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Significance of objects in the perirhinal cortex

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The perirhinal cortex is known to play a role in recognition memory and visual perception of objects. A recent single-unit recording study adds to our understanding of perirhinal cortex function, suggesting that it may also play a role in evaluating the significance of objects in a context-dependent manner.

In real-life situations, the significance and value of an object can be context-dependent. For example, a ticket purchased at a county fair can be used in exchange for food, rides and games, but beyond the fairgrounds that same ticket would have little value. For visitors, information about the significance of the ticket inside and outside of the fair environment can be used to guide behavior and impact decisions such as how much to spend on tickets for a single day of fair attendance. Lesion and single-unit recording studies in non-human primates have identified the perirhinal cortex (PRc) and ventral temporal area TE as critical for object processing, but little is known how context influences object representations in these regions. A recent study addressed this question by using single-unit recordings to explore how neurons in PRc code for the significance of objects in different reward contexts relative to visual area TE [1].

Many theories argue that because the PRc is at the apex of the ventral visual processing stream, it can form highly specific representations that disambiguate visually similar objects in both perceptual and mnemonic tasks [2]. However, in addition to receiving visual inputs from area TE, the PRc has strong reciprocal connections with the hippocampal formation, amygdala, and prefrontal cortex [3]. Accordingly, recent theories have suggested that the PRc is an important component of a broader anterior-temporal system that is principally involved in representing the meaning and significance of entities [4]. In line with this theory, studies in humans have demonstrated that the PRc represents object-specific semantic information [5], conceptual implicit memory [6], and is a site of cross-modal integration, where object features are bound into a conceptual representation [7]. Taken together, these findings strongly indicate that the PRc is crucial for representing conceptual, as well as perceptual, object features.

Building on this prior work, Eradath and colleagues used single-unit recordings to investigate how the PRc encodes the motivational significance of objects [1]. In their experiment, two monkeys were exposed to sets of four highly visually similar objects while performing a simple task in which each object was deterministically followed by a fixed outcome. Within each visually similar set, two of the objects were followed by a reward and two objects were not rewarded. Thus, this experimental design pitted visual similarity against motivational significance (i.e., reward or no reward). Eradath and colleagues found that cells in both PRc and TE represented information about the visual object sets and reward outcomes during the cue period, but the prevalence of these signals differed sharply across the two areas. Cells in area TE were more likely to show responses that differentiated between the object sets, whereas a higher proportion of cells in PRc showed responses that differentiated between rewarded and non-rewarded objects within each set. These results support the idea that neurons in PRc carry information beyond higher-order visual or perceptual properties represented by strictly visual areas, and that PRc is particularly involved in supporting generalizations about the motivational significance, and possibly the 'meaning,' of items.

To further explore how the PRc supports this type of generalization, Eradath *et al.* systematically altered the 'time context' of cue-outcome associations. Specifically, 'time context' was manipulated by creating two-part trials composed of two consecutive cue-outcome sequences. The first part of each trial consisted of a deterministic cue-outcome contingency that had been previously learned. In the second part of the trial, a learned object was presented, but the outcome that followed was randomly determined. In other words, in the first half of each trial, the significance of each object was known, but in the second half of the trial, the significance of each object could not be known. After monkeys spent approximately 17 weeks performing the two-part deterministic-random trials, the order of trial parts was switched. In this stage, cue-outcome contingencies in the first half of the trial were random and in the second half of the trial they were deterministic. After approximately 19 additional weeks, the order of trial parts was again reversed, with deterministic cue-outcome contingencies in the first half of the trial, followed by random cue-outcome contingencies.

In these experiments, Eradath and colleagues found that PRc signaled reward associations about each object only in the deterministic parts of the trial, whereas neurons in TE signaled outcome information following presentation of object cues in both parts of the trial. Eradath *et al.* interpret these results as evidence that PRc neurons are sensitive to both cue-outcome associations as well as the 'time context' within which they occur. It should be noted that this operationalization of 'time context' differs from

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Box 1. Outstanding questions

- Does PRc assign similar representations to visually dissimilar objects that have a similar meaning or motivational significance? Multivariate analyses of population-level activity patterns could be useful in addressing this question and provide a clearer picture of the different roles of PRc and TE in object representation.
- Is context-dependent significance coding in PRc dependent on inputs from the hippocampus, parahippocampal cortex, prefrontal cortex, and/or ventral striatum? In particular, the hippocampus or prefrontal cortex might be expected to signal changes in task context that could modulate responses to objects in PRc.
- How are object representations in PRc updated in response to environmental feedback? Eradath *et al.* suggest that PRc neurons do not represent reward prediction errors, but it is not clear whether PRc responses to cues differentiated between unexpected and expected reward outcomes during non-contingent trial periods.
- Does the PRc encode information about the temporal context of an object, relative to other ongoing events, independently of reward outcomes? Alternatively, is the PRc more specifically engaged in using context to determine the motivational significance of an object?

the typical use of the term to refer to associations between temporally contiguous events, which has been strongly associated with hippocampal function [8]. The results of Eradath *et al.* might be better described as showing that that the PRc is involved in representing the significance of objects in a manner that is context-sensitive. In other words, PRc neurons might encode the significance of an object only in situations in which the meaning is clear. In situations where the significance of the object is ambiguous, however, the PRc no longer signals this information.

The results of Eradath and colleagues raise many new questions about how the PRc integrates various attributes of an object and how different regions signal the current significance of an object to PRc (Box 1). For now, however, it seems likely that PRc represents information involved in the purchase of far too many ride tickets at the fair, as well as the decision to trash them as soon as you get home.

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