

Social Cognition: LIP Activity Follows the Leader

A new study has found that, when a macaque monkey chooses where to look, activity in parietal cortex reflects anticipated reward value, whether from fluid to drink or from social information such as dominance.

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As we go about our everyday activities, we seem to generate movements effortlessly, but the process is not as easy as it may seem. Decisions to move to a particular location are made on the basis of signals received from the environment, such as the location of the all-important cup of coffee in the morning, but they are also influenced by intrinsic signals about the importance of that cup of coffee. Several functions of the posterior parietal cortex are involved in such tasks. The posterior parietal cortex is critical for allocating spatial attention [1] to the most salient sensory information, and for effector selection [2,3] during goal directed actions. This

brain region also plays a critical role in perceptual decision-making related to these tasks [4,5]. Human functional neuroimaging studies have supported the role of parietal cortex in the integration of multiple factors during decision-making, including categorization of visual features [6] and perceived reward [7].

A study on the macaque monkey, published recently in *Current Biology* [8], has expanded the notion of attentional and intentional selection in parietal cortex to include the integration of expected reward value, independent of reward modality, in the decision-making process. Earlier work on reward behavior has emphasized the use of juice as a motivator, which may create an environment atypical for normal behavior. Klein *et al.* [8]

sought a more ecologically plausible scenario in which they investigated the effect of social cues and juice rewards on macaque lateral intraparietal (LIP) activity during a decision-making task. In their study, monkeys chose to make a saccade to one of two cued locations for a reward. Saccades made towards the LIP receptive field target were followed by presentation of an image — of either a familiar dominant or submissive monkey, a female hindquarter, or a neutral gray square — paired with juice reward that varied in quantity. Both types of reward were held constant within blocks of trials and, thus, were predictable before making a saccade choice.

Klein *et al.* [8] found that LIP neural activity reflected the anticipated ‘value’ of the decision to look at one target over another. This variance in LIP firing activity correlated with the behavioral value of the choice regardless of the type of reward — juice or social cue. Critically, expected reward was only encoded in macaque LIP when animals made a choice between two locations or had the expectation that the following trial would require a choice. During blocked presentations of a single target, LIP activity no longer reflected anticipated reward value. This finding elegantly illustrates the importance of both the focus of attention and modality-independent reward information relative to the act of decision making. There are two broad implications of these findings for our understanding of the function of parietal cortex. First, they enhance our understanding of multiple levels of coding in macaque LIP to include behaviorally relevant reward information. Second, incorporation of a more natural basis for making saccadic decisions may help identify the role of parietal cortex in a broader network linking perception and action.

An interesting question arising from this work is whether or not the relative value of the decision is encoded by the same neurons that also encode saccade direction, effector choice or spatial focus of attention. Is relative reward value encoded orthogonally to other features coded in parietal cortex, or is it rather coded in an additive or multiplicative fashion within the same pool of neurons? In humans, parameters of the blood oxygen level dependent (BOLD) signal that underlies functional magnetic resonance imaging

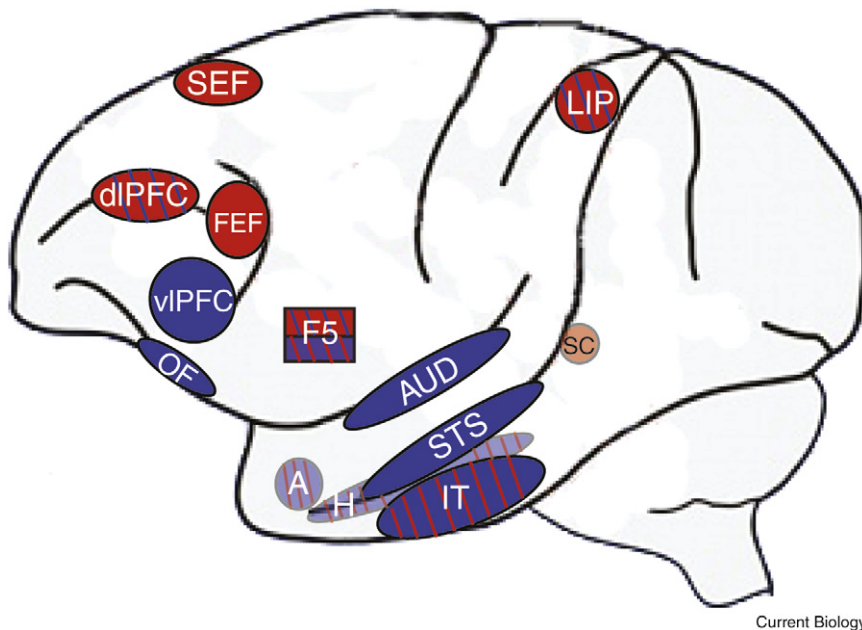


Figure 1. A diagram of brain regions associated with the oculomotor system (red) and the perception of social cues (blue).

Hatched lines in red or blue indicate evidence for oculomotor modulation or social stimulus modulation, respectively. The depicted regions are not exhaustive, since many brain areas have not been tested for sensitivity to eye movements and social stimuli. A, amygdala; AUD, auditory cortex; dIPFC, dorsolateral prefrontal cortex; F5, frontal area 5; FEF, frontal eye field; H, hippocampus; IT, inferotemporal cortex; LIP, lateral intraparietal area; OF, orbito-frontal cortex; SC, superior colliculus; SEF, supplementary eye field; STS, superior temporal sulcus; vIPFC, ventrolateral prefrontal cortex.

(fMRI) were shown to correlate with attentional demands during a visuospatial attention task [9]. These systematic changes in the fMRI signal occurred in spatially selective regions of human parietal cortex. A component of the BOLD signal was low when the task was either too easy or too hard, and high when attentional demands were intermediate. This human neuroimaging work is an example of additive activity of both the focus of spatial attention and attentional load. In light of the new macaque LIP study [8], perhaps changes within the BOLD signal represent not only the attentional focus, but also the value placed on responses at varying levels of difficulty. Further electrophysiological recordings in the macaque will be required both within and outside of the spatial receptive fields of LIP to address the issue of coding within parietal cortex.

Thus, it remains to be clarified whether, or how, multiple levels of information are encoded by cells in LIP. Indeed, this topic has already been the focus of much attention; the novel approach taken in the study by Klein *et al.* [8] is to incorporate more naturalistic motivations for allocation of attention and choices, to shed light on the neural activity used for choice behavior in real social settings. While this goal is commendable, and proved fruitful, on this point the authors leave room for further advances.

The testing paradigm described by Klein *et al.* [8] was many steps removed from 'naturalistic'. Static images of monkeys were presented on a computer monitor, in the laboratory setting removed from the monkey colony. These images were artificially associated with juice rewards, and repeated hundreds upon hundreds of times over the course of many daily recording sessions. Despite these unnatural conditions, the images were given a value that was consistent with their importance in the monkeys' actual social settings. This suggests an almost compulsory importance placed on social dominance and reproductive salience, and may indicate neural specializations that are associated with parietal cortex to extract this 'valued' information.

Visual social cues independently modulated LIP activity, but only in the context of *choice* behavior. Other brain areas are apparently responsible for attaching attentional salience or reward value to visual social cues,

implying a complex link between perceptions of — and behaviors towards — social cues (Figure 1). Brain regions important for processing visual social cues [10] also show modulation associated with eye movements [11] or show altered eye movements when lesioned [12]. Yet, to date, the connection between the perception of — and orienting towards — social cues remains to be tested in these areas. Other brain regions that might link the processing and valuation of social cues to behavioral responses include the orbitofrontal cortex, the inferior prefrontal convexity, the auditory cortex, and the hippocampus, all of which contain neurons that respond differentially to stimuli such as faces, body parts, and/or expressions and gestures (Figure 1; see [13] for review).

The data of Klein *et al.* [8] do not address the neural substrates for *perceiving* social cues; nevertheless, it is one of the first studies to show a neural link between evaluations of and actions towards social signals, as part of a broader network of regions concerned with processing social signals. Moreover, the addition of social cues as reward-associated modulators of LIP 'choice' activity may provide another framework from which to view the growing number of attention- and intention-based studies of parietal cortex function in human and non-human primates alike.

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Organelle Evolution: What's in a Name?

Plastids are organelles derived from cyanobacterial endosymbionts and the evolutionary process that gave rise to them is well understood. Or is it? The complete genome sequence of a recently evolved photosynthetic body in *Paulinella chromatophora* is cause for reflection on the distinction between 'endosymbiont' and 'organelle', and how the boundaries between these terms can blur.

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On Christmas Eve 1894 the German biologist Robert Lauterborn discovered

a strange new eukaryotic microbe, which he called *Paulinella chromatophora* [1,2]. The organism had blue-green photosynthetic bodies — 'chromatophores' — reminiscent of