

Walk the line: parietal neurons respect category boundaries

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Categorization of objects has been considered a function of the temporal ‘what’ pathway, but a new paper shows that neurons in the lateral intraparietal area of the ‘where’ pathway show learned responses based on category boundaries.

In everyday life, we are subjected to a continuous stream of visual images, no two of which are exactly alike. We might find this barrage of input overwhelming were it not for the brain’s ability to rapidly extract critical features and sort stimuli into familiar categories. Categorization can be thought of as a process by which we assign importance to the similarities and differences among stimuli. These distinctions can be innate for some classes of stimuli, but often they are learned. The critical values of the stimulus dimensions that distinguish categories define the category boundaries. Freedman and Assad¹ provide an important insight into how these boundaries are learned and represented by neurons in visual cortex, in a recent *Nature* paper.

The authors trained monkeys to categorize the direction of moving random dot patterns presented on a computer screen. If one thinks of the hour hand of a clock, all the directions between 10:30 and 4:30 were arbitrarily assigned to category 1, and the remainder belonged to category 2. Such experiments always raise a concern that the abstract categorical decision could be confounded with the motor response used to express that decision. To avoid this confound, the investigators used a ‘match-to-category’ task: monkeys viewed two successive motion stimuli whose directions were chosen randomly and judged whether the two stimuli belonged to the same or different categories. Hence, the monkeys’ behavioral responses were correlated with the same/different decision but were randomized with respect to any particular category. This is a crucial methodological point because there is evidence that perceptual decisions are functionally distinct from movement plans^{2,3}.

The investigators then recorded from neurons in two cortical areas that respond to

visual motion: the middle temporal area (MT) and the lateral intraparietal area (LIP). They found that the direction tuning of neurons in LIP was systematically biased away from the category boundary to which the monkeys were trained. Specifically, the difference in response to any two arbitrary stimuli was significantly greater if the stimuli were in different categories than if they were in the same category. In contrast, the responses of neurons in area MT, which provides direct input to LIP, did not show any such bias. These results imply that, across the population, the preferred directions of LIP neurons were shifted independently of changes in the input signals from MT.

Freedman and Assad then went a step further by retraining the same monkeys on a new category boundary that was orthogonal to the original. After retraining, they recorded a fresh population of LIP neurons whose tuning now reflected the newly learned categories. Although they did not directly show that individual neurons change their tuning during retraining, this conclusion is virtually inescapable. Their results therefore provide evidence for a form of plasticity wherein neurons can change their tuning to reflect behaviorally relevant classes of stimuli. The new data suggest that the transformation from a sensory representation of motion to a categorical representation could occur in a single synaptic layer between MT and LIP, and that this synapse could be a site of plasticity for category learning.

These results are striking for several reasons. Perhaps the most significant is that visual object recognition, which is intimately related to categorization, has long been considered a function of the temporal ‘what’ pathway and not the parietal ‘where’ pathway⁴. Damage to visual areas of the inferior temporal lobe can result in category-specific visual agnosia⁵. Such patients might be unable to recognize fruits and vegetables or different makes of car. The most famous form of visual agnosia is prosopagnosia or ‘face-blindness’, which is often caused by lesions of the medial occipitotemporal cortex⁶. In contrast, damage to parietal cortex almost never results in problems with object recognition.

Rather, parietal lesions typically result in spatial neglect⁷, a complex disorder that involves an inattention to stimuli in the contralesional visual space. Although visual pattern selectivity has been described in LIP (ref. 8), Freedman and Assad now provide some of the first evidence for categorical representations in parietal cortex.

Although LIP is only a few synapses removed from the retina (the shortest path from the retina to LIP comprises four synapses: retina to LGN to V1 layer IVb to MT to LIP), it is gaining recognition as a critical watershed for transforming stimulus-bound visual activity into more abstract representations related to spatial attention, decision making and movement planning. Current theories posit that LIP is a ‘salience map’ that tags important locations in the visual scene for perceptual or motor tasks⁹. LIP is also involved in evaluating the quality of sensory information during motion discrimination tasks¹⁰. Although the results of Freedman and Assad were not anticipated based on previous work in LIP, they nevertheless make sense in this context. After all, categorization involves attending to specific stimulus features and evaluating the relationship of those features to the category boundary.

The new results point to possible mechanisms of category learning. One such mechanism is based on reward expectation (or spatial attention related to expectation of reward), which modulates neuronal responses in LIP (ref. 11). In the experiments of Freedman and Assad, stimuli that were near the category boundary were associated with lower behavioral performance in terms of percent correct. This means that these stimuli were rewarded with lower probability than other stimuli. It would be reasonable to infer that monkeys had a lower expectation of reward for these stimuli.

One possible model argues that reward expectation modulates the gain of visual neurons in LIP. We call this the ‘reward-gain’ model (Fig. 1a). If one assumes that a reward expectation signal varies with behavioral performance and that this signal interacts with the stimulus-driven response of direction-tuned neurons, then the preferred directions could be biased so that they cluster around an axis orthogonal to the category boundary.

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Freedman and Assad examined their data to evaluate the reward-gain model. One prediction of the model is that overall neuronal responses to stimuli near the category boundary should be weaker than responses to stimuli far from the boundary. The authors found that the average population response was the same for all stimuli regardless of their proximity to the boundary. The reward-gain model also predicts that neurons with preferred directions near the boundary should be more broadly tuned than those with preferred directions far from the boundary (J. Ditterich, personal communication). This prediction also was not supported by the data.

The fact that some stimuli are more predictive of reward than others seems not to explain the change in tuning of LIP neurons after category learning in any straightforward manner. However, at some level, reinforcement must be involved in category learning. Parkinson and Huntington disease patients are impaired in certain kinds of category-learning tasks, implying a role for the dorsal striatum¹², a structure involved in reward expectation¹³. A model (Fig. 1b) in which the synaptic strength of MT-to-LIP connections is modulated by a reinforcement signal originating in the striatum might explain changes in LIP tuning better than the reward-gain model. The reinforcement-learning model tends to broaden the tuning curves for LIP neurons such that they respond only to stimuli in one category and do not discriminate well within that category (yellow tuning curve, Fig. 1b).

So does categorization 'happen' in LIP? It seems clear that LIP can contribute to the representation of some category boundaries. However, categorization requires more than this. At a minimum, categorization involves comparing sensory data against a category boundary. Neurons that are involved in making this comparison should encode the relationship of any given stimulus to the category boundary. For example, a categorization neuron might respond more strongly to stimuli near the boundary than to those far away. It is not clear that this

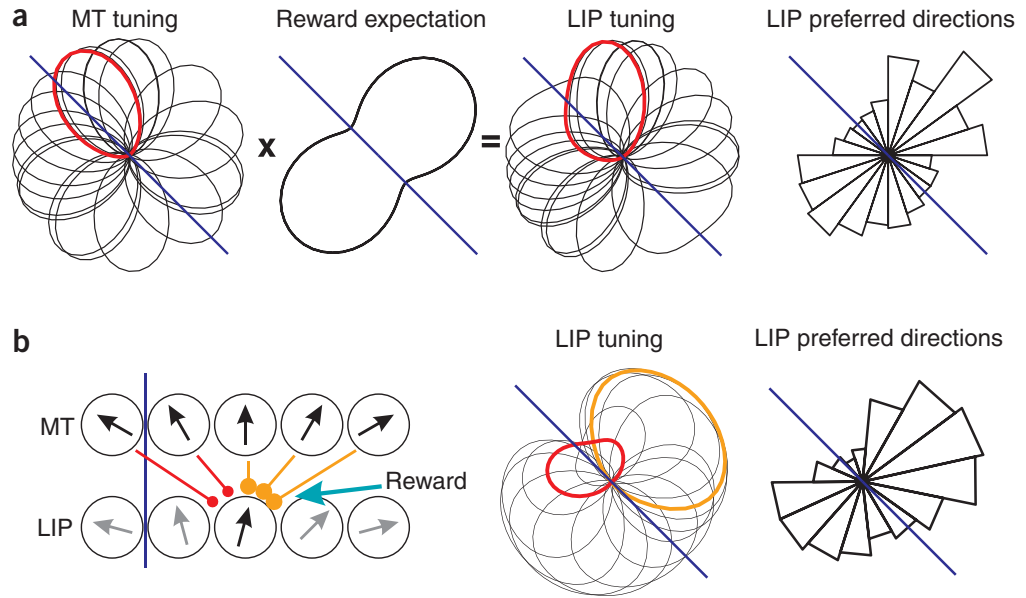


Figure 1 Reward-based models of LIP category learning. **(a)** Reward-gain model. This model starts with a population of MT cells that have random preferred directions. Upper left, each ellipsoidal curve represents the direction tuning of a single MT neuron. Only a random subset of the total neurons (500) in the simulation is shown. The response of each MT neuron is multiplied by the peanut-shaped reward expectation signal to produce the LIP tuning curves. Reward expectation follows the animal's behavioral performance and is lowest near the category boundary (blue line). The effect is to bias the preferred directions in LIP toward an axis orthogonal to the category boundary. (Compare red tuning curves in MT and LIP.) It also tends to broaden tuning curves near the boundary. The distribution of preferred directions in LIP (upper right) shows a preponderance of cells with preferred directions orthogonal to the category boundary. **(b)** Reinforcement-learning model. MT-to-LIP synapses are modified according to a simple rule: if an MT neuron was active on a trial that was rewarded, its output is strengthened (yellow connections, left); if the MT neuron was active on trial that was not rewarded, its output is weakened (red connections). Because reward probability is lower near the category boundary, the response of those LIP neurons tends to shrink (red curve, lower middle), whereas the response of LIP neurons tuned to directions away from the boundary tends to broaden (yellow curve). This model also produces LIP tuning functions with preferred directions biased away from the category boundary (lower right).

comparison occurs in LIP, as, on average, LIP activity did not vary with stimulus direction. Other work on categorical decision making has identified several regions, including the striatum, medial prefrontal cortex and anterior insula, in which activity varies depending on the proximity of the stimulus to the category boundary¹⁴. Previous work¹⁵ showed that some neurons in ventrolateral prefrontal cortex are more strongly activated for stimuli close to the category boundary. Thus, it is possible that LIP is involved in representing categorical boundaries, whereas the frontal cortex is involved in performing the comparison between the stimulus and the boundary to categorize the stimulus.

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