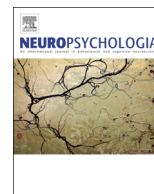




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# Spatial and non-spatial aspects of visual attention: Interactive cognitive mechanisms and neural underpinnings

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## ABSTRACT

In humans and non-human primates, the parietal lobe plays a key role in spatial attention – the ability to extract information from regions of space. This role is thought to be mediated by “priority” maps that highlight attention-worthy locations, and provide top-down feedback for motor orienting and attentional allocation. Traditionally, priority signals within the parietal cortex have been characterized as being purely spatial, i.e., encoding the desired locus of gaze or attention regardless of the context in which the brain generates that selection. Here, we highlight evidence from human behavior and neuroimaging as well as monkey physiology, to argue that non-spatial responses are critical to the establishment of priority maps in parietal cortex. This review offers an integrative view of the role that parietal cortex plays in attentional selection, providing evidence that priority maps reflect spatial and non-spatial priorities that ultimately act on sensory information in a spatial way.

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## 1. Introduction

Selective attention allows us to focus on significant sources of sensory information. Decades of research starting in the early 1970s provided strong evidence that attentional selection operates on spatial representations (Eriksen and Eriksen, 1974; Eriksen and Hoffman, 1972; Posner, 1980). Research conducted in 1980s and 1990s offered additional evidence that attention is also highly sensitive to mid-level visual properties such as features (Treisman and Gelade, 1980; Wolfe, 1994), surfaces and objects (Duncan, 1984; He and Nakayama, 1995; Shomstein, 2012b), either in isolation or in combination with spatial selection (Egley et al., 1994; Egeth & Yantis, 1997; Kravitz and Behrmann, 2011). These studies greatly expanded our knowledge of the visual system and constrained computational models of visual attention (e.g., Itti and Koch, 2001; Lanyon and Denham, 2005; Zaharescu et al., 2005).

Attentional selection is also guided by non-spatial high-order properties established by the task associations and rewards of sensory cues. For example, a street sign in a busy intersection may

not be conspicuous based on low-level features, but will be closely attended because of its association with an action that leads to a desired goal (e.g., walking to a destination). The neural mechanisms by which these properties influence attention are much less well understood.

Here, we will review recent studies pointing to an integral role that the posterior parietal lobe (PPL) in humans and inferior parietal lobe (IPL) in non-human primates play in service of attentional selection based on different types of representations. These studies suggest that, even though the parietal cortex is traditionally associated with spatial attention, it conveys a much richer signal that combines spatial information with a range of non-spatial higher-order factors such as reward, object properties, and semantic associations. We review the behavioral and neural correlates of these interactions and their possible significance for attention mechanisms.

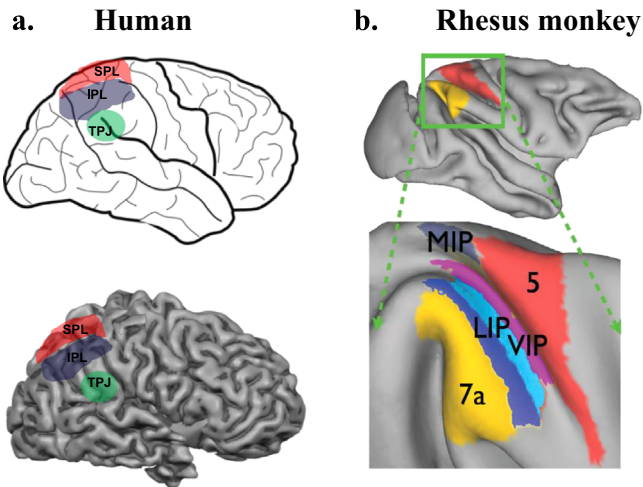
## 2. Spatial encoding in the posterior parietal cortex

The parietal lobe forms about 20% of the human cerebral cortex. Posterior parietal cortex (PPC) is the association cortex that is thought to play an important role in attentional selection. In humans, the PPC is further subdivided into three major regions: the superior parietal lobe (SPL) that is dorsally located, the inferior parietal lobe (IPL) that lies more ventrally, and the temporo-parietal junction (TPJ) (Fig. 1a). SPL/IPL regions are implicated in

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**Fig. 1.** Anatomical regions and subdivisions of the human and monkey parietal cortex. (a) Schematic depiction of relevant parietal cortex subdivisions projected onto the lateral surface of the right hemisphere (top); and same regions projected onto the lateral surface of a structural anatomical cortical surface (bottom). The intraparietal sulcus divides posterior parietal cortex (PPS) into the superior parietal lobe (SPL) and the inferior parietal lobule (IPL). The superior temporal gyrus (STG) runs along the superior extent of the temporal lobe and terminates at the temporo-parietal junction (TPJ). (b) Lateral view of the macaque monkey brain indicating the approximate location of individual parietal areas. Our discussion focuses on areas LIP and 7a, which are located laterally to the intraparietal sulcus and belong to the inferior (or posterior) parietal cortex. Area 5 located medially and dorsally relative to the IPS, is part of the functionally distinct superior parietal lobe. The inferior parietal lobe includes areas 7a, LIP (the lateral intraparietal area, ventral and dorsal divisions) and VIP (ventral intraparietal area). Reproduced with permission from Gottlieb and Snyder (2010b).

volitional (top-down) control of attention, while TPJ is thought to be responsible for low-level (involuntary) capture of attention (Behrmann et al., 2004; Shomstein, 2012a). In monkeys, parietal areas that are dorsal to the intraparietal sulcus (area 5 and area MIP) are predominantly somatosensory, whereas areas that are more ventrally located (the lateral intraparietal area (LIP), ventral intraparietal area (VIP) and area 7a) are implicated in vision and visual attention (Fig. 1b). The human PPC and the monkey IPL are located at the junction of multiple sensory regions. They project to several cortical and subcortical areas and are engaged in a number of cognitive operations, many of which involve spatial representations (Kravitz et al., 2011; Margulies et al., 2009).

Studies of the effects of visual attentional selection have revealed behavioral facilitation in attended spatial locations. Since 1970, benefits of spatial selection have been consistently and robustly demonstrated, mostly relying on variants of a spatial cuing paradigm originally described by Posner (1980). In this paradigm, a spatial location is cued either directly with a salient sensory event (“exogenous” cue) or indirectly through a symbolic instruction (“endogenous” cue). Following the cue, visual targets are detected and identified more quickly if they appear in or near the cued location, relative to the non-cued locations, indicating that the cue has attracted attention toward its location (for review see Carrasco (2011), Eriksen and Eriksen (1974) and Posner et al. (1980)). Unilateral damage to the parietal lobe impairs the ability to orient attention, and particularly to shift attention from the unimpaired hemifield (the hemifield ipsilateral to the damage) into the impaired, contralateral hemifield (Mesulam et al., 1999).

Consistent with a role of the PPC in spatial attention, studies employing functional magnetic resonance imaging (fMRI) found that corresponding frontal (frontal eye fields, FEF) and parietal areas in humans (IPL, SPL, and TPJ) contain topographic representations related to saccade planning and attention (Husain

and Nachev, 2007; Molenberghs et al., 2007; Serences and Yantis, 2007; Sheremata and Silver, 2015; Silver and Kastner, 2009). For example, one robust finding is that when cues direct attention to specific visual field locations, activation is noted in superior frontal, inferior parietal, and superior temporal cortices (for review see Corbetta and Shulman (2002)). Voluntary deployments of spatial attention are associated with neural activity in regions of the dorsal parietal cortex (IPL, SPL) and frontal area FEF while involuntary spatial orienting, such as attentional capture by a perceptual singleton, is associated with ventral parietal cortex (TPJ) and ventral frontal cortex (VFC) (Downar et al., 2000; Serences et al., 2005).

The degree to which the representations in these regions are lateralized remains an open question. For example, a large number of neuroimaging studies have reported bilateral activations following shifts of attention to either hemifield (e.g., for review Corbetta and Shulman (2011), Hopfinger et al. (2000), Kastner et al. (1999) and Shomstein and Yantis (2006)). However, just as many reports provide evidence for a strong right lateralization (Szczepanski and Kastner, 2013; Szczepanski et al., 2010; Yantis et al., 2002). Laterality within the spatial attentional orienting system remains an active topic of investigation, with recent findings suggesting that perhaps the level of right lateralization greatly depends on the degree of visual short term memory (VSTM) involvement (Sheremata et al., 2010; Sheremata and Shomstein, 2014) and attentional load (Sheremata and Silver, 2015).

Concordantly with the observed activity over the parietal cortex, directing spatial attention to the left hemifield results in increased stimulus-evoked neural activity in early visual areas in the right hemisphere, whereas directing spatial attention to the right hemifield is accompanied by increase of activity in the early visual areas of the left hemisphere (Yantis et al., 2002). Such sensory enhancement of attended information has also been demonstrated with other neuroimaging techniques. For example, studies employing event-related potentials (ERPs) take advantage of the fact that visual stimuli typically elicit two early waveform components, which are termed P1 (first positive, occurring 100–200 ms after stimulus onset) and N1 (first negative; 100–200 ms after stimulus onset). When attending to a lateralized stimulus, the contralateral P1 and N1 components show enhanced amplitude (with no change in latency) in response to an attended item as opposed to when spatial attention is diverted elsewhere in the scene (Luck et al., 2000).

In monkeys, single-unit recordings support a role in spatial attention for two subdivisions of the IPL, areas LIP and 7a. Area LIP receives strong visual input from multiple visual areas (including V2, V3, V3A, V4 and the middle temporal area (MT)), and has strong connections with the oculomotor system including the frontal eye field (FEF) and the superior colliculus (Blatt et al., 1990; Lewis and Van Essen, 2000). Consistent with these connections, a large fraction of LIP neurons have visual receptive fields (RF) that are typically confined to the contralateral hemifield (Barash et al., 1991b; Ben Hamed et al., 2001; Blatt et al., 1990; Platt and Glimcher, 1998).

A hallmark of the LIP visual neurons is that, rather than signaling any object that enters their RF, the cells respond selectively for task-relevant or physically salient stimuli, suggesting that they encode a sparse “priority” representation of complex visual scenes (Bisley and Goldberg, 2010). Neurons in LIP respond robustly to stimuli that pop-out by virtue of an abrupt onset or contrasting color (Balan and Gottlieb, 2006; Bisley and Goldberg, 2003; Gottlieb et al., 1998), and also encode the top-down selection of informative but inconspicuous cues (Balan et al., 2008; Gottlieb et al., 1998a, 1998b; Oristaglio et al., 2006). Prior studies have linked the selective activity in LIP to overt saccades (Bracewell et al., 1996; Ipata et al., 2009; Snyder et al., 1997) as well as covert

(internal) shifts of attention (Balan et al., 2008; Bisley and Goldberg, 2003; Oristaglio et al., 2006), and it was recently suggested that these two functions may be differentially represented in, respectively, the dorsal and ventral subdivisions of this area (Liu et al., 2010). Reversible unilateral inactivation of LIP using local injections of muscimol (a GABA<sub>A</sub> receptor agonist that transiently silences neural activity) produces deficits in saccades and attention in the contralateral hemifield (Balan and Gottlieb, 2009; Liu et al., 2010; Suzuki and Gottlieb, 2013; Wardak et al., 2002, 2004), although these deficits are typically more subtle than the full-blown spatial neglect syndrome that is seen in humans.

A more lateral subdivision of the PPC called area 7a may also be important for spatial attention, but its role is less well understood. Area 7a shares many of the same connections as LIP, but has weaker links to early visual and oculomotor areas and stronger connections with parts of prefrontal cortex (e.g., area 45), cingulate and parahippocampal cortex (Cavada and Goldman-Rakic, 1989a, 1989b). Visually responsive cells in area 7a have large RF that may cover the entire contralateral hemifield (Barash et al., 1991a; Ben Hamed et al., 2001; Blatt et al., 1990; Platt and Glimcher, 1998) and have been shown to encode a priority map that selectively responds to salient objects within their RF but is silent for inconspicuous “background” features (Constantinidis and Steinmetz, 2005; Katsuki and Constantinidis, 2012).

Along with the findings that emphasize the visuo-spatial functions of the parietal cortex, there is mounting evidence suggesting a more domain general contribution to attentional selection. Given multisensory inputs to the parietal cortex, it is reasonable to hypothesize that the contribution of parietal cortex extends well beyond exclusively spatial and exclusively visual processing. In fact, recent studies investigating domain specificity have found that IPL plays an important role in cross-modal attentional selection and spatial and non-spatial auditory attention and memory (Kong et al., 2014; Michalka et al., 2016; Shomstein and Yantis, 2004b, 2006). Further, converging evidence has accumulated suggesting that parietal cortex integrates non-spatial information about object-based, semantic and motivational effects (Gottlieb and Snyder, 2010a; Husain and Nachev, 2007; Shomstein, 2012a).

### 3. Object-based selection

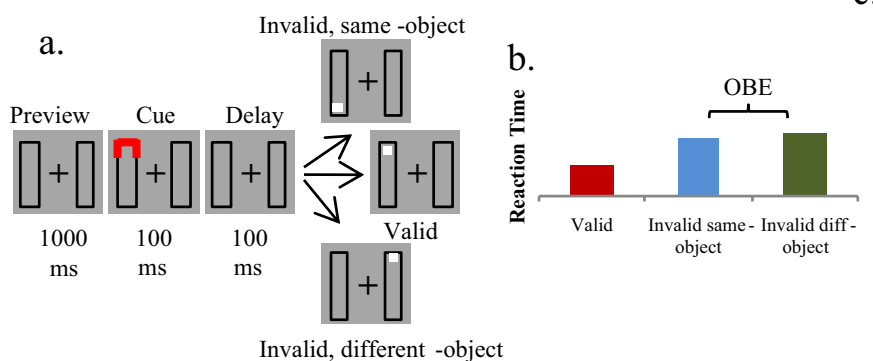
In natural scenes, spatial locations are occupied by objects, and the efficiency with which we interact with the world suggests that object-based selection plays an important role. Starting in the

early 1980s, evidence began to accumulate that some tasks engage a selective mechanism that operates on an object-based, rather than purely location or feature-based, representation (Duncan, 1984; Kahneman and Henik, 1981; Kanwisher and Driver, 1992; Rock and Guttman, 1981).

A large body of evidence in support of object-based attention has been derived from the two-rectangle paradigm, originally developed by (Egly et al., 1994; Marrara and Moore, 2003; Shomstein, 2012b). In this paradigm, two adjacent rectangles, oriented either vertically or horizontally, are presented and one end of one of the rectangles is illuminated briefly, cueing the observer to direct attention to that location while maintaining fixation at the center of the display (Fig. 2a). After a brief delay, a target is presented either at the location previously occupied by the cue (the *valid cued* location), at the opposite end of the cued rectangle (an *invalid same-object* location), or at the other (un-cued) rectangle (an *invalid different-object* location) at the same distance from the cue as the *invalid same-object* location.

This paradigm yields two main findings. First, items in the *validly cued* location are detected faster and more accurately than items at any other location (Fig. 2b, red vs. blue and green). This result implies that the spatial distance between the cued location and the target affects the quality of one's perceptual representation (Desimone and Duncan, 1995; Egly et al., 1994; Müller et al., 2003; Posner et al., 1980) and is consistent with space-based attentional orienting. Second, targets in the *invalidly cued locations* are detected faster and more accurately if they fall on the same objects rather than a different object. This effect, labeled as object-based effect (OBE) in Fig. 2b, reflects the contribution of object-based attention to the quality of perception (Müller and Kleinschmidt, 2003; O'Craven et al., 1999; Serences et al., 2004). This paradigm has been extended in several subsequent studies (Behrmann et al., 1998; Martinez et al., 2006; Moore et al., 1988; Müller and Kleinschmidt, 2003; Shomstein and Behrmann, 2006, 2008; Shomstein and Yantis, 2004a; Watson and Kramer, 1999), including a recent study showing that the laboratory object-based phenomenon observed with simple objects extends to complex objects in complex real world scenes (Fig. 2c) (Malcolm and Shomstein, 2015). Therefore, attentional allocation is guided by spatial location as well as non-spatial object membership.

Several neuroimaging studies have directly probed whether object-based orienting activates attention-related regions in the IPL (Arrington et al., 2000; Lee and Shomstein, 2013; Müller and Kleinschmidt, 2003; O'Craven et al., 1999; Serences et al., 2004; Valdes-Sosa et al., 1998). One such study (Shomstein and Behrmann, 2006), adapted the two-rectangle method for fMRI to



**Fig. 2.** (a) Example of a typical trial in a two-rectangle experiment. Note that the same-object and the different-object target locations are equidistant from the cue. (b) Idealized pattern of results (RT, reaction time) for targets appearing in the same location as the cue (valid, red), in the same-object as the cue (same-object, blue) and in the object that was not cued (different-object, green). (c) Four examples of displays used in the real-world object-based attention study. The target (light bulb) is superimposed on the scene in three possible locations (for representation purpose): same-object as the cue, different-object, and floating. Only a single target was present in the experiment. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

examine (i) the sensitivity of the attentional control signals in SPL/IPL to space- versus objects-based shift of attention; and (ii) whether object-based sensitivity within SPL/IPL results in corresponding facilitations of object locations within the early sensory regions (visual areas V1 through V4). Participants were asked to execute shifts of attention either within an attended object or between two objects, or to hold attention in place (Fig. 3a).

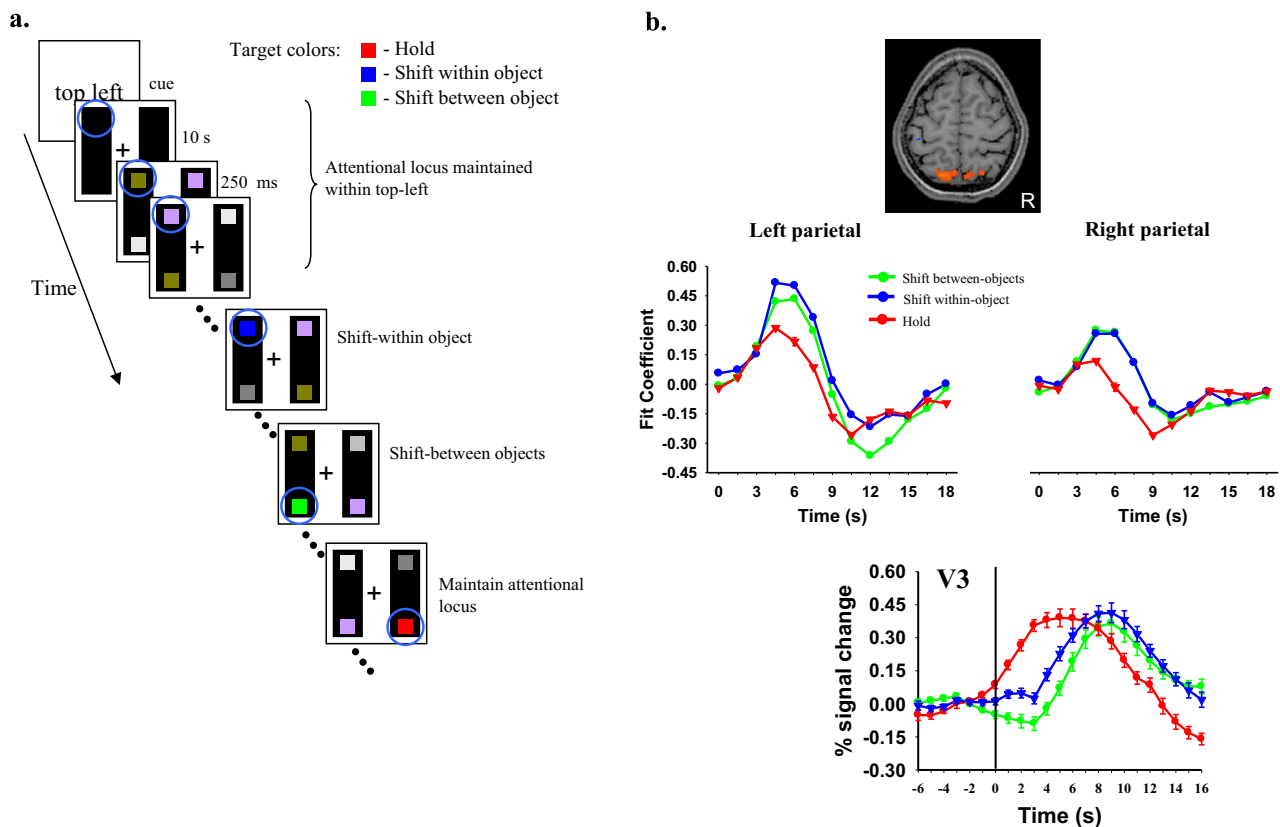
The blood oxygenation level dependent (BOLD) activity in the posterior parietal cortex was enhanced following instructions to shift versus hold attention, independent of whether the shifts were executed within or between objects (Fig. 3b, blue and green vs. red traces). This result replicated existing findings that spatial shifts engage left and right SPL/IPL (Liu et al., 2003; Serences et al., 2004; Shomstein and Yantis, 2004b; Yantis et al., 2002). Of particular interest however, was a novel observation that activity in IPL showed specific enhancement for within-object over between-object shifts of attention. Notably, this object-based sensitivity was only seen in the left IPL (Fig. 3b; blue vs. green traces). Consistent with the suggestion that priority maps within the parietal cortex integrate both spatial and non-spatial attentional signals, it is important to note that these object-based effects were observed in the very same area of the IPL that was responsible for eliciting spatial shifts of attention. Object-based representations directly modulated the magnitude of the responses related to spatial shifts. Concurrently with the object-sensitive shift-related activity observed over IPL, object-sensitive modulations were also found within extrastriate regions of the occipital cortex (areas V1 through V4; Fig. 3b, bottom panel, blue vs. green traces), evidenced by greater increases of activity for within-object relative to between-object shifts.

These data were among the first to suggest that the attentional control signal issued by the parietal cortex (a seemingly spatial area) is object-sensitive and differentiates between attention directed to within- versus between-object locations. The neuroimaging results suggest that the neural mechanisms underlying object-based attention involve integration of space- and object-based representations within the left IPL and earlier sensory regions of the visual system. A dynamic circuit between the parietal and earlier visual regions may enable observers to preferentially focus on objects of interest that appear in complex visual scenes.

Object-based effects have not yet been reported in the parietal cortex of monkeys. However, in addition to their retinotopic visual responses – which depend purely on the location of a stimulus on the retina – LIP and 7a neurons also carry extraretinal signals that could support computations in head- or body-centered coordinates (Mullette-Gillman et al., 2005; Snyder et al., 1998) and, importantly, in world- or object-centered reference frames (Crowe et al., 2008; Rawley and Constantinidis; Snyder et al., 1998). Additionally, visual responses as early as V1 are modulated by object representations (Grossberg and Raizada, 2000; Roelfsema et al., 1998), making it likely that the parietal and visual areas are involved in object-based attention in human and monkey.

#### 4. Semantics

In addition to segmenting the visual stream into recognizable objects, an important task of the brain is to assign *meaning* to those objects. The meaning – or semantics – of an object are of



**Fig. 3.** Modulation of PPC and V3 by object representations. (a) Each run started with a cue indicating the starting to-be-attended location, top left in this example. Locus of attention is represented by a blue circle and was not present on the screen. Participants then waited for a target to appear in the attended location. Three types of targets were used: (i) shift attention to the same object; (ii) shift attention to the different object; or (iii) remain attending in the same spatial location. (b) *top*, bilateral activation of SPL/IPL following shifts of attention as compared to maintaining attention in the same location; *middle*, activation profiles of event-related time courses extracted from the corresponding left and right parietal cortex; *bottom*, activity extracted from V3 of visual cortex shows greater responses for targets that appear in the same-object (blue) as compared to different-object (green), with even larger modulations of targets that appear within the locus of attention (valid, red). Similar patterns were observed in areas V2 and V4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

course not dictated strictly by the visual input, but depend on learnt, task-specific associations between an object and subsequent actions, events, or outcomes. For example, to understand the meaning of a red traffic light at an intersection, we must have learnt that a red light is associated with stepping on the brake and ultimately, success in driving. In addition to allowing us to interpret visual inputs, semantic properties dictate whether and when an input is worthy of attention, and therefore may be expected to influence areas implicated in attention control. In this section we review evidence supporting this hypothesis in humans and monkeys. Please note that, throughout this section we use the term “semantic” to refer not only to a narrow language based property, but more broadly to the sensory, motor or reward associations that an object acquires in a task context.

Natural environments readily elicit high-level, context-specific, activation (Bar and Aminoff, 2003) suggesting that observers can extract the “gist” of a scene from as little as ~100 ms viewing duration (Biederman et al., 1974; Fei-Fei et al., 2007; Greene and Oliva, 2009; Potter, 1975). At the level of individual objects, Yang and Zelinsky (2009) showed that a category-defined target (as opposed to an item belonging to a different category) is fixated faster and with greater probability than would be expected by chance, and that this effect is derived from observers using a categorical model of common features from the target class (see also Schmidt and Zelinsky (2009)). Other studies show that distracting stimuli that are related to the target also capture attention (Belke et al., 2008; Moores et al., 2003; Telling et al., 2010).

A recent neuroimaging study (Cukur et al., 2013), for example, demonstrated that searching for a target that belongs to a category, during natural vision, causes semantic tuning changes, as measured by fMRI, that alter the cortical representation of the attended categories. Participants were presented with movie clips that contained different object categories (e.g., people and vehicles) and were asked to search for a target in one of these categories (e.g., a person appearing in a movie). The important aspect of the study was that instead of focusing on specific regions of the brain, category influences were examined within individual voxels across the cortex. Many voxels across the ventral visual cortex (from occipital to the temporal pole) and within the IPS shifted their tuning toward the attended category. Importantly, these shifts in tuning expanded the representation of the attended category, as well as of semantically related, but not currently attended, categories. These results provided a neural footprint for an attention mechanism that facilitates representations of not only the target category, but other categories that are strongly semantically related (Hickey et al., 2015; Huth et al., 2012).

It should be noted that while left lateralization has been implicated in derivations of semantic relationships, this lateralization is restricted to the left inferior frontal gyrus (LIFG) and left posterior middle temporal gyrus (Badre et al., 2005; Corbett et al., 2009; Jefferies and Lambon Ralph, 2006; Noppeney et al., 2004; Thompson-Schill et al., 1997), involvement of IPL is bilateral (Cukur et al., 2013; Whitney et al., 2012). Therefore, while semantic computations themselves are left lateralized, semantic influence on attentional selection seems to be accomplished via bilateral IPL.

With some exception (Hwang et al., 2011; Kravitz and Behrmann, 2011, Exp. 2; Lupyan et al., 2010), research into semantic/category influences on attention have been restricted to instances when semantic information is directly relevant to the task. Thus, it is not evident whether semantic content constrains attentional selection only when it is task relevant, or whether it operates continually, independent of task-relevance.

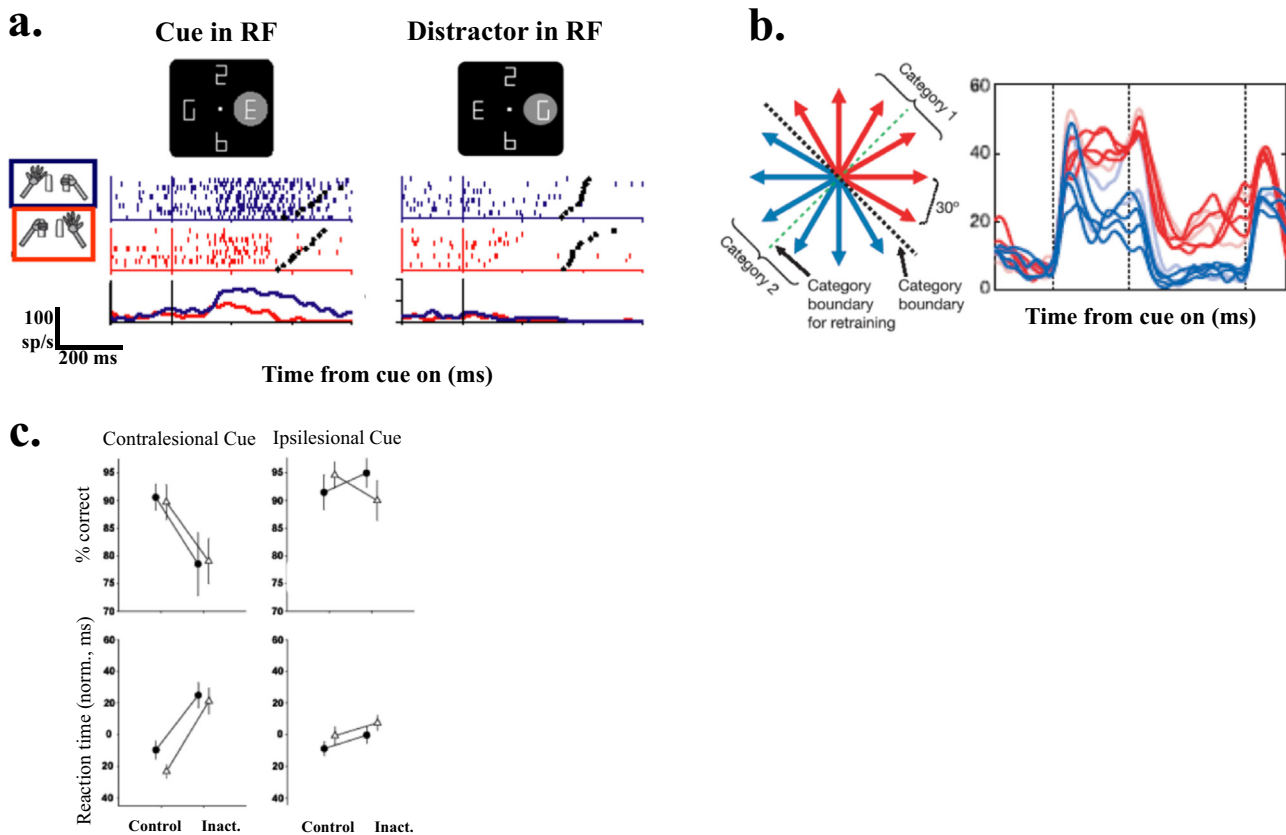
In order to examine this question, a recent study (Malcolm, Rattinger, and Shomstein, in press) presented participants with three objects, two of which were semantically related, and asked them to identify a target that was superimposed on the objects.

Importantly, the objects served only as background and were completely irrelevant to the task – i.e., did not predict target’s location or its identity. First, participants were presented with a single object that was located at the center of gaze and remained on the screen for over a second. Then, two peripheral objects appeared, one semantically related and the other semantically non-related to the central object. For example, if the central object was a toothbrush, the peripheral object may be a comb (semantically related) and a hammer (semantically unrelated). After a variable delay, a target and distractors appeared on each of the two peripheral objects. Consistent with a hypothesis that task-irrelevant semantic information influences attention, responses to targets appearing on semantically related objects were faster than those to targets on unrelated objects. Follow-up experiments showed that, even when the target was more likely to appear at a specific location – thereby validly cueing attention toward that location – semantic facilitation remained significant, although the effects occurred later in time. These results suggest that i) the visual system continually utilizes semantic information to constrain attention allocation, and ii) this influence is mandatory. Whether SPL/IPL is responsible for semantic-based speeding of responses is an open question. In fact, current research in the Shomstein lab is focused on directly addressing this very question.

Consistent with the role of semantic processing in humans, single neuron recordings in monkeys show that parietal target selective neurons are sensitive to a range of learnt associative properties of visual cues (Gottlieb and Snyder, 2010b). One such property is related to the motor affordances of a visual cue. In natural behavior action affordances are key ingredients for top-down attention allocation (Navalpakkam and Itti, 2005). For instance, our motivation to attend to a traffic light is based on the knowledge of the association between the light and subsequent actions – i.e., that red and green lights are related with, respectively, stopping or crossing the street. However, very little is known about the encoding of such stimulus-action associations in attention-related cells.

To examine this question, Oristaglio et al. (2006) trained monkeys to perform a covert visual search task where the monkeys had to attend to a peripheral cue (an “E” like shape) embedded among distractors, and report the orientation of the cue by releasing a bar held, respectively, in the right or left paw (Fig. 4a). Similar to the traffic light example, the relevance of the cue in this task was determined by its action associations – i.e., the fact that the right facing “E” instructed a right bar release and the left-facing “E”, a left bar release. Most LIP neurons responded more strongly when the cue relative to a distractor fell in the RF, providing the expected signal of visuo-spatial selection (Balan et al., 2008; Oristaglio et al., 2006). The novel result however, was that in about half of the cells this response was modulated by the manual release: some cells had stronger responses to the RF cue if the cue instructed a left bar release (Fig. 4a, left column, red vs. blue trace), while others only spatially selected the cue if it instructed a right bar release. This modulation could not be explained by spatial factors but was specifically related to the limb (right or left paw) that was associated with a visual shape.

Subsequent experiments showed that LIP neurons also reflect visuo-visual associations (Fitzgerald et al., 2011) and the categorical membership of an attended cue (Freedman and Assad, 2006). A study demonstrating category selectivity trained monkeys on a delay-match to category task, where each trial began with the presentation of a sample motion cue and the monkeys had to report whether a subsequent test stimulus fell in the same or a different category as the sample (Fig. 4b, left) (Freedman and Assad, 2006). Monkeys were first trained to divide a set of motion directions into two arbitrarily assigned categories, and were later



**Fig. 4. Modulation of LIP responses by action affordances and categorical membership a. Modulation by manual release.** Monkeys maintained gaze at the center of a display containing several letter-like shapes (panels, central dot). One shape, a right or left-facing “E” appeared at variable location, which could fall inside the neuron’s RF (left column, gray shading) or at a non-RF location (right column). Monkeys were rewarded for maintaining fixation and reporting the orientation of the “E” – right or left facing – by releasing a bar held, respectively, in the right or left paw. The bars themselves were outside of the field of view. Rightward-facing cues could appear on the left and vice versa, so the laterality of the motor response was independent of the laterality of the visual cue. The lower panels show activity of a neuron with dual sensitivity to “E” location and manual release. The neuron responded only if the “E” appeared in the RF but was silent if a distractor did (left vs. right column). In addition, when an “E” appeared in its RF, the cell was more active if the monkey released the left bar than the right bar (blue vs. red traces). Raster plots in the top panels show individual trials. Each dot represents the time of an action potential aligned on cue onset, and the black dots show the time of manual release. Trials are sorted offline in order of manual reaction time. The bottom panel shows the corresponding averaged spike density histograms (smoothed with a Gaussian kernel, sigma 10 ms). Adapted, with permission, from [Oristaglio et al. \(2006\)](#) **b. Modulation by stimulus category.** The *top left panel* illustrates the behavioral task. Monkeys viewed a sample stimulus containing random dot motion in one of 8 possible directions. After a delay period (650–1650 ms) a test motion stimulus appeared and monkeys had to release a bar if the test stimulus matched the category of motion of the sample, but continue to hold the bar otherwise. Monkeys were initially trained to categorize directions according to one category boundary (black dotted line) and then retrained to use a different boundary (green dashed line). *Top right panel* shows representative LIP neuron that had visual and delay period activity following presentation of a sample inside its RF as well as sensitivity to sample category. Firing rates were much more strongly modulated by changes in direction across, relative to within a category boundary, dissociating this modulation from simple selectivity for motion direction. Modified, with permission from [Freedman and Assad \(2006\)](#) **c. Unilateral inactivation of LIP impairs spatial but not non-spatial aspects of performance.** Performance on the “E” search task shown in [Fig. 4a](#), segregated according to the hemifield of the cue (left vs. right column) and the active limb (white vs. black symbols). Symbols show mean and standard error. Reaction times are normalized by subtracting the session mean. Inactivation (24–26  $\mu$ g muscimol at 8 mg/ml) lowered accuracy (top left) and elevated reaction times (bottom left) if the cue was in the hemifield contralateral to the inactivated hemisphere (left column) but not if the cue was in the ipsilesional hemifield. Modified, with permission, from [Balan and Gottlieb \(2009\)](#). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

re-trained using the orthogonal category boundary. LIP neurons responded to the presentation of a cue in their RF, consistent with a spatial attention response, but also responded more strongly to a stimulus if it belonged to one or the two categories ([Fig. 4b](#), right). The latter response reflected the new categorization scheme after retraining with a new boundary, clearly distinguishing it from a sensory, motion-selective response.

The wide range of non-spatial modulations that are found in LIP ([Gottlieb and Snyder, 2010b](#)) suggests that these modulations may not indicate contributions to specific functions – such as motor planning or categorization – but may be part of a mechanism for attentional selection of stimuli with different action or semantic associations. Two specific results support this contention. First, the non-spatial responses found in LIP cells do not arise independently but are primarily modulations of a visuo-spatial response. For instance, the neuronal modulations by a manual report or categorization were very strong if the attended object

was in the neurons’ RF, but much weaker if attention was directed elsewhere and a distractor was in the RF ([Freedman and Assad, 2009](#); [Oristaglio et al., 2006](#)) ([Fig. 4a](#) and [b](#), blue vs. red). This suggests that, rather than having bona fide contributions to motor planning or categorization, LIP neurons receive feedback about these processes from other brain structures, and use this feedback to modulate their visuo-spatial response.

A second result that strongly supports this interpretation comes from a study by Balan and Gottlieb ([Balan and Gottlieb, 2009](#)) showing that reversible inactivation of LIP produces deficits in visuo-spatial processing, and not in performing a limb motor response. After muscimol inactivation of LIP in one hemisphere, the monkeys’ performance was impaired if the cue was in the contralateral but not in the ipsilesional field, suggesting a role in visuo-spatial selection ([Fig. 4c](#)). In contrast, the inactivation did not cause global or limb-specific deficits in manual release, supporting the idea that LIP is not critical for limb motor planning per se ([Fig. 4c](#)).

In sum, the studies described in this section suggest that attention-related areas in human PPC and monkey LIP incorporate information about abstract, learnt properties of stimuli such as semantic relatedness, category membership, motor affordances or visual associations. While we have emphasized the hypothesis that this information plays a key role in guiding attention, and that this role is common in humans and monkeys, we must also note that attention networks also have some important differences between the two species that are likely to be important for this interpretation. Species differences in attention networks are especially pronounced in the organization of temporal areas and their connections with the frontal lobes, which are implicated in object recognition and semantic (including language) processing (Mantini et al., 2013; Patel et al., 2015; Thiebaut de Schotten et al., 2012). These differences in architecture are very likely to underlie species differences in the mechanisms by which attention is deployed based on linguistic and higher level understanding of a task context.

## 5. Reward

Rewards play central roles in learning and decision making, and recent evidence indicates that they are also powerful determinants of attention. Rewards modulate attention in a top-down fashion, with observers allocating more priority to task-relevant stimuli that are associated with higher probability or amounts of reward, consistent with an adaptive, reward-maximizing strategy (Della Libera and Chelazzi, 2006; Hickey et al., 2015; Hickey and Peelen, 2015; Navalpakkam et al., 2010; Serences, 2008). More surprising, however, are reports that rewards also operate in a bottom-up fashion, increasing the salience of stimuli that are *not* relevant and may interfere with an action or task (Kiss et al., 2009; Kristjansson et al., 2010).

The effect of rewards on visual salience, also known as value-driven attentional capture, is typically demonstrated in two-part experiments in which participants initially receive monetary rewards for correctly selecting a color-defined targets in a training phase (e.g., red color is associated with high reward, and green color is associated with low reward) and subsequently complete a test phase involving a different search task in which color is task-irrelevant (Anderson et al., 2011). On half of the trials during the test phase, one of the non-targets is rendered in the color of a formerly rewarded target from the training phase. The presence of a reward-associated distractor (e.g. a red stimulus in the search display) significantly slows the response times for the relevant target and this slowing can persist for several days after the training phase. A recent study by Lee and Shomstein (2014) showed that a reward effect that was established in an easy pop-out search task transfers to a conjunction search task, increasing search efficiency for targets previously associated with higher reward by both enhancing target salience and distractor filtering, depending on whether the target and distractors shared a critical feature. Therefore the learning of stimulus-reward associations produces persistent changes in stimulus salience that transfer to unrelated tasks, where it can facilitate performance or be a source of distraction (Anderson et al., 2011; Della Libera and Chelazzi, 2009). Additionally, recent report by Hickey and Peelen (2015) showed that effects of reward are pervasive, extending not only to rewarded stimuli in different contexts (i.e., not directly tied to the stimulus), but also guiding attention to categories of stimuli rather than individual rewarded exemplars.

Neural recordings in monkeys shows that reward-based salience profoundly affects LIP cells (Peck et al., 2009). Monkeys were trained on a task where they had a 50% chance of obtaining a reward, and each trial began with presentation of an abstract

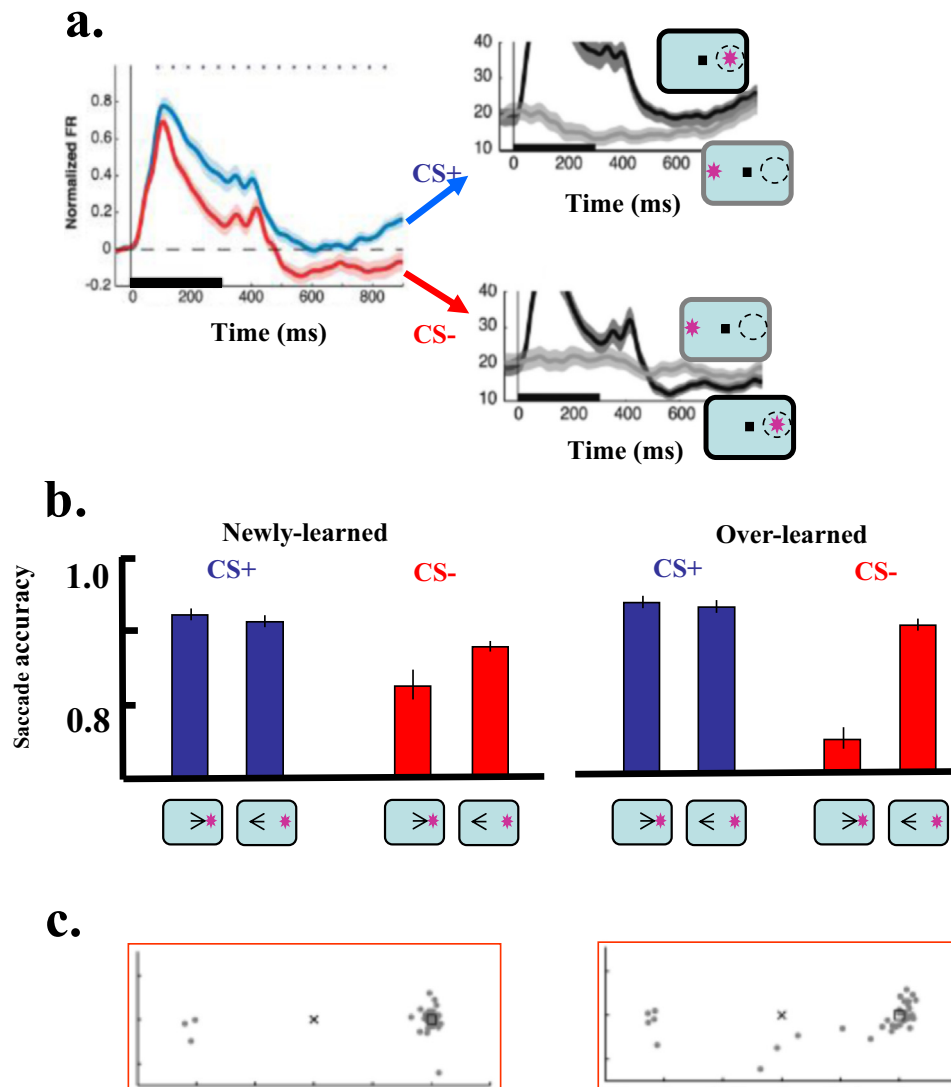
pattern that indicated whether the trial would end in a reward (CS+) or a lack of reward (CS-). The CS appeared at a peripheral visual location inside or opposite the RF of the cell, and had the opportunity to bias attention toward its location. However, the location of the CS was irrelevant to the task. After a brief delay period following the disappearance of the CS, the monkeys had to make a saccade to a second target that appeared unpredictably at the same or at the opposite location as the preceding CS.

Even though the CS was irrelevant for the subsequent action, it evoked sustained spatially selective responses in LIP cells (Fig. 5a). When a CS+ appeared in the RF, neurons had a fast transient visual response followed by sustained excitatory activity that persisted during the delay period. In contrast, when a CS- appeared in the RF, the neurons had a weaker visual response followed by sustained firing rate *suppression*. These modulations appeared specifically at the location that had been occupied by the CS showing that they could not be interpreted as global changes in arousal or motivation (Fig. 5a, right panels, black vs. gray).

The monkey's saccades reflected the spatial biases in LIP cells. Saccades were slightly facilitated if the target happened to fall at the location of a CS+ (whose representation was enhanced in LIP; Fig. 5b, blue bars), but strongly *impaired* if it happened to coincide with a CS- location (whose representation was suppressed in LIP; Fig. 5b, red bars). In the latter trial types, when the saccade target was congruent with a CS- location, the monkeys often made dysmetric saccades that failed to reach the target, which were scored as errors and lowered the overall rate of reward (Fig. 5c). Strikingly however, despite its detrimental effect, the suppression evoked by the CS- *increased* rather than decreasing with training, becoming worse for a familiar relative to newly learned CS- (Fig. 5b and c). This result rules out any interpretation in terms of a deliberate strategy or even learning based on Bayesian priors – which would predict that the bias should become weaker with training. It suggests that reward-based salience is a distinct phenomenon which is entirely independent of the task significance or the actual rewards associated with acting based on visual cues.

To examine the effect of rewards in human IPL, Lee and Shomstein (2013) conducted two experiments that combined reward manipulation with space- and object-based visual attention. A variant of a two-rectangle paradigm, mentioned above, was used in conjunction with a payoff schedule that differentially rewarded shifts of attention within a single object or between different objects. In one condition a same-object shift was associated with a high reward while a different-object shift was associated with a low reward. In another condition, the object to reward mapping was reversed, such that a different-object shift was associated with a high reward and a same-object shift was associated with a low reward. Incorrect responses were followed by a subtraction of points. A third manipulation completely removed the reward schedule (Fig. 6a).

Without a reward schedule, BOLD activity evoked by spatial shifts of attention in the IPL was modulated by object-based structure as described above. However, when the reward schedule was introduced, activity in IPL evoked by spatial shifts of attention was modulated by reward, such that shifts that were associated with a high reward evoked greater responses than those associated with low reward. Importantly, in the presence of a reward schedule the IPL and FEF no longer showed object-based effects, suggesting that the object-based signal was completely replaced by the reward associations (Fig. 6b). Similarly to the results observed in IPL, target and cue-related activity in early sensory cortex (V1-V4) reflected spatial and reward-based modulations, but not object-based modulations. These results are striking and suggest that priority signals in posterior parietal cortex are flexible: when objects are relevant for the task, it is the object signal that is integrated with the spatial representation; however, if reward is



**Fig. 5. Modulation of LIP visuo-spatial responses by expected reward.** **a.** Population firing rates (normalized) following presentation of a CS+ (blue) or CS- (red) in the RF. Each CS category contained several individual, abstract patterns that were initially novel to the monkey and were equated for size and luminance. CS presentation (300 ms, thick horizontal bar), was followed by a 600 ms delay period during which monkeys maintained fixation. The stars show time bins when firing rates were significantly modulated by reward. The right panels show, for each CS category, a comparison of activity when the CS appeared inside the RF (black) or opposite the RF (gray). Cartoons indicate trial configurations, with the dashed oval showing the RF and the magenta star, the CS location. The y axis is truncated to highlight delay-period activity. After a CS+ (top panel) or CS- (bottom panel), sustained activity was, respectively, higher or lower at the CS location relative to the opposite, non-stimulated location, indicating a spatial bias toward or away from the CS. **b.** After the end of the delay period a saccade target appeared unpredictably at either location and monkeys made a visually-guided saccade to the target. Bars show saccade accuracy for each configuration (mean and standard error), defined as the normalized angular distance between the target and the saccade endpoint). Accuracy was impaired specifically on CS- trials in which the target happened to coincide with the CS- location, indicating a repulsion from the location of the CS-. This impairment increased with training, being stronger following an over-learned relative to a newly-learned CS. **c.** The insets show saccade endpoints on CS- congruent trials on a representative session. Each point represents one saccade, and coordinates are rotated so that the target appears on the right horizontal. Saccades show a large degree of scatter, especially after an over-learned CS-. This is remarkable given that the target remains lit and clearly visible until the end of the movement. Modified, with permission, from Peck et al. (2009). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

relevant, it is the reward signal that is integrated with the spatial signal.

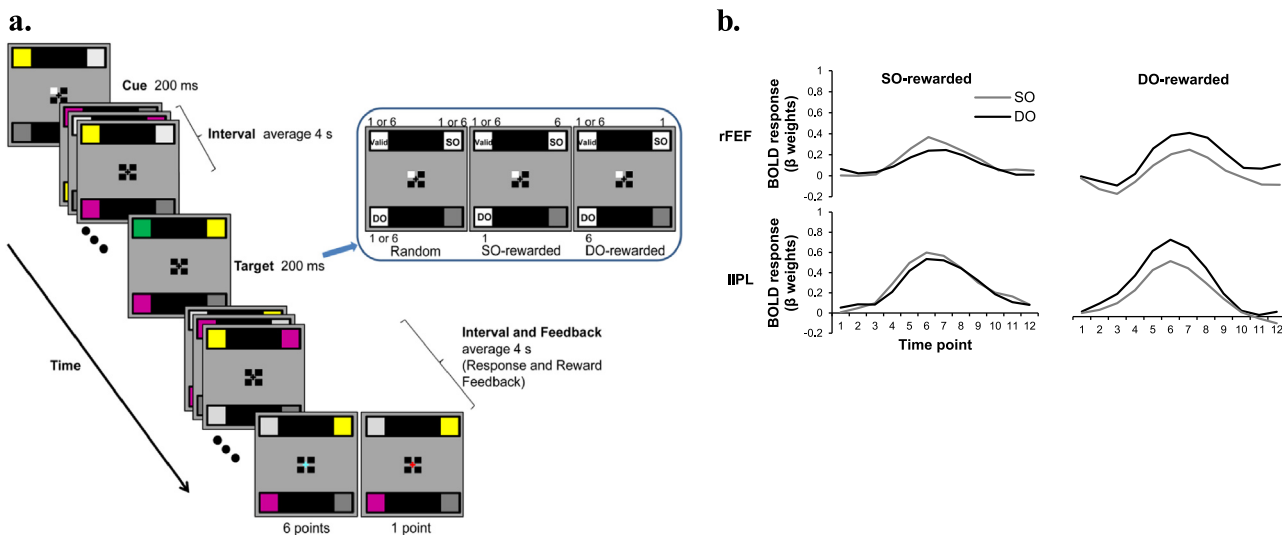
## 6. Conclusions

We have reviewed evidence that the parietal cortex in humans and monkeys multiplexes visuo-spatial information with non-spatial properties of stimuli such as object representations, motivational aspects and semantic, category and action associations. The properties of these neural responses, together with the results of reversible inactivation studies in monkeys, suggest that the non-spatial responses do not indicate parietal involvement in an unrelated array of functions – e.g., object segmentation, decision

making or categorization – but instead contribute to a common set of computations related to attentional allocation.

If correct, this view suggests a significant expansion of traditional models of spatial attention in several important respects. First, in contrast with the traditional view that parietal and frontal areas encode a purely spatial signal – a “mental spotlight” – for guiding attention, the results suggest that the parietal response is multi-dimensional, integrating multiple factors that are relevant for orienting attention. Second, rather than being segregated in different areas or neural populations, these factors seem to impinge on a common population of cells, supporting the idea that an integrated priority map guides top-down and bottom-up attention (Bisley and Goldberg, 2010; Gottlieb et al., 1998) (Shomstein, 2012a). Third, the integration is dynamic and task dependent, with different factors –





**Fig. 6.** Modulation of PPC by reward. **(a)** Each trial started with a central endogenous cue indicating the likely location of the target. Target, a green patch, appeared either in the cued location (valid), same-object (SO), or different object (DO). Three reward schedules were used separated by different scanning sessions: random, SO-rewarded, and DO-rewarded. Reward feedback was provided by changing the color of fixation. **(b)** event related timecourses extracted from right FEF and left IPL, regions that showed greater activity for spatial shift of attention (invalidly cued trials). Activity in FEF and IPL were modulated by reward. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

e.g., object assignment or rewards – influencing attention to different extent in different behavioral contexts. Finally, the correspondence between non-spatial effects in the IPL and earlier visual areas suggest that non-spatial responses are propagated to these areas – i.e., that the top-down control signal is high dimensional and produces modulations based on more than merely spatial location. Therefore, these findings can provide important constraints and inspiration for expanded models of attention control based on higher-level task factors.

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