Dopamine reward prediction errors are modulated by an internal bias during stimulus discrimination

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Under uncertain stimulation conditions dopamine (DA) responses to relevant task cues reflect cortical perceptual decision-making processes, such as the certainty about stimulus detection (de Lafuente and Romo, 2011) and evidence accumulation (Nomoto *et al.*, 2010), in a way compatible with the reward prediction error (RPE) hypothesis (Sarno *et al.*, 2017). This suggests that the midbrain DA system receives information from cortical circuits about decision formation and transforms it into a RPE signal. If so, DA phasic activity should reflect a variety of phenomena, including internally generated biases. This is because biases influence decisions and performance and hence they are expected to modulate the error in the prediction of reward. To test this hypothesis and acquire further insight into how DA neurons behave under uncertainty we used the two-interval, two-alternative forced-choice paradigm. These tasks present a contraction bias whereby the sensory feature of the first stimulus is perceived as if its value were shifted to the center of its range. Specifically:

1. We analyzed the firing rate of DA neurons recorded in monkeys discriminating the frequency of two vibrotactile stimuli.
2. Although naively the response to the first stimulus should only code the predicted average reward, it was modulated (but not tuned) by the value of the frequency in the way expected from the bias.
3. Similarly, the response to the second stimulus depended on the stimulus pair in a way consistent with the bias.
4. The activity during the comparison period was modulated by confidence, defined using a Bayesian model for the choice.
5. The reward prediction error obtained from a reinforcement learning model reproduced the phasic response to the second stimulus and its dependence on confidence.
6. The DA activity was above baseline throughout the delay (memory) period. It was neither tuned nor modulated by the first frequency, pointing to quite different roles of delay and phasic activities.

The results support the notion that the phasic and delay activities of DA neurons have quite different roles. The phasic activity of DA neurons coded RPEs that were modulated by internal biases. Instead their activity during the delay period was not tuned to the stimulus, did not exhibit bias effects and changed throughout the duration of that period; these properties point to a role in stabilizing working memory in frontal areas.

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