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Dopamine and proximity in motivation and cognitive control

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Cognitive control — the ability to override a salient or prepotent action to execute a more deliberate one — is required for flexible, goal-directed behavior, and yet it is subjectively costly: decision-makers avoid allocating control resources, even when doing so affords more valuable outcomes. Dopamine likely offsets effort costs just as it does for physical effort. And yet, dopamine can also promote impulsive action, undermining control. We propose a novel hypothesis that reconciles opposing effects of dopamine on cognitive control: during action selection, striatal dopamine biases benefits relative to costs, but does so preferentially for 'proximal' motor and cognitive actions. Considering the nature of instrumental affordances and their dynamics during action selection facilitates a parsimonious interpretation and conserved corticostriatal mechanisms across physical and cognitive domains.

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Introduction

Cognitive control is essential for flexible, context-sensitive planning and decision-making. Recent studies have shown that striatal dopamine (DA) signaling can alternatively promote cognitive control, boosting accuracy and speeding reaction times, and undermine it, yielding impulsivity. Here, we review evidence for these opposing effects and propose a novel hypothesis to explain why DA sometimes promotes and sometimes undermines cognitive control, in terms of cortico-striatal action selection mechanisms and biases.

DA offsets effort costs, promoting control

Although cognitive control is necessary for flexible, adaptive functioning, it is also subjectively costly [1,2•,3], causing demand avoidance [4] and reward discounting [5,6]. Control is thought to be recruited in proportion to potential benefits less effort costs [7]. The nature of subjective effort costs is yet unresolved: they may reflect mechanisms to reduce cross-talk interference among multiplexed control signals, or opportunity costs incurred by resource allocation [2•]. Nevertheless, the consequences are real: higher subjective costs erode control under fatigue [8], and in advanced cognitive aging [5]. Deficient motivation may also partly account for cognitive deficits in schizophrenia [9–12] and disorders including depression and ADHD [1].

Incentives, conversely, promote cognitive control [3], and these effects are likely mediated, in part, by dopamine (DA) signaling in the striatum [13]. Phasic DA signals train cortico-striatal synapses to gate cognitive actions, such as working memory updating and task-set selection, according to their relative reward and punishment histories, by modulating synaptic plasticity in direct and indirect pathways, respectively [14,15•]. Extracellular DA can also convey momentary motivation, biasing high-benefit, high-cost actions over low-benefit, low-cost actions during action selection [15•,16–20,21••]. Momentary, DA-mediated motivational signaling explains both why incentives boost apparent control for speed, accuracy, and distractor resistance in a saccade task, and also why these incentive effects are attenuated in Parkinson's disease [22••].

Importantly, striatal DA dynamics during goal-directed behavior suggest that they are well-suited to convey an evolving willingness to work over extended intervals that cognitive control requires [21••,23]. Key features include protracted ramps during goal approach which adapt to unanticipated state transitions, encode temporally discounted rewards, and predict action likelihood [21••,24]. Computational theory has highlighted the influence of costs in arbitrating between cheap and efficient 'model-free' (MF) action selection, and precise but costly 'model-based' (MB) planning over complex state-action-outcome transitions [25–27]. Evolving striatal DA dynamics may thus be important for conveying the expected values of costly MB processes. Indeed, decision-makers rely more on MB over MF control when the

stakes are higher [28] and with increased striatal DA signaling [29–31].

DA also undermines control

If DA promotes control by conveying incentives that offset effort costs, there is also evidence that it undermines control. Notably, the DA precursor levodopa yields impulse control disorders in 17% of Parkinson's disease patients [32] and may also drive impulsive responding to irrelevant stimuli as a function of patients' trait impulsivity [33]. Trait impulsivity itself has been linked with higher adolescent DA function [34], higher striatal D2 receptor density in healthy adults [35], and D2 autoreceptor density and amphetamine-induced DA release [36]. Experimentally, DA can both promote and undermine control within a single task: during a Stroop task, trial-wise incentives enhance performance (reduce conflict costs) for those with low striatal DA synthesis capacity, while incentives undermine performance (increase conflict costs) for those with high synthesis capacity [37••]. Beyond altering control performance, DA can also increase the degree to which individuals explicitly choose to avoid high versus low control-demanding tasks. Specifically, the DA transporter blocker methylphenidate caused high trait-impulsive participants to avoid control demands more [38••], suggesting that DA may undermine control by altering when individuals choose to exert it.

DA may also undermine control, in part, due to DA's well-established effects on behavioral vigor [39,40••,41–43]. In short, higher extracellular DA tone in the striatum increases the likelihood, and reduces the latency of action commission [21••,24,40••,41]. Thus, prepotent actions that control is intended to override (e.g. reading a Stroop word) are also potentiated by higher DA, just like controlled actions. That is, DA can potentiate actions that require incentive motivation for overcoming effort costs, but also actions which do not require motivation. Indeed, DA-mediated incentives can simultaneously potentiate both performance-contingent and non-contingent behaviors like speeding saccades both when rewards depend on reaction times and when they do not [44].

DA interacts with proximity to modulate control

What determines when DA will promote control and when it will undermine it? One suggestion comes from an elegant series of studies which implicate both DA and spatial proximity in conditioned approach to instrumental apparatus [45]. Subpopulations of striatal neurons respond to discriminative stimuli and their activity determines whether rats approach and engage instrumental apparatus. Critically, this activity is DA-dependent [40••,46] and is modulated by spatial proximity: more proximal apparatus evoke more firing, greater likelihood of approach, and shorter latency reaction times [47]. As a consequence, rats are biased toward closer low-cost, low-reward levers, even if they otherwise prefer a high-cost, high-reward lever [47].

Striatal proximity effects themselves reflect early cortical dynamics of competing action proposals (e.g. in premotor cortex) that are evoked as instrumental affordances and filtered by mutual inhibition, biased by multiple factors predicting action probability [48–50]. Filtered actions are then 'proposed' to the striatum where they are gated, via thalamic disinhibition, according to the relative activity in the direct and indirect pathways [14,15•]. Thus, actions which are proposed more rapidly and robustly, will be earlier and stronger candidates for action gating. Generalizing to any factor which causes cortical action representations to be evoked rapidly and robustly, we can see that spatial proximity as well as attention, salience, prepotency, familiarity, concreteness, etc. will all have similar effects, thus *proximity* is hereafter used to refer to *psychological* rather than strictly *spatial* proximity.

Striatal DA tone will also interact during action selection by increasing direct versus indirect pathway excitability [15•,21••,24,40••], functionally equivalent to more benefit and less cost evidence across all candidate actions [14,19]. If an instrumental apparatus is more proximal, then, it will be an earlier candidate for potentiation by striatal DA tone. We therefore propose the following hypothesis concerning the interaction of DA and proximity: *DA will potentiate action commission, by up-weighting benefit over cost evidence, preferentially for proximal actions* (Figure 1). Thus, when DA tone is high, proximity will strongly determine output. If no actions are uniquely proximal, high-benefit, high-cost alternatives (e.g. controlled over automatic responses) will win out. However, as one action becomes relatively more proximal, it is more likely to be selected. Conversely, when DA tone is low, preferences will shift toward low-benefit, low-cost alternatives, but, since the general likelihood of action commission is reduced, proximity effects will also be attenuated. Moreover, even under high DA tone, proximity biases can be overcome by raising the gating threshold when detecting the need for cognitive control, via recruitment of prefrontal-subthalamic nucleus circuits [51,52••], as less proximal actions will have more time to compete.

We can formalize key features of the proposed DA–proximity interaction in a choice between a low-cost, low-benefit action b, that has a proximity advantage ΔP over a high-cost, high-benefit action a. Specifically, we can write the net action value of a as the linear combination of activity evoked in the direct (D_a) and indirect pathway (I_a; following [15•]):

$$Act_a = \beta_D D_a - \beta_I I_a \quad (1)$$

where β_D and β_I weights reflect D1 and D2 receptor effects and increase, and decrease with striatal DA levels,