Multiple gates on working memory
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The contexts for action may be only transiently visible, accessible, and relevant. The cortico-basal ganglia (BG) circuit addresses these demands by allowing the right motor plans to drive action at the right times, via a BG-mediated *gate* on motor representations. A long-standing hypothesis posits these same circuits are replicated in more rostral brain regions to support gating of cognitive representations. Key evidence now supports the prediction that BG can act as a gate on the *input* to working memory, as a gate on its *output*, and as a means of reallocating working memory representations rendered irrelevant by recent events. These discoveries validate key tenets of many computational models, circumscribe motor and cognitive models of recurrent cortical dynamics alone, and identify novel directions for research on the mechanisms of higher-level cognition.

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Introduction
The world is rich with information, much of it only transiently available to the senses. And yet, an animal must leverage a small, but crucial, fraction of this input in order to provide a context for its behavior. Working memory is a central adaptation to confront this problem, selecting behaviorally relevant information, maintaining it in time, and referencing it when appropriate in order to make decisions about how to act in the world. Indeed, the elaborated working memory system of higher primates partly underlies their distinguishing intelligence and flexible behavior.

Working memory is capacity limited. Measures of capacity predict individual differences in cognitive ability, including scholastic aptitude, intelligence, and aging-related cognitive change [1,2]. Moreover, changes in working memory capacity accompany neurological and psychiatric disease [3] and may underlie behavioral and cognitive deficits associated with these disorders [4]. However, just as the world is dynamic, so is the working memory system adapted to address these dynamics. Thus, control processes are required in order to rapidly and selectively store information in memory (input control), to rapidly and selectively deploy subsets of that information for use in behavior (output control), and to selectively eliminate an obsolete representation from memory when its predicted utility declines (reallocation). Such control functions would seem to be crucial for strategically making use of capacity-limited working memory. And indeed, though less understood, individual differences in these control processes could be equally or even more important than the size of a static capacity for intellectual ability.

Though still in its early stages, the last few years have yielded rapid advances in our understanding of how the brain solves the input, output, and allocation control problems facing working memory. These experiments have associated all three functions with interactions between frontal and basal ganglia systems. Below, we review this work to outline an account of how the brain manages working memory.

From motor control to cognitive control
There is a clear parallel between the problems addressed by working memory control processes and the fundamental challenges faced by an animal's motor system. Consider the task of hunting for dinner. For example, a predator must program motor actions on the basis of transiently observed information about prey (input control); maintain these programs until the time is right, enacting only the most appropriate motor program at that time (output control); and finally, refrain from perseveratively considering outdated motor programs, should the prey escape (reallocation; Figure 1a). Thus, demands on selective encoding, maintenance, utilization, and clearing of information face a variety of species.

This similarity motivates the search for neural solutions that might also be shared across species. Indeed, recent phylogenetic analyses show that the basal ganglia (BG) has been highly conserved evolutionarily — all its major structures preserved since their debut in an unknown ancestor common to all vertebrates [5]. This conservation of structure may attest to the BG's efficacy in solving the action selection problems faced by many species.

Figure 1
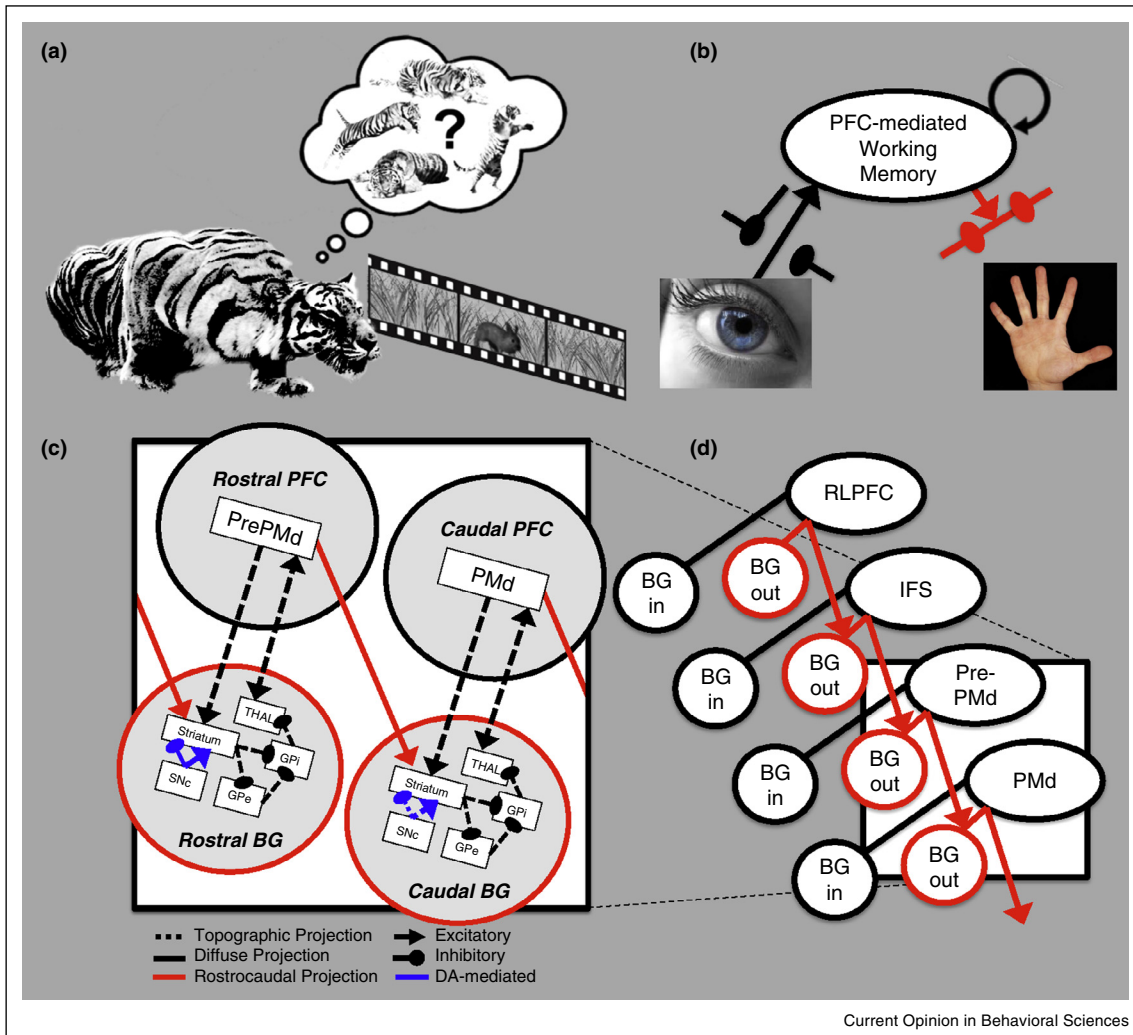
Theoretical overview. **(a)** All behaving animals must be capable of selecting useful motor actions at the right times. A long-standing hypothesis [11] holds that the same frontostriatal mechanisms supporting this kind of action selection might also support higher-order cognitive functions. **(b)** Frontostriatal mechanisms can implement a gate to select useful but transient information for rapid storage in working memory, as well as a gate to select of information from working memory to inform motor planning [6,10,13]. **(c)** Models involving rostral to caudal nesting of corticostriatal input and output gating loops have been shown to solve abstract, multiply contingent action problems [18] as well as forms of Bayesian inference [22••] and symbolic referencing [23••]. A key feature of these models is the presence of a 'diagonal' rostrocaudal projection (red arrows) allowing rostral areas to modulate the striatal input to more caudal basal ganglia; one implemented model is shown here. **(d)** Multiple such frontostriatal circuits are thought to exist, each modulated in a top-down manner by more rostral circuits (PMd by pre-PMd; pre-PMd by the inferior frontal sulcus [IFS]; and IFS by the rostrolateral prefrontal cortex [RLPFC]). The diagonal rostrocaudal projections are thought to be particularly important for modulating output gating mechanisms ('BG out') as opposed to input gating mechanisms ('BG in').

One way to describe the dynamics of this selection function is as a *gate* that regulates the passage of information from one neural circuit to another [6], such as in the case of motor selection, between thalamus and motor cortex. Theoretical models posit that motor gating occurs via the opposing circuit-level effects of the two classes of medium spiny neurons of the striatum: *Go* and *NoGo* cells. The net effect of D1-receptor - expressing *Go* cells is to 'open the gate' by facilitating recurrent thalamo-cortical information flow, whereas D2-receptor-expressing *NoGo* cells 'close the gate' by blocking thalamo-cortical information flow. By this scheme, a planned motor action represented cortically might trigger the activation of *Go* cells via a corticostriatal projection, in turn facilitating a projection from thalamus to the primary motor neurons responsible for enacting specific movements. At the same time, alternative action plans would trigger *NoGo* cells and so would have negligible thalamocortical influence.