Expectancy-related changes in the firing of dopamine neurons depend on the hippocampus

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Abstract:

The orbitofrontal cortex (OFC) and hippocampus (HC) both contribute to cognitive maps that support flexible behaviors. Previously, Takahashi et al. (2011) recorded dopamine neurons in sham and OFC-lesioned rats performing an odor-based choice task, in which reward prediction errors (RPEs) were induced by manipulating the expected reward across blocks. They found that OFC supports dopaminergic RPEs in the VTA, particularly when those errors depend on hidden or inferred information. Here we extended this approach to examine the contribution of the HC. Dopamine neurons recorded from ipsilateral HC lesioned rats showed intact responses to the odor cues, but not to the delivery and omission of rewards. To explain these phenomena, we developed a hierarchical temporal difference reinforcement learning model in a partially observable semi-Markov framework. By assuming HC is necessary for estimating the upper-level hidden states that distinguished the trial blocks, we successfully reproduced the results observed in HC-lesioned rats. The results contrast the respective roles of the OFC and HC in cognitive mapping and demonstrate that dopamine neurons access a rich set of information from distributed regions.

Keywords: dopamine; hippocampus; reward prediction error; learning.

Results

We recorded single-unit activity from dopaminergic neurons in the VTA of male Long-Evans rats with ipsilateral sham (n=5, 72 neurons) or neurotoxic lesions targeting the HC (n=9, 117 neurons) during an odor-guided choice task. On each trial, rats sampled odors and then responded at one of two fluid wells. The odors signaled the availability of sucrose reward in the left or right wells. To induce errors in reward prediction, we manipulated either the timing or the number of rewards expected in each well across blocks of trials (Fig. 1). Positive prediction errors were induced by making a previously delayed reward immediate or by adding more rewards, whereas negative prediction errors were induced by delaying a previously immediate reward or by decreasing the number of rewards.

Rats changed their choice behaviors across blocks in response to the changing rewards, responding more quickly and accurately when the earlier or larger reward was at stake. Moreover, there were no significant effects of the ipsilateral HC lesions on these choice behaviors.

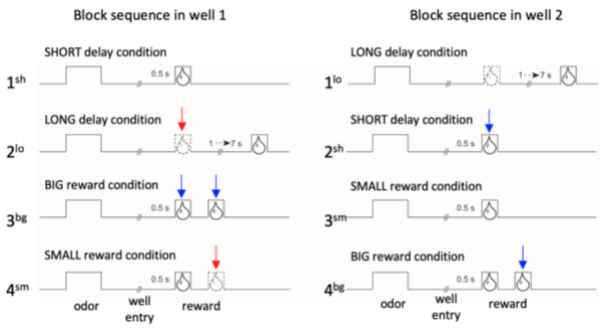

Figure 1: Deflections show the timing of stimuli presented to the animal across different trial blocks.

Deflections show the timing of stimuli presented to the animal on each trial across different trial blocks. Positive and negative RPEs are indicated by red and blue arrows, respectively.

Ipsilateral Hippocampal Lesions Affect Reward-evoked but Not Cue-evoked Activity in VTA Dopamine Neurons

RPE signaling was observed in response to changes in reward in dopamine neurons in control rats. The neural activity was elevated for unexpected rewards and suppressed for omitted expected rewards. In contrast, dopamine neurons in HCx rats did not increase firing when the unexpected reward was delivered, nor did they suppress firing when an expected reward was omitted. Thus, dopamine neurons recorded in rats with ipsilateral HC lesions showed degraded bidirectional changes in firing in response to manipulations of reward.

The activity of dopamine neurons in control rats also differed for the odor cues. Dopamine neurons exhibited higher firing during the presentation of the high-valued cue than during the presentation of the low-valued cue, a difference that reversed in each block early in learning. Surprisingly, roughly similar effects were also evident in dopamine neurons recorded in HCx rats, and no significant differences between groups were found (ANOVA, $p > 0.10$). Thus, dopamine neurons recorded from rats with ipsilateral HC lesions showed normal changes in firing in response to the cues.

Hippocampal Lesions Disrupt the Segregation of States Available across Blocks

To better understand how the hippocampus contributed to the pattern of results, we developed a temporal difference reinforcement learning model within a partially observable semi-Markov framework (Daw et al., 2006) to describe the task and reproduce neural findings. Recognizing the extensive training history of the rats, we created separate sets of states for each block, reflecting the unique reward contingencies of each block (Fig. 2). This resulted in a hierarchical state space in which lower-level states described the process within individual trials and upper-level states provided priors of transitions to states that belonged to each block, which were updated based on recent reward history. This model reproduced the pattern of RPEs at the time of reward delivery and cue sampling in dopamine neurons from control rats.

We modeled the effect of HC lesions as a blurring of transitions between the upper-level states, reflecting the hypothesis that HC would be necessary to maintain hidden information for identifying blocks. The imprecise transition probabilities caused the estimation of the current block to be more heavily influenced by external observations. As a result, the lesioned model quickly altered its current estimated state to states belonging to other blocks and adapted to changes in reward outcome, rather than evoking RPEs and adjusting the state value accordingly. This model also captured the RPE signals in response to the cues observed in the HCx rats by updating the transition probabilities based on reward history, leading to an update in the estimated belief state behind the odor cues after initial trials in a block and resulting in changes in cue-evoked activity.

Overall, our model, simulating HC lesions as a blurring of high-level internal information across blocks, captured the dopamine neurons' firing in lesioned rats, suggesting that HC may be important for maintaining and updating higher-order state representations, which capture the task block structure in the cognitive map.

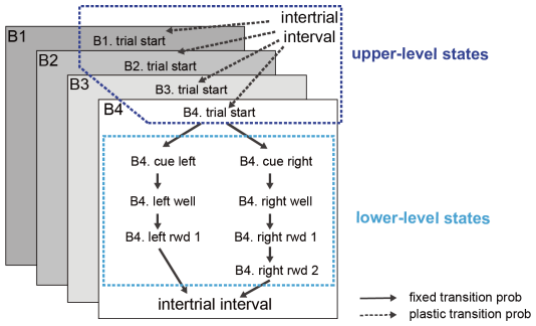

Figure 2: Hierarchical state space representation.

Available transitions between states are marked by arrows. Dashed arrows indicated plastic transitions, whose probabilities are updated over trials. Solid arrows are transitions with fixed probabilities.

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