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Attention as a decision in information space

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Decision formation and attention are two fundamental processes through which we select, respectively, appropriate actions or sources of information. Although both functions have been studied in the oculomotor system, we lack a unified view explaining both forms of selection. We review evidence showing that parietal neurons encoding saccade motor decisions also carry signals of attention (perceptual selection) that are independent of the metrics, modality and reward of an action. We propose that attention implements a specialized form of decision based on the utility of information. Thus, oculomotor control depends on two interacting but distinct processes: attentional decisions that assign value to sources of information and motor decisions that flexibly link the selected information with action.

Eye movements serve visual exploration

To successfully negotiate our world we are constantly called on to make decisions, ranging from the simple (look right or left when crossing the street) to the very complex (choose a mate or a career path). Decision making occupies most of our cognitive capacity, and its failure results in devastating behavioral and psychiatric disorders. Thus, understanding the neuronal mechanisms of decision formation is a central goal of cognitive neuroscience.

In recent years, significant progress in the study of decision formation was made possible by the development of behavioral tasks suitable for use in experimental animals. In these tasks animals are trained to make simple decisions based on sensory evidence or rewards and express these decisions through specific actions [1,2]. This strategy has been particularly fruitful in the oculomotor system, where monkeys report decisions by making a rapid eye movement (saccade) to one of several possible targets. Although many areas contribute to decision formation, most studies of oculomotor decisions have focused on the lateral intraparietal area (LIP), a cortical area located at the interface between visual input and oculomotor output [1,2]. LIP has been an attractive target of investigation because its neurons encode the direction of an upcoming saccade in a manner that depends on the evidence for that saccade, suggesting that they provide a window onto the mechanisms of decision formation [1–3].

In this article we examine the decision literature from the perspective of a second line of investigation that has

also been prominent in LIP: studies of visuo-spatial attention. Experiments examining the role of LIP in attention show that, in addition to its saccade-related activity, its neurons have robust responses to salient or task-relevant stimuli that are not saccade targets [4]. These attentional responses are similar to saccade-related activity in that they encode a form of visual orienting; however, they diverge from the predictions of decision models because they can be dissociated from the metrics, modality, probability and even the reward of an action. We propose that responses to attention represent a distinct form of decision that assigns value to sources of information rather than to specific actions. Thus, we propose that oculomotor control entails two distinct types of decisions: attentional decisions that select sources of information and motor decisions that select an appropriate action. In the following sections we survey the key findings emerging from the decision and attention literatures in LIP, and end by proposing a synthesis that incorporates findings from both lines of investigation.

Parietal neurons encode saccade decisions

The control of saccades relies on a distributed network encompassing subcortical and cortical areas [5]. In the neocortex, two areas that are particularly important for oculomotor control are the LIP and the frontal eye field (FEF) [6,7]. Neurons in both areas have visual receptive fields (RF) and selectively encode the locations of salient or task-relevant objects [8–10]. These neurons are thought to provide spatially organized 'priority representations': sparse maps of the visual world that mediate orienting toward selected objects or locations [8–10].

Studies of oculomotor decisions, which have focused primarily on area LIP, have shown that neurons in this area reflect not merely the final outcome of a decision – the metrics of an upcoming saccade – but also the accumulation of evidence leading to that decision. In one well-known paradigm saccade decisions are based on a sensory cue. On each trial, monkeys see a patch containing random dot motion directed toward one of several saccade targets and are rewarded for selecting the target whose location is congruent with motion direction ([11]; Figure 1a). As expected, LIP neurons encode the direction of the upcoming saccade and respond more if the monkey plans a saccade toward the RF relative to the opposite direction (Figure 1a). Importantly, these responses depend on the strength (signal to noise ratio) of the sensory evidence supporting the saccade (Figure 1b). Activity ramps up slowly if the discriminandum contains low coherence
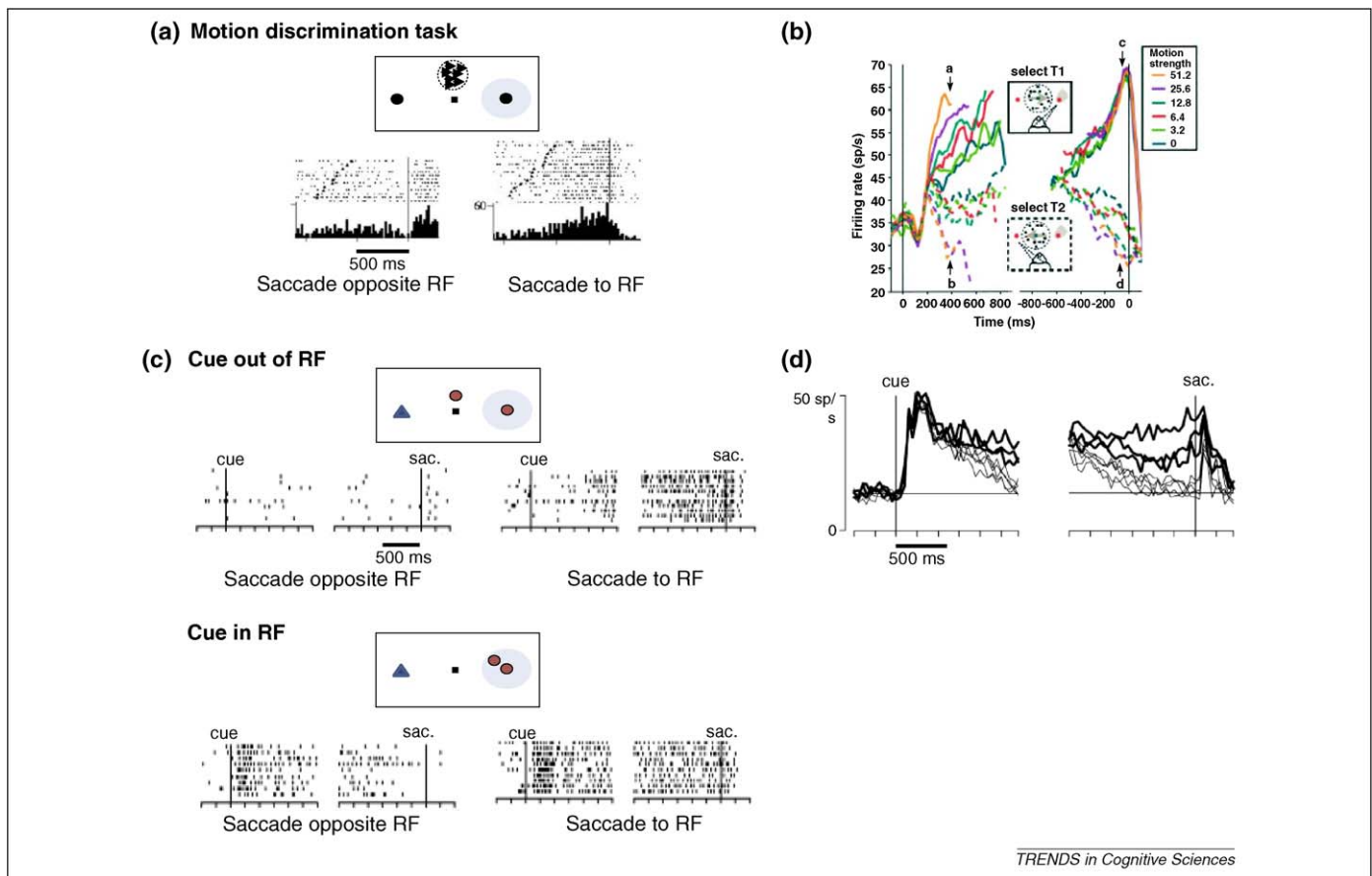
Figure 1. Overlap of visual and saccade responses in LIP. **(a,b)** Encoding of saccade direction on the random dot discrimination task. **(a)** Task layout (top) and single-neuron response (bottom panel). Saccade targets (black dots) are placed in and opposite the RF (pale oval). The motion cue appears near the center of gaze, outside the RF. Bottom panels show responses of a representative neuron encoding saccade direction. Activity is aligned to saccade onset (vertical bar) and carets show the time of cue onset. The average histograms show average firing rate in spikes per second. Reproduced, with permission, from Ref. [12]. **(b)** Population responses Activity preceding a saccade to the RF increases at a rate proportional to motion coherence, but converges to a common level immediately before the saccade. Reproduced, with permission, from Ref. [12]. **(c,d)** Encoding of saccade direction and cue location in a match-to-sample decision task. **(c)** Two task layouts, with the cue outside (top) or inside the RF (bottom). Monkeys viewed a circular array containing 8 peripheral saccade targets (only two are depicted here for clarity of presentation). On each trial a cue was flashed for 200 ms and, after a 600–800 ms delay, monkeys were rewarded for making a saccade to the target matching the cue. Rasters show responses of a representative neuron. If the cue was out of the RF (top) the neuron encoded saccade direction. If the cue was in the RF (bottom) the neuron responded first to the cue and later encoded saccade direction. Modified, with permission, from Ref. [25]. **(d)** Population responses when the cue appeared in the RF. The 8 traces correspond to the 8 different saccade directions (bold traces marking the 3 best directions). The saccade directional response was preceded by a strong saccade-independent response to the cue. Modified, with permission, from Ref. [25].

motion but faster for high-coherence cues, and converges to a common, coherence-independent level immediately before the saccade [12–15]. In other studies saccade decisions are based not on sensory evidence but on the reward history of the alternative targets [9,16–18]. Monkeys learn to track the targets' histories and typically choose the optimal (higher-reward) target; again, neural responses are not stereotyped but increase as a function of the subjective desirability of the selected action [2,3].

Taken together these findings led to a view of LIP as a sort of 'final path' for saccade motor decisions (Figure 4a). LIP is thought to integrate multiple sources of evidence and encode the accumulation of that evidence into an evolving motor plan, culminating in the final selection of an action. This idea has been implemented in several computational models, including models based on probabilistic decision variables [19], attractor networks [20] or saccade probability in a Bayesian framework [21]. A common idea implemented by these models is that LIP represents a final stage for the selection of specific courses of action.

Neurons also encode covert attention

Studies of the role of LIP in attention have targeted a similar population of neurons as that studied in decision experiments: neurons with spatially tuned visual, sustained and pre-saccadic activity [22–24]. However, these studies have examined a different aspect of the neural response, asking how neurons encode not only saccade targets but also salient or informative non-target stimuli.

A consistent outcome of these studies is that LIP neurons with saccade-related activity also have strong motor-independent visual responses. A particularly good example of this is an early experiment where, similar to the motion discrimination task, monkeys choose a saccade target based on a visual cue [8,25]. One difference was that the saccade decision in this task was based not on visual motion but on a match between cue and target properties (Figure 1c). A more important difference, however, was that we placed not only the target but also the cue in the RF, allowing us to examine neural responses to both stimuli. This manipulation showed that, that if the target was in the RF, then neurons had directionally tuned delay

and pre-saccadic activity similar to that described in decision paradigms (compare Figure 1a with 1c, top). However, if the cue appeared in the RF then neurons had an additional early cue-evoked response that was independent of the subsequent saccade (Figures 1c (bottom), 1d).

While the cue-evoked responses are consistent with a role of LIP in attention (see below), they are problematic for models of decision formation because they break the presumed relation between LIP activity and the probability of an overt saccade. Rather than scaling with saccade probability as indicated by the results in Figure 1b, activity in our task was strongest in response to the cue, even though this stimulus was practically never targeted with a saccade (cue-directed saccades were penalized in the context of the task). Given the similarities in other aspects of the data and in particular the strong saccade-related activity found in both studies, it is unlikely that this apparent discrepancy was due to sampling of different neuronal populations. The most likely explanation is that cue responses were not observed in studies with the motion discrimination task simply because the cues were always placed outside the RF (near the center of gaze) (Figure 1a). However, our findings show that such responses are readily elicited under the appropriate experimental conditions.

The dual visual and saccadic nature of the LIP response significantly complicates the readout of this response in downstream areas. The common assumption of decision models is that the readout involves a simple comparison to a threshold, whereby a saccade is triggered whenever activity in some portion of the LIP map reaches or exceeds a certain level [19,20]. However, this scheme is no longer tenable if one considers all components of the LIP response. Given the strong visual responses shown in Figures 1c and 1d a simple comparison to a threshold would trigger more erroneous saccades to the non-target cue than correct saccades to a target.

One possibility is that saccade thresholds are variable, for example being set high throughout a delay period and lowered upon receipt of the 'go' signal (extinction of the fixation point). To address this possibility we carried out another experiment in which monkeys were required to make an immediate saccade opposite a salient cue (an antisaccade) [26]. After achieving central fixation monkeys saw a cue that flashed either inside the RF or at the opposite location. The fixation point disappeared simultaneously with cue onset and monkeys were rewarded for making a saccade opposite the cue. This created an acute spatial conflict between the salient cue and the required saccade. In this condition neurons encoded *only* visual not motor selection: neurons responded whenever the cue appeared in their RF but did not encode saccade direction even as monkeys were executing the saccade itself. In other words the motor decision was generated in downstream areas, and information about this decision was not expressed in LIP. These findings show that significant decision computations unfold in structures downstream from LIP. Rather than merely setting a motor threshold, these structures may generate their own action selection, contravening or supplementing the visual signal from LIP if this is necessary in a given task. Moreover, these decisions need not be expressed in LIP, suggesting that this area "reads out" decision computations only in variable, task-specific manner.

In a subsequent series of experiments we asked whether, in addition to responding to salient visual stimuli, LIP is also important for effortful, top-down attention [4,27]. To examine top-down attention we trained monkeys on a task in which the relevant cue (an 'E'-like shape) was not physically conspicuous but appeared in the visual periphery among similar distractors [22,28,29]. The cue appeared at an unpredictable location and could face to the right or to the left (Figure 2a). While holding central fixation, monkeys were rewarded for reporting cue orientation by releasing a bar held in their right or left hand. Performance declined as a function of the number of distractors, revealing a set-size effect that is diagnostic of attentionally demanding visual search [29].

Consistent with a role in attention, over 80% of LIP neurons encoded the location of the cue in the visual array, responding strongly if the 'E' appeared in their RF but much less if a distractor was in the RF [22,29]. These responses declined as a function of the number of distractors, consistent with a competitive normalization mechanism [30] and correlated with the behavioral set-size effect [29] (Figure 2b). These findings are consistent with prior reports that transient unilateral inactivation of LIP with muscimol (a GABA-A receptor agonist) impairs performance of attentionally demanding visual search [31,32], a result confirmed by a subsequent inactivation experiment carried out in our laboratory ([28]; Figure 2c). This indicates that LIP is important for top-down attention whether attention guides ocular or skeletal motor output.

In addition to requiring top-down attention, an important aspect of the "E" search task was that it separated the workspaces of attention and motor planning. Attention selected a target within the visual display, while the motor action was linked to a limb and was performed outside of the field of view. Thus, we expected that the cue selection signal in LIP would be independent of the manual release. Surprisingly however, this signal was strongly modulated by the motor action [22]. This effect is shown for a representative neuron which, as described above, responded more if the cue than if a distractor appeared in its RF (Figure 2d). However, its response to a cue in the RF was stronger when the monkey released the left limb than when she released the right limb. Although for this neuron the preferred limb was congruent with the hemifield of the RF, other neurons preferred the RF-incongruent limb (the limb ipsilateral to the recording hemisphere), with the relative proportion of contralateral and ipsilateral limb preferences varying across subjects. Control experiments showed that this selectivity described the active limb rather than the orientation of the cue because it persisted when the monkey discriminated a second set of shapes. In addition, selectivity was linked to the effector and not to the effector's location in space because it was unchanged if monkeys performed the task with their limbs crossed over the body midline [22].

Taken together, these findings support a different view of LIP activity relative to that indicated by studies of decision formation. First, the findings show that LIP
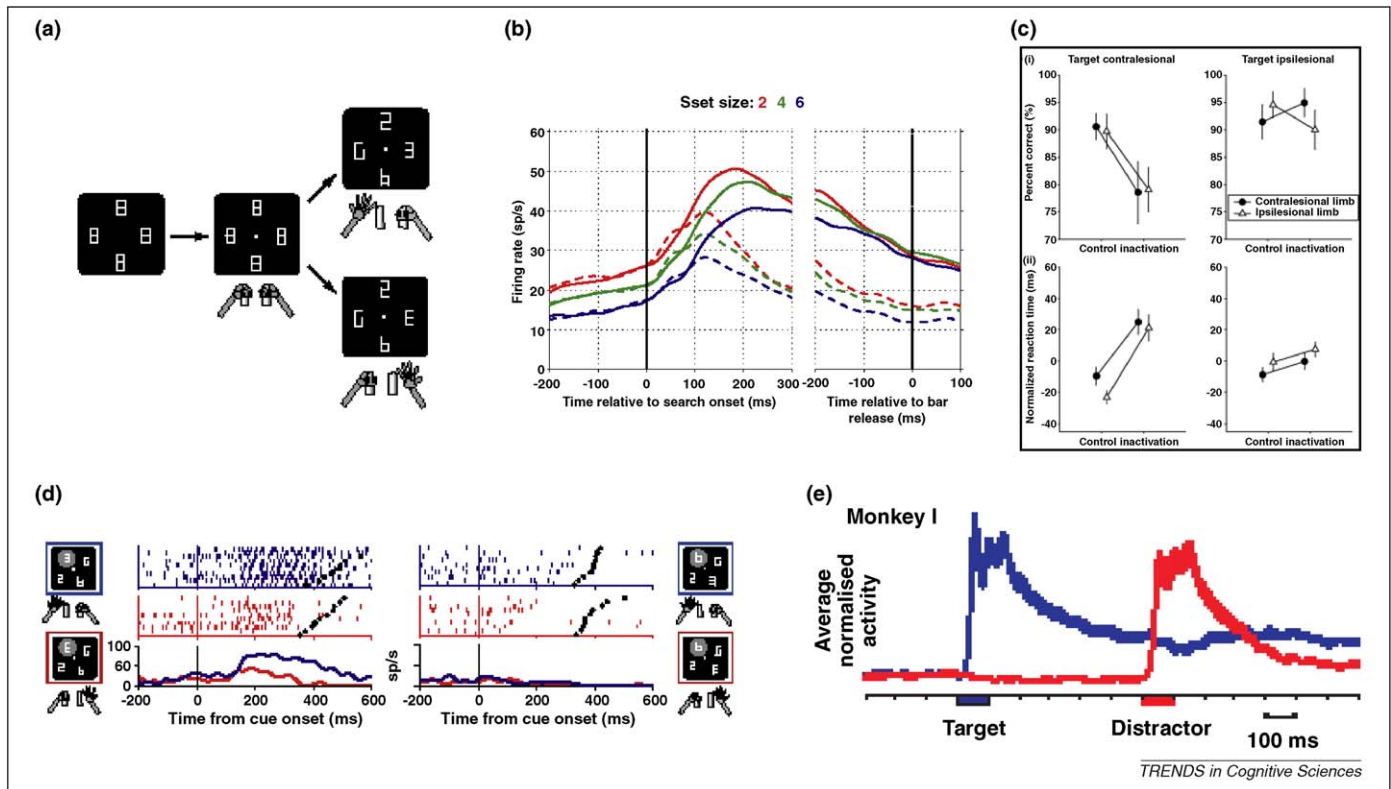
Figure 2. LIP encodes top-down and bottom-up attention. **(a)** Monkeys reported an orientation discrimination using a manual report. A display containing several figure-8 placeholders remained stable on the screen. A trial began when the monkeys achieved central fixation and grasped two response bars, leading to presentation of several distractors and a cue (a letter 'E'). Monkeys reported 'E' orientation by releasing the right or left bar. **(b)** Population responses for search with displays of 2, 4 or 6 elements. After presentation of the search the display (time 0) firing rates strongly increased if the 'E' was in the RF (unbroken traces) but not if a distractor was in the RF (dashed traces). Increasing set-size lowered firing rates. Reproduced, with permission, from Ref. [29]. **(c)** Effects of reversible inactivation during covert search. If the cue is in the hemifield contralateral to the inactivation site, inactivation lowers accuracy (top left) and elevates reaction time (bottom left). Deficits are not seen for ipsilateral cues (right panels) and do not depend on the limb used to indicate the decision (black vs. white symbols). Modified, with permission, from Ref. [28]. **(d)** Neuron selective for cue location and bar release. The neuron increased its activity if the 'E' was in its RF (left column) but not if a distractor was in the RF (right column). The neuron also responded more if the monkey released the left relative to the right bar (blue vs. red). Trials are sorted offline in order of manual latency. Reproduced, with permission, from Ref. [22]. **(e)** Population activity encoding bottom-up shifts of attention. Monkeys kept in mind the location of a briefly presented target for a later saccade; a salient distractor was presented at an unpredictable location during the delay period. When the target was in the RF (blue) LIP neurons maintained sustained activity encoding the target's location. If the distractor appeared in the RF (red), the distractor-evoked response far surpassed the target-related activity for a brief period before returning to baseline. Reproduced, with permission, from Ref. [23].

encodes visual selection in conjunction with ocular or skeletal actions. Second, they show that LIP receives feedback from multiple motor modalities, including ocular and skeletal non-targeting actions. Finally, the results indicate that motor feedback is expressed in a variable fashion, gated by visual and attentional demands. Earlier we mentioned the fact that saccade activity is found in LIP in some cases (e.g. before visually guided or delayed saccades, Figure 1) but not in others (e.g. before an antisaccade to an unmarked location [26]). Likewise, sensitivity to limb movement on the 'E' search task appeared *only* if attention was deployed to the RF (Figure 2d, left panels) but not if attention was deployed outside the RF (right panels), even though the manual release was equivalent in both cases. Moreover, the deficits produced by muscimol inactivation were fully explained by the location of the cue but were equivalent regardless of the active limb, indicating that LIP was not crucial to the manual response [28] (Figure 2c). Based on these findings we propose that LIP encodes a stage of visual selection that communicates with but is distinct from downstream motor selection (Figure 4b). Although neurons receive feedback about the selected action they express this feedback variably depending on visual or attentional demands.

Attention is based on the utility of information

A central tenet of the decision literature is that every decision requires an estimate of the utility of the available options [2,3]. The attention-related responses described above encode a form of selection and as such also require the weighting of alternative options. However, although in decision studies utility is determined by a physical reward – the food or drink that can be harvested by an action – the relationship with reward is more complex in the case of attention. Instead, as we discuss in this section, attention seems to be based on a more abstract metric related to the value of information.

Consider for example the cue selection response on the 'E' search task (Figure 2b). As we described above, this response encodes a shift of attention to the cue and may be viewed as an incipient plan to make a saccade to the cue. However, whether overt or covert, such orienting is not the decision in the task: monkeys were rewarded for releasing a bar and would have been *penalized* had they directed gaze to the cue. Had LIP simply reported the desirability of an action then its cue response might have been expected to diminish and perhaps disappear with prolonged training, as the monkeys learned that it is not desirable to make a saccade to the 'E'. One possibility is that in this task the

cue had indirect reward value by virtue of its ability to inform the later manual action. However, the evidence we discuss below shows that attention can be even more starkly dissociated from a physical reward. When driven by physical conspicuity or emotional significance attention is automatically allocated to salient or predictive stimuli even when this consistently interferes with an optimal action [23,33,34].

As we mentioned above, LIP neurons have strong responses to abruptly appearing stimuli (Figures 1c, 1d), and several experiments have linked these responses with reflexive, bottom-up attention. Neurons respond selectively to abruptly changing, relative to stable, inconspicuous stimuli, and the strength of the visual response correlates with the distracting effects of such stimuli on a current task [8,23,33,35]. The dynamics of bottom-up attention were examined in one experiment in which monkeys remembered the location of a target for a later saccade while viewing a salient distractor presented during the memory interval [23]. Neurons responded both to the target and to the distractor (Figure 2e). Attention (measured at several time points through a secondary contrast sensitivity task) was allocated to the locus of the highest activity in LIP, switching first from the target to the distractor and back to the location of the target as the distractor response waned in LIP. Notably, attention and LIP activity were inexorably driven by the distractor even though this stimulus could only impair, never improve, the odds of harvesting a reward.

An additional source of automatic influence on attention is the biological significance - the Pavlovian or emotional associations of external objects. In human subjects emotional stimuli automatically attract attention [36] and bias visual activity in primary visual cortex independently of their relevance to the task [37,38]. However, little is known about the substrates of Pavlovian attention in single neurons in the monkey brain.

To address this question we tested LIP responses to reward predictors: cues that signaled an upcoming outcome but not the required (optimal) action [34]. Each trial began with a brief conditioned stimulus (CS), an abstract pattern announcing whether the trial would end in a reward (CS+) or no reward (CS−). The CS appeared randomly either inside or opposite the neuron's RF but its location was irrelevant to the task. To complete a trial the monkeys had to make a saccade to a second target that appeared after extinction of the CS, and was located unpredictably at the same or at the opposite location relative to the CS.

Despite their lack of operant significance, the CS automatically biased attention based on their salience and Pavlovian associations. Immediately upon their onset both CS+ and CS− produced a strong visual response, suggesting that they transiently attracted attention to their location. However at longer delays (after disappearance of the CS) this early response gave way to a sustained bias that was specific to the reward valence of the CS. In the wake of a CS+ neurons had slightly higher delay activity if the CS+ appeared in the RF relative to the opposite location indicating that the CS+ produced an attractive bias toward its location (Figure 3b, left). By

contrast, after an over-learned CS− neurons had lower activity at the CS− location relative to the opposite location (Figures 3a, right and 3b, right) indicating that a CS− produced an inhibitory bias at its location. Consistent with this, saccades were slightly facilitated if they were congruent with the location of a recent CS+ (Figures 3c, 3d, left) but were impaired (in both accuracy and reaction times) if they were directed to the location of a recent CS− (Figures 3c, 3d, right). Thus, following its initial bottom-up effect, a CS+ automatically attracted attention whereas a CS− automatically repelled attention from its location.

The fact that CS-evoked responses were modulated by expected reward is consistent with prior reports of strong reward influences in this area [9,16]. However, this finding is not consistent with an interpretation in terms of reward-based action selection. Because the CS were not saccade targets, the attentional biases they evoked interfered with the monkey's ability to make the required (optimal) saccade. Reinforcement models predict that the CS-evoked attentional biases should subside with training as subjects learn the value of the optimal action [9,39]. However, the experiment yielded precisely the opposite result. The repulsion evoked by a CS- increased with training (was stronger for an over-learned relative to a newly-learned CS), indicating that learning only exacerbated an initial maladaptive effect (Figures 3a, 3d). This, we propose, is a very strong result. It indicates that learning in the system of attention was not based on the expected reward of an action; instead it was based on the value of information, increasing as monkeys had more opportunity to learn the predictive properties of the CS.

The need for autonomous visual and motor selection
We reviewed evidence that, in addition to its saccade-related activity, LIP encodes signals of visual selection that are consistent with a role in spatial attention. While these responses represent a form of spatial orienting and possibly incipient saccade motor plans, they are not captured by current action-based decision models because they do not reliably encode the occurrence, reward or metrics of an overt action. This indicates that LIP is not near the end point of a motor decision stage as suggested by the current decision literature (Figure 4a); instead it represents an earlier stage encoding visual or attentional selection (Figure 4b). This stage can provide top-down feedback to sensory systems as proposed in computational models of attention [40]. In addition, this stage interacts with downstream motor areas, being influenced by and influencing processing in these areas. The decision regarding the final action, however, rests with structures downstream from LIP.

A longstanding and important question concerns the purpose of such an explicit representation of attention. Given that eye movements are often congruent with the locus of attention, why would the brain have a stage of *visual* selection that is distinct from that of saccade *motor* selection? The findings we reviewed suggest that the purpose of such representation is twofold. First, this stage might be required for behavioral flexibility: the ability to variably link selected information with actions. Second, it
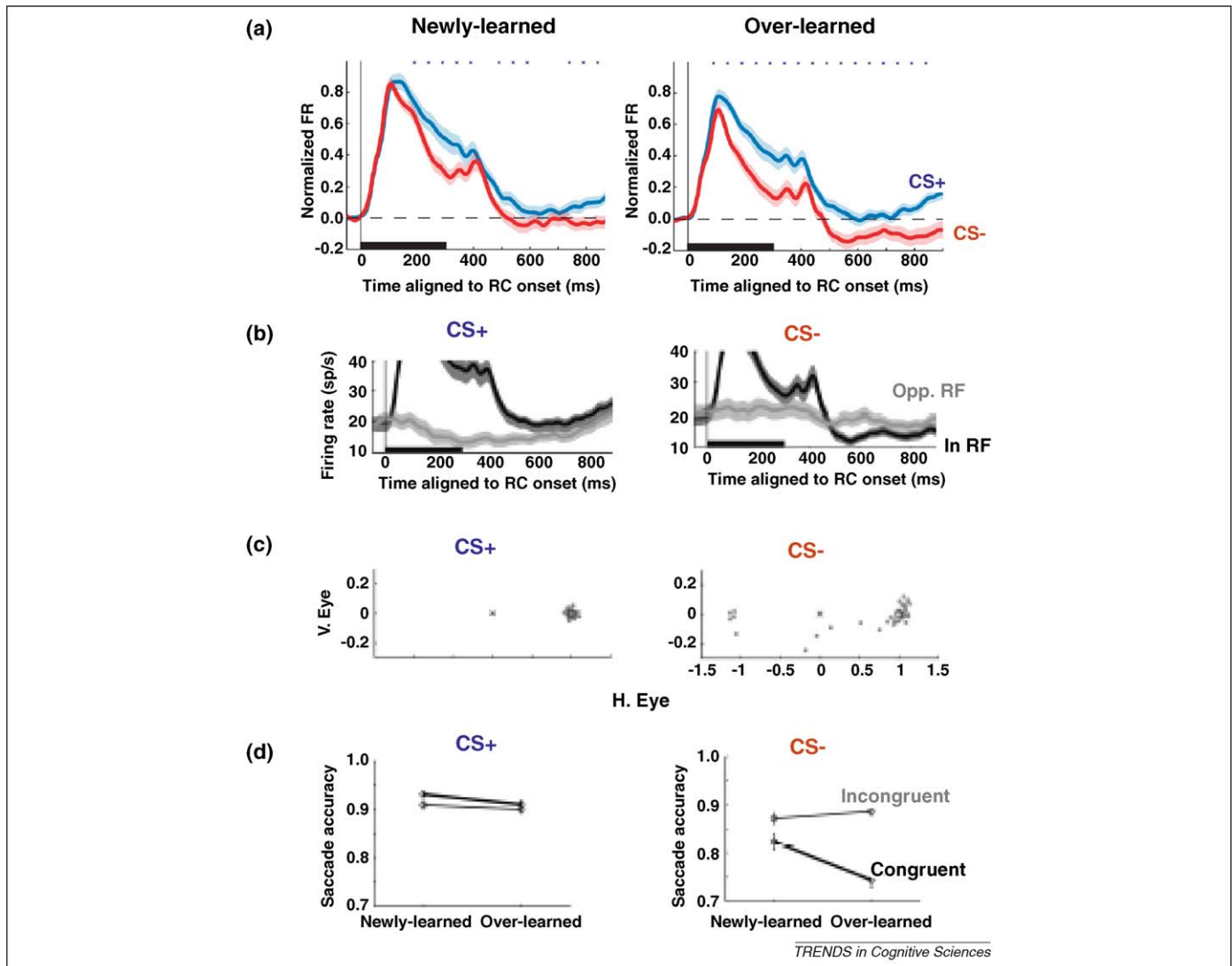
Figure 3. Pavlovian cues bias attention and LIP activity. **(a)** Neurons have valence-selectivity activity that grows with training. Normalized population firing rates to CS+ (blue) or CS− (red). Monkeys had been trained with over-learned stimuli for several months before recordings began. In each session the monkeys also learned to discriminate sets of novel stimuli, acquiring discriminatory licking within the first 5–10 trials. Only trials that followed the acquisition of discriminatory licking were analyzed for these newly-learned stimuli. Shading represents standard error of the mean (SEM). Stars show time bins of significant differences. The CS was present for 300 ms (black bar) followed by a 600 ms delay period where two identical placeholders were visible at each location. **(b)** CS-evoked responses are spatially specific. Traces show population responses for over-trained CS, appearing inside (black) or opposite the RF (gray). The vertical axis is truncated to highlight delay period activity. **(c)** Saccade accuracy is impaired for CS− congruent saccades. Landing positions of saccades in a representative session, when the saccade target was congruent with the location of an over-trained CS+ (left) or CS− (right). Each gray dot shows one saccade. Axes show horizontal and vertical eye position, normalized so that the target appeared at position (1,0). Saccades on CS− trials were often dysmetric, falling outside the allowed accuracy window. **(d)** Saccade impairment is spatially specific. Panels show mean and SEM for saccade accuracy across all sessions. On CS+ trials accuracy is slightly but significantly higher for saccades that are spatially congruent with the CS. On CS− trials, accuracy is much lower for CS− congruent relative to incongruent saccades, and this difference increases with training. Modified, with permission, from Ref. [34].

is needed for implementing a distinct form of decision: decisions that identify and assign priority to sources of information. We discuss each point in turn.

To succeed in complex environments we must act in a flexible manner as appropriate for a given task. The need for flexibility is clear in the case of skeletal actions. We are not limited to reaching to an attended object but can perform actions that are unrelated to the locus of attention, such as shifting gears while looking at the traffic light, running *away* rather than toward a ball, or playing the piano while reading the musical score. Although less obvious, flexibility is also required for oculomotor control. In complex environments we look at some stimuli while covertly attending to others [41–43] and we separate attention from gaze in social situations.

Such flexible coordination might be difficult to achieve with a single stage that equates visual and motor selection. By contrast, a two-stage model of the type shown in Figure 4b allows for both autonomy and coordination between visual and motor selection. By virtue of its feedforward projections the visual selection in LIP can bias downstream areas to generate a saccade to the locus of attention. However, these biases do not amount to a motor command, as downstream areas can block or supplement this descending signal as required in a given task. The sites computing final oculomotor decisions are not fully understood but probably include visuo-movement and movement neurons in the FEF and the superior colliculus along with related basal ganglia circuitry [44–47].
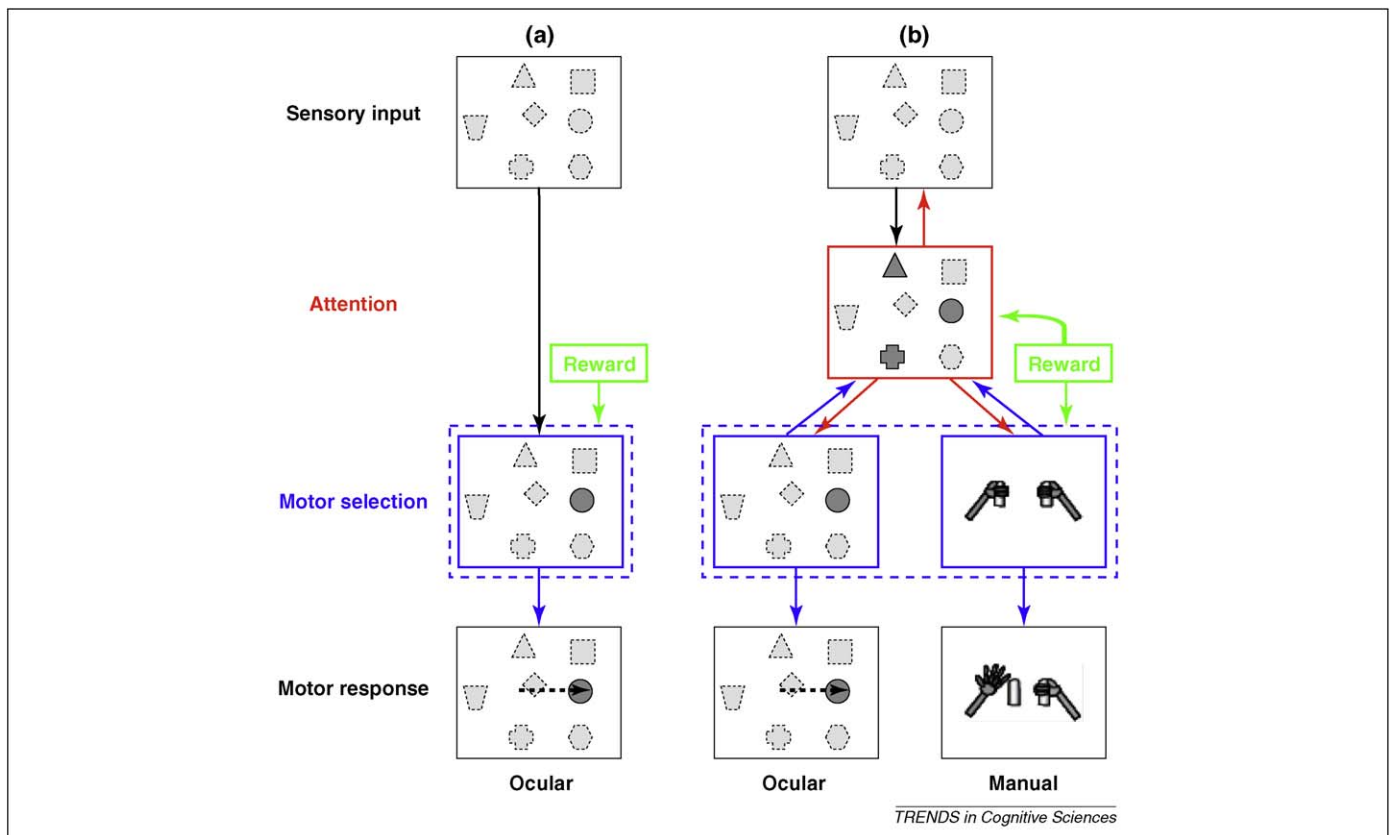
Figure 4. Computational stages involved in decision formation. **(a)** In the decision literature an internal decision layer (proposed to be encoded in LIP) selects among alternative actions based on sensory and reward information. **(b)** Proposed expansion of the internal decision layer to include a stage of visual selection (attention) that is distinct from action selection. The visual selection stage can highlight several objects or locations, for example those that are cues or targets for action. This stage communicates with downstream ocular or skeletal motor areas that select an appropriate action. Feedback from action selection layers modulates the dynamics of visual selection.

A second crucial function of an explicit attentional representation is, we propose, to assign priority to sources of information. Although many studies have examined the effects of attention on sensory perception [30], these studies tell us little about how the brain identifies the relevant stimulus to begin with – how it decides which stimulus is worthy of attention. In Box 1 we outline some of the most obvious questions regarding the metric, or metrics, that might guide an attentional decision. Briefly, the above discussion suggests three possible answers. One metric guiding attention could be the task-relevance or information provided by a stimulus: the ability of a stimulus to enhance the reward of a later action (Figure 2; [48,49]). Another metric could be based on biological significance, the Pavlovian associations of specific stimuli (Figure 3). Yet other metrics could be related to the conspicuity of stimuli or their ability to change an existing belief, which might be important for learning or exploration [40,50,51]. Understanding these three types of "attentional decisions", together with other questions outlined in Box 1, will be critical for understanding how the brain controls attention.

A moment's consideration shows that, as action selection requires the learning of action-reward associations so too might attention need to rely on associative learning regarding visual stimuli. A visual stimulus is not valuable in and of itself but it only becomes so if it predicts other variables of interest such as an action or an expected reward. Thus, the 'E' in our search task is only relevant because it predicts an optimal action, and a CS in the Pavlovian task is only relevant because it predicts a specific reward. One possibility is that the reward and motor modulations found in LIP are part of a broader mechanism by which the brain learns to identify predictive stimuli based on their task-specific associations. Thus the feedback in systems of attention might not serve solely visuo-motor coordination; it might be part of a broader mechanism where motor, emotional and cognitive factors define which stimulus should be attended in the context of a task.

Concluding remarks

We highlighted a few crucial open questions emerging from the study of attention and oculomotor decisions in the parietal cortex. Our discussion suggests that a synthesis between these lines of research can significantly expand the outlook provided by each camp alone. On the one hand, the presence of attention-related activity indicates the need to expand the current study of decision formation, to account not only for choices of action but also for decisions regarding sources of information. On the other hand, these studies call for a more principled account of the factors controlling attention than has been available so far. Rather than intuitively defining attention as a form of 'focusing' we can attempt to understand it as a distinct

Box 1. Questions for future research

Our view of attention as involving decisions about the value of information opens several fundamental questions that have not been addressed in the literature. Below we highlight a few of these questions.

- Identifying valuable sources of information is one of the most difficult problems faced by the brain, and it is unlikely that it involves only LIP. What is the relation between the associative coding we find in LIP and the frontal lobe, which is thought to provide memory-based, top-down control of attention [52,53]?
- How is attention related to a reward or, more generally, to the goal of a task? We have seen that attending to task-relevant cues can increase the reward of a later action (Figure 2). Is the 'relevance' of a cue related to the strength of its action associations? If so, do animals track cue-action associations independently of a physical reward? How is a metric of information based on the validity of a cue (the strength of its predictive associations) related to a metric based on its sensory strength (signal to noise ratio) [54]?
- How is attention related to learning and exploration? Is more attention allocated to more reliable cues, or is attention allocated to more *un*certain stimuli to facilitate learning about them? How do other factors that influence saccadic exploration, such as visual conspicuity or surprise relate to an information metric [50,51]? A recent study in adaptive systems indicated that a metric of acquired information could be used to motivate exploration, guiding it toward situations that increase learning [55]. Can this framework be fruitfully applied to neuroscientific studies of attention and learning, and can it provide a bridge for crosstalk between studies in neuroscience and robotics?

- What are the mechanisms that motivate attention? A recent study proposes that dopamine neurons encoding prediction error for physical rewards also encode a cognitive reward signal related to the anticipation of information [56]. Is this reward signal crucial for motivating attention? If so, how is it computed and how does it affect attention? Is attention deficit disorder related to deficits in processing delayed or cognitive rewards?
- What is the relation between the phenomenology described by decision and attention experiments? Does the coherence-dependent rise of activity in the motion discrimination task (Figure 1b) truly reflect the 'accumulation of evidence' or does it reflect competitive interactions between the saccade target and the attentionally demanding cue [29]? If information accumulation does occur, does it apply to covert attention (when it is not necessary to cross a motor threshold) and if so, how?
- Is the task-related feedback we find in LIP transmitted to sensory areas (e.g. [57]) and from there to perception? Is attention directed differently depending on the information content of stimuli, i.e. whether the stimuli describe actions, emotionally significant outcomes or abstract categorical variables [58]? Does the perception of a stimulus depend on the action or category associated with that stimulus?
- The attentional maps in LIP and FEF inform both ocular and skeletal motor output [22,59]. Are these maps important for allowing flexible selection and coordination across motor modalities and, if so, how?

form of cognitive decision. By using tasks in which monkeys choose between alternative cues we can understand the metric or metrics that guide these more abstract decisions. This will provide important insights into the control of attention and, in so doing, into broader processes of learning, exploration and the active search for information.

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