it has a contrasting, unique color on a uniformly colored background [4••]. In this experiment, the pop-out stimulus is also task-relevant, serving as the sample in a spatial match-to-sample task. However, an earlier study showed that physical salience and task-relevance could independently drive LIP neurons [5]. Task-relevance can gate not only the presence, but also the feature selectivity of parietal activity [6]. Furthermore, task-relevance can have long-term effects on parietal responses. Although LIP neurons do not normally respond to ecologically insignificant auditory stimuli (pure tones), a small fraction becomes responsive after the animal is trained to make saccades to these stimuli [7]. Neurons in LIP also respond preferentially to stimuli that are more strongly associated with a reward [8] (see also [3]). In the more recent study [8], monkeys were shown two visual targets and, after a brief delay, were rewarded for making a saccade to one of the targets. The magnitude and probability of the reward associated with a saccade to each target were systematically changed in blocks of trials. Early in the trial (during the cue and early delay period) LIP neurons responded preferentially to the target that was associated with the largest or more likely reward, regardless of the saccade the monkey eventually made. However, during the late delay and presaccadic periods, neurons became selective for the next saccade’s target, regardless of that target’s reward value. Thus, neurons responded selectively to an object that was behaviorally significant, whether this significance was established by virtue of the object’s association with a reward or by virtue of being selected as a saccade target.

Parietal neurons seem to participate actively in locating potential behavioral targets and do not merely reflect the

Figure 1

Schematic representation of the location of the parietal areas mentioned in this review. In this lateral view of the cortex of the macaque monkey, the intraparietal sulcus (IPS) is 'opened' to show its lateral and medial banks. The parietal lobe is divided broadly into the SPL and the IPL, which lie, respectively, medial and lateral to the IPS. CS, central sulcus; LS, lateral sulcus; STS, superior temporal sulcus; V6A, area V6A.



outcome of a selection process completed elsewhere, because the rate of increase of LIP neuronal responses for a saccade target is inversely proportional to the difficulty of the selection process itself [9**]. Interestingly, competitive mechanisms similar to those recently described in extrastriate visual areas [10] may also operate in the IPL. The weak response to multi-element displays is due in part to lateral suppression from surrounding array elements in both area LIP (J Gottlieb, unpublished data) and area 7a [4**], and this suppression is overcome by rendering a stimulus salient or task-relevant.

Parietal contributions to movement

Area 7a is considered primarily visual and does not appear to contribute directly to movement preparation [11]. However, the LIP is strongly interconnected with the brain's saccadic system and has been implicated in the control of saccadic eye movements — the fast eye movements that foveate animals use to scan their environments (for a review see [12]). A large proportion of neurons in area LIP have spatially specific responses before saccades to visual or auditory targets, and reversible inactivation of LIP can affect saccade metrics in some circumstances (e.g. [13,14*]).

Detailed analysis shows that, although LIP neurons respond before saccades in some circumstances, their activity does not always reflect the monkey's oculomotor behavior. This suggests that area LIP may select targets for potential eye movements, but the final specification of these movements depends on downstream structures, such as the frontal eye field and the superior colliculus. A clear example of dissociation between LIP activity and saccade preparation is provided by an antisaccade task, in which the monkey makes immediate saccades opposite a visual stimulus [15] (Figure 3). In this spatial conflict situation,

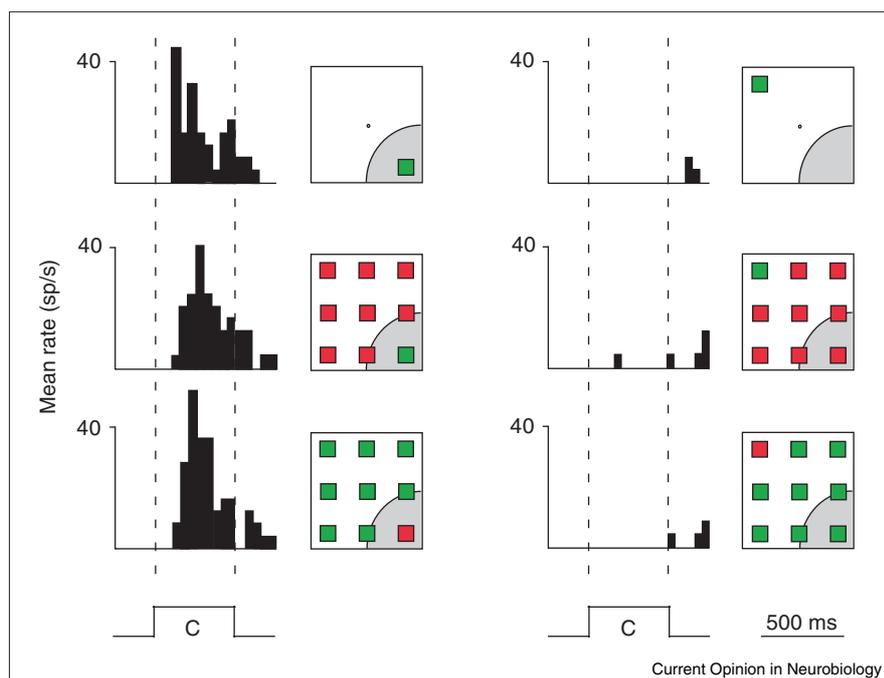
LIP neurons faithfully encode the location of the visual stimulus but fail to provide information about saccade direction, even as the monkey is making that saccade. In general, LIP neurons, including those that project to the superior colliculus [16*], are active not only when the monkey makes an eye movement in their preferred direction, but also in response to salient stimuli, if the monkey plans to withhold a movement or to move in the opposite direction [5,15,17]. Furthermore, LIP neurons have very little activity before voluntary, goal-directed saccades made in the absence of sensory guidance [5,15].

Parietal contributions to attention

Attention is defined as an improvement in the ability to discriminate, detect or memorize an attended object relative to an unattended object, and can be directed independently of overt motor orienting behavior toward the attended object. Saliency representations, such as those found in LIP and 7a, which integrate information from a variety of sources but do not necessarily lead to movement, are clearly suited for directing spatial attention. Indeed, selective spatial representations with properties similar to those found in the parietal lobe are proposed to act as attentional controllers in most computational models of attention [18].

Responses of area LIP and area 7a neurons correlate with spatial shifts of attention in tasks requiring perceptual detection or spatial memory [19,20*]. Pharmacological manipulations of LIP cause deficits in peripheral detection tasks [21,22]. Finally, although the visual representation in area LIP was traditionally thought to be dedicated to the visual periphery, a substantial representation of the central visual field was also recently described, consistent with the importance of attentive fixation during normal behavior [23**].

Figure 2



Responses of a single neuron in posterior parietal area 7a to the single and multiple stimulus cues illustrated in the frames next to each histogram. In this task, the monkey was required to remember the location of the salient cue and release a lever only if a subsequent stimulus appeared at the cued location. The neuron responded for salient stimuli presented inside the receptive field (shaded area in each frame), either alone (top left) or along distractors (middle and bottom left). It did not respond when the salient stimuli appeared outside the receptive field (right panels), even when distractors appeared inside the receptive field (middle and bottom right). C, cue. Data obtained from [4**].

In humans, unilateral parietal damage often causes spatial neglect — a complex neurological syndrome characterized by profound loss of awareness of the space contralateral to the lesion. Consequent to this lack of awareness, neglect patients have a wide array of impairments of sensory perception, movement planning, and memory and imagery specific for contralesional objects and events (for review, see [24]). Functional imaging of the brains of healthy individuals suggests that parietal cortex provides control signals for directed attention in the absence of both movement and sensory stimulation [25–27]. Activation of parietal areas occurs in a variety of tasks engaging spatial attention [28], is sensitive to attentional load [29**], and predicts the conscious detection of peripheral visual events [30**]. In monkeys as well as in humans, the IPL appears crucial for the selective allocation of perceptual resources.

Perceptual and motor selection

What is the relation between motor planning and attention, and why has it proven so difficult to decide whether LIP activity is more closely related to one or the other function? The answer lies in the fact that there is no independent behavioral assay that can indicate the formation of a covert motor plan. Preparing a voluntary eye movement — a saccade [31] or a smooth-pursuit movement [32] — leads to improvements in the perception of that movement's target that are very similar to those caused by covert attention alone. It is not possible, even with considerable effort, to attend to one location while simultaneously preparing a saccade to another location. Because attentional selection is the only known signature of a motor plan, it is impossible to

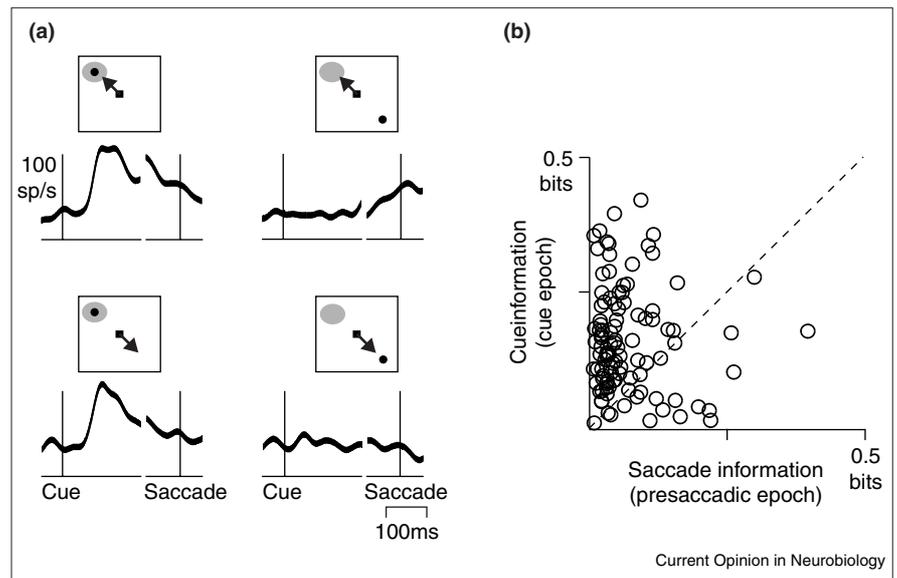
distinguish, except through indirect and uncertain inferences, between attention and motor planning.

The fact that many parietal neurons are active on both perceptual and motor tasks suggests that they may represent a neural substrate that is common to perceptual and motor selection. A very recent experiment illustrates how this idea may be realized in area LIP [33]. The authors trained monkeys on a dual-task paradigm, in which monkeys had to carry out a difficult perceptual discrimination while simultaneously preparing a delayed saccade to the remembered location of a target. They found that discrimination was best for targets presented at the spatial goal of the anticipated saccade, showing that monkeys, like humans, naturally attended to the saccade goal while preparing the movement. As expected, LIP neurons encoded the saccade goal during the saccade preparation period. If a salient visual distractor (to which the monkey was forbidden to make a saccade) was flashed at a remote location during the saccade preparation epoch, the monkey's attention shifted transiently to the distractor location. LIP neurons also responded to distractor onset and the balance of activity in LIP transiently shifted to the distractor. However, attention, as well as the balance of LIP activity, returned to the saccade goal immediately prior to the movement. Thus, LIP activity specified the perceptually advantaged location throughout the trial. This location coincided with the goal of the upcoming saccades at some, but not all, stages of the task.

The above discussion has centered on area LIP, in which most of the issues pertaining to perceptual versus motor

Figure 3

LIP neurons encode cue location but not saccade direction in an antisaccade task. **(a)** The spike density histograms illustrate the activity of one LIP neuron in four trial types. Top left and bottom right panels represent prosaccade trials in which the monkey made saccades (arrow) to the location of a briefly flashed cue (black dot) that appeared either in the receptive field of the neuron (grey oval) or at the opposite location. Top right and bottom left panels represent antisaccade trials in which the cue and saccade goals were opposite each other. The cue was presented for 50 ms and its onset was simultaneous with the saccade-go signal. The neuron responded transiently to the cue's onset only if the cue appeared inside its receptive field (compare left and right panels). By the time of the saccade, activity was equivalent when the monkey made an antisaccade to the receptive field, when he made an antisaccade to the opposite location, and when he made a prosaccade to the receptive field. Therefore, the neuron did not reliably encode saccade direction even as the monkey made that saccade. **(b)** A sample of LIP neurons ($n = 103$) transmit much more information about cue location early in the reaction time (50–150 ms) than they do about



the saccade goal immediately before the movement (50 ms before the saccade initiation). Transmitted information estimates the reliability with which a particular code (in this

case, spike rate) encodes a particular variable. Because there are only two possible cue and saccade goal locations, the maximum possible transmitted information is 1 bit.

selection have been investigated. However, similar reasoning may apply to parietal areas within the superior parietal lobule (SPL), which respond in relation to arm reach movements (see Figure 1). A stronger visual than motor dependence also characterizes neurons in area 5d, suggesting that, like those in area LIP, these neurons provide a relatively early input to premotor reach-related structures [34]. Consistent with this idea, parietal neurons encode arm movement targets in retinotopic coordinates, a representation that is not appropriate for the specification of an arm motor command, although it is well-suited for target selection and the online, or adaptive control of reach [35,36*]. Attentional selection of the movement target obligately precedes an arm reach movement, much as it precedes eye movements [37].

It is worthwhile to consider a few important characteristics that are common to movement planning and attention, and are also consistent with properties of the parietal spatial representations.

Cross-modal integration

Just as movements can be made to targets in different modalities, so attention selects a unified object regardless of the modality of its sensory manifestations [38]. Consistent with this, some parietal neurons have bimodal responses, and their activity refers to a common object across modalities. The visual and auditory receptive fields of bimodal LIP neurons occupy the same spatial locations [39,40] and, in the ventral intraparietal area (VIP), there is close correspondence between the location, size and

directional selectivity of the visual and somatosensory responses of individual neurons [41].

Frames of reference

Planning various movements requires access to several spatial reference frames, which are centered on the eye, head, limb or external objects. Similarly, covert attention can be directed relative to several reference frames, as contralesional neglect is manifest simultaneously relative to the eye, head, trunk, limbs or external objects [42].

Most parietal neurons encode stimulus location in retinocentric coordinates [12,35,36*,43,44] and carry information about postural variables — that is, the position and/or movement of the eyes, head and arms — either explicitly or as gain modulations of retinotopic receptive fields [12,44–47]. Parietal neurons are thought to integrate retinotopic and postural information to allow accurate spatial localization in several frames of reference [5,35,48–54,55*,56,57]. Remarkably, exactly the same computations that achieve nonlinear spatial transformations for movement also reproduce the pattern of perceptual deficits in contralesional neglect [58**].

Near versus far space

Specific motor effectors operate at specific egocentric distances: mouth movements explore near peripersonal space; arm and hand movements reach farther peripersonal space; and eye movements reach both peripersonal and extrapersonal space. Similarly, parietal lesions can cause neglect specifically for near or far objects [59]. The definition

of 'near' and 'far' is dependent on context: a hand-held tool can act as a spatial extension of the arm and redefine far space as near space. This redefinition is reflected in reach-related neural activity in the medial intraparietal area (MIP) [60] and also in spatial neglect [61[•]]. Neurons in area VIP are selective for very close stimuli, and a complementary specialization for farther peripersonal space may exist in area MIP [62].

Motor specificity

Many parietal neurons appear specialized for particular motor modalities. For example, LIP neurons respond more strongly before eye than before arm reach movements, whereas the converse is true for neurons in more medial parietal areas ([45,46,63], see also [64]). The anterior intraparietal area (AIP) is specialized for hand manipulation movements [65]. This specificity suggests that, although some parietal neurons may participate in a general-purpose attentional mechanism, others are dedicated to individual motor modalities [66].

However, the prevalence of putative attentional and motor-related neurons has not been conclusively established. For example, whereas only about 20% of LIP neurons have spatially tuned activity preceding simple arm reaches toward stationary visual targets [63], 50% encode target motion in a more demanding hand-tracking task in which monkeys track (but do not make saccades to) intermittently disappearing moving stimuli with a joystick-controlled cursor [6]. Furthermore, most neurons with reach-specific or saccade-specific tonic (delay period) activity also respond phasically to salient visual objects, regardless of the type of movement the monkey is required to make. The preferential responses in LIP for saccadic eye movements may simply reflect the tendency for perceptual attention to be linked with eye, rather than with arm or hand movements. This preferential linkage may be overcome by making the hand/arm manipulation task more challenging.

An additional, unexplored question is to what extent neurons in different parietal subdivisions represent attended targets at specific ranges of egocentric distances, which, as discussed above, are relevant for different types of movement [62].

Perspectives

Tight correlations are yet to be established between parietal activity and the dynamics of attentional orienting in a variety of perceptual tasks. Furthermore, much remains unknown about the precise localization of attentional functions in the human and monkey parietal lobe and about homologies between the two species [67[•],68[•],69^{••}].

Another major issue to be resolved concerns the role of parietal neurons in representing physical properties of objects, in particular shape. Recent experiments strongly implicate the caudal intraparietal area (CIP) in the perception of three-dimensional shape [70,71,72^{••}] and show that area LIP also contains neurons that are selective

for three-dimensional [73^{••}] and two-dimensional [74] shape. The prevalence and behavioral importance of the feature selectivity of parietal neurons, and its interaction with spatial control signals is a central topic for further research.

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