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Fictive Reward Signals in Anterior Cingulate Cortex

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Summary

Monkeys adjust their behavior in response to outcomes that they have observed but not directly experienced, and single neurons within the anterior cingulate cortex respond to these fictive rewards they same way they respond to experienced rewards.

The neural mechanisms supporting the ability to recognize and respond to fictive outcomes, outcomes of actions that one has not taken, remain obscure. We hypothesized that neurons in anterior cingulate cortex (ACC), which monitors the consequences of actions and mediates subsequent changes in behavior, would respond to fictive reward information. We recorded responses of single neurons during performance of a choice task that provided information about the reward values of unchosen options. We found that ACC neurons signal fictive reward information, and use a coding scheme similar to that used to signal experienced outcomes. Thus, individual ACC neurons process both experienced and fictive rewards.

People routinely recognize and respond to fictive outcomes – rewards or punishments that have been observed but not directly experienced (1–3). Fictive thinking affects human economic decisions (4) and is disrupted in disorders such as anxiety and impulsivity (5). Moreover, monkeys respond to information about rewards they have not directly experienced (6) or were received by other monkeys (7). To understand the neural mechanisms that mediate these processes, we investigated how fictive reward information is encoded in anterior cingulate cortex (ACC), part of a neural circuit that mediates outcome-contingent changes in behavior (8, 9, 10) and processes fictive information in humans (11). ACC is interconnected with orbitofrontal cortex (OFC), which mediates fictive thinking in humans (5, 12).

In our task, monkeys chose from among eight white targets arrayed in a circle (28). Seven low value targets (LV) provided small rewards (100 μL), while the eighth target (high value, HV) provided a variable reward with a larger expected value (EV). Its value on each trial was selected randomly from 6 possibilities (0, 200, 267, 300, 333, 367 μL). Once the monkey selected a target, the values associated with all eight of the targets, represented by their colors, were revealed (Fig. 1A–B). After a half-second delay, the monkey received the reward associated with the chosen target. On the next trial, the position of the HV target either remained in the same position (60% probability) or moved one position clockwise (40% probability).

Only trials when monkeys maintained fixation were analyzed (90.6% of trials). Because the HV target had a greater EV than LV targets (243 μL vs. 100 μL), we expected that monkeys

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would prefer it. Indeed, in a control task that explicitly cued HV location, monkeys chose it on 93.4% of trials. In the standard task, monkeys chose the HV target (45.6% of trials) more often than chance ($p < 0.005$, binomial test, Fig. 2A). Monkeys earned 165.0 μL per trial, 88.5% of the amount earned by an omniscient observer with access to information about the value of all targets on all preceding trials (28). Monkeys chose targets adjacent to potential HV targets more often (37.7% of trials) than more distal targets (16.7% of trials, $p < 0.005$, binomial test, Fig. 2A), suggesting that they understood the probabilistic relationship between the HV target on the current trial and its likely location on the next.

Large fictive rewards promote gambling in humans (13, 14); we hypothesized that monkeys would likewise preferentially choose HV options after large fictive rewards. We observed this pattern (Fig. 2B, black line, $r = 0.300$, $p < 0.001$). This effect may reflect an increased willingness to switch from to a new target, as likelihood of switching increased with larger fictive outcomes (Fig. 2C, $r = 0.199$, $p < 0.001$). One alternative explanation for these effects is that HV targets may have positive associations that influence behavior. This explanation is unlikely for several reasons. First, obtained rewards never depended on unselected targets on that trial, so any associations between these fictive stimuli and reward values would be eliminated over the thousands of training trials that preceded recording. Second, immediately following choices, monkeys were no more likely to make a second saccade to (Fig. 2D, $r = -0.02$, $p > 0.2$), nor faster to shift gaze to (Fig. 2E, $r = 0.008$, $p > 0.2$) high-value fictive targets than to low-value fictive targets, indicating that attention and motivation were roughly similar following all fictive outcomes. Third, we performed a control task in which the HV target remained white and a colored square appeared in the center of the monitor during the delay following the trial. This square's color did not indicate what reward could have been received - and thus provided no fictive information - but had the same associations as the fictive targets. Monkeys' choices on subsequent trials did not depend on the color of this stimulus (Fig. 2F, $r = 0.005$, $p > .6$).

An example ACC neuron showed clear phasic responses around the time of gaze shifts to targets; the amplitude of these responses was correlated with the size of both the experienced reward (Fig. 3A, $r = 0.056$, $p < 0.001$, the 6 rewards are grouped into 4 categories to simplify presentation) and the size of fictive outcomes on trials when the monkey chose the LV target (Fig. 3B, $r = 0.037$, $p < 0.001$). The amplitude of phasic responses of most neurons reflected experienced reward size (n = 46/68, 67.7%), and were usually greater for larger rewards (n = 39/46 neurons, 84.8%). Responses of 50% of neurons reflected fictive reward size (n = 34/68); these responses were usually greater for larger fictive rewards (n = 30/34, 88.2%, $p < 0.05$). A substantial proportion of neurons (35.5%, n = 24/68) showed tuning for both experienced and fictive outcomes; most were tuned in the same direction for experienced and fictive rewards (91.7%, n = 22/24). The majority of neurons showed matching tuning for experienced and fictive outcomes (97.0%, n = 66/68). For the population, the average response strength was greater for experienced than for fictive reward outcomes ($p < 0.01$, bootstrap t-test). These phasic neural responses are tightly coupled to gaze shifts to visual targets. These responses may thus reflect visual stimulation, reafferent oculomotor signals, or attention to the cue. Importantly, the amplitude of these phasic responses carries information about the value of fictive outcomes.

To test the hypothesis that responses to fictive rewards may contribute to behavioral adjustment, we calculated the trial-by-trial correlation between firing rate and likelihood of choosing the optimal target following LV trials for all neurons (Fig. 4A). To control for the different neuronal responses to different fictive outcomes, we analyzed data separately for each fictive reward. We found a positive correlation for four of the six fictive outcomes ($p<0.001$), and no correlation for the remaining two ($p>0.05$). These results raise the possibility that firing rate signals subsequent changes in behavior and not fictive outcomes

(15). However, a second analysis revealed that firing rates were correlated with fictive outcome preceding trials in which monkeys chose optimally ($p<0.001$). This analysis controls for any adjustment signal, and confirms that ACC neurons do not merely predict behavioral switching. Finally, reaction times did not correlate with likelihood of choosing the optimal target across all recording sessions ($p>0.5$, correlation test), thus controlling for the possibility that the correlation between firing rate and adjustment merely reflects uncontrolled variations in arousal.

One alternative explanation for these data is that fictive outcomes, by influencing behavior and thus future rewards (Fig. 2B), serve as the first predictive cue of the reward on the next trial. We find this alternative explanation unlikely for several reasons. First, a choice intervenes between the time of the fictive cue and the reward at the end of the next trial, which is itself probabilistic. The value of the subsequent reward is therefore not strictly predicted by the fictive cue. Second, the reward signal would have to skip the next salient/rewarding event (the reward on the present trial) and signal the subsequent one (the reward on the next trial); such a signal would be highly unusual, and has not to our knowledge been observed in ACC or any other brain area. Third, if fictive outcomes are perceived as reward-predicting cues, they should elicit faster reaction times and greater accuracy on the next trial (16). We did not observe these effects ($p>0.5$ for both RT and accuracy, Student's t-test). Fourth, if the reward on the next trial is larger than the value cued by the fictive outcome on this trial, we should see positive deflections in the neuronal response. Similarly, if the reward on the next trial is smaller than the value cued on this trial, we should see negative deflections in the neuronal response. However, we did not observe any dependence of HV neuronal response on previous fictive value ($p>0.3$, Fig. 4B). Collectively, these data indicate that the behavioral and physiological correlates of fictive rewards are not an artefactual consequence of simple extended reward associations.

In summary, the most parsimonious explanation for monkeys' behavior in this task is that they recognize and respond to fictive outcomes, and responses of ACC neurons are sufficient to guide such fictive learning. Neural markers of fictive outcomes have so far been limited to non-invasive measures. Hemodynamic activity in the ventral caudate, which is connected with ACC, reflects fictive learning signals (14) and ACC activity tracks the correlation between craving for cigarettes and fictive learning (11). The error-related negativity, an ERP component with a possible source in the ACC, tracks fictive outcomes (17). Here we show that the same neural circuit carries information about fictive outcomes in monkeys. Moreover, information about both experienced and fictive outcomes is encoded by the same neurons and is represented using a similar coding scheme. The correlation between firing rate and behavior suggests that these neurons do not simply tag the incentive salience of a stimulus (18, 19), but also reflect neuronal processes that translate outcomes into behavior. Thus, ACC may integrate information about obtained rewards—likely signaled by the dopamine system (20, 21)—with information about observed rewards--presumably computed in the prefrontal cortex (22)—to derive a model of the local reward environment in the near future. These findings are consistent with the idea that ACC represents both real and fictive reward outcomes to dynamically guide changes in behavior (9, 23–26). Such a mechanism may be crucial in complex social environments, where the behavior of others provides a rich supply of fictive information (14, 27).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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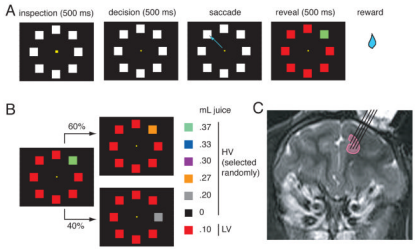

Fig. 1.

Task and recording location. **A.** Schematic of standard task. Fixation point and eight white squares appear; 500 ms after fixation, monkey chooses one target, and all targets change color, revealing their value. A half-second later, reward is given. **B.** Between trials, HV target either remains at the same position (60% chance) or moves to adjacent position (40% chance). **C.** MRI of monkey E. Recordings were made in ACC-sulcus.

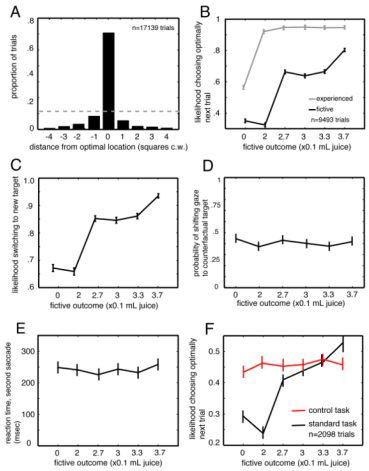

Fig. 2.

Fictive outcomes influence behavior. **A.** Histogram of distance between monkeys' choices and optimal target, measured in squares clockwise. Dashed line: chance performance. **B.** Likelihood of choosing optimally increases as a function of both fictive and experienced reward outcome on previous trial. Black: trials following choice of LV. Gray: trials following choice of HV. **C.** Likelihood of switching to new target increases with size of fictive outcome on previous trial. **D. and E.** Likelihood and latency of immediately shifting gaze to HV location are not affected by fictive reward. **F.** Likelihood of choosing optimally is not influenced by a colored square presented during delay between trials (red line).

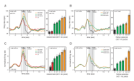

Fig. 3.

ACC neurons signal both experienced and fictive rewards. **A.** Left: PSTH showing responses of example neuron following choice of HV target. Response grows with reward size. Vertical dashed lines indicate, successively, the time outcomes are revealed and reward is given. Shaded gray region indicates epoch used for bar graph showing average (+− 1 SE) response of neuron for each experienced reward size. **B.** Responses of same neuron for fictive rewards. Experienced reward was identical (100 μL) in all cases. **C.** Population response (n = 68 neurons) for experienced rewards, normalized to maximal firing rate for each neuron. **D.** Population response for fictive rewards.

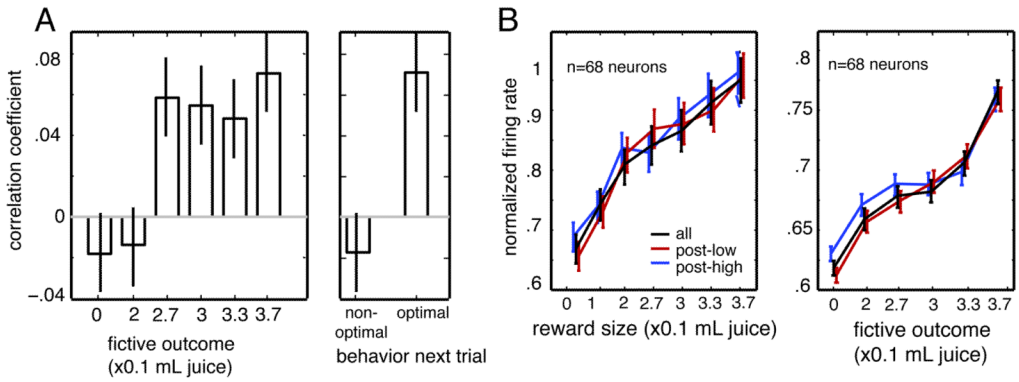

Fig. 4.

Neuronal responses signal both fictive rewards and subsequent adjustments in behavior. **A.** Firing rates following LV trials predict optimal choice on next trial for four of the six fictive outcomes. **B.** Neuronal responses to experienced rewards are identical on the trial that follows low (0 μL, red line) and high (>= 300μL, blue line) fictive outcomes, and thus do not signal reward prediction errors.