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Executive control and decision-making in the prefrontal cortex

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The prefrontal cortex (PFC) subserves decision-making and executive control. Here we review recent empirical and modeling works with a focus on neuroimaging studies, which start unifying these two conceptual approaches of PFC function. We propose that the PFC comprises two arbitration systems: (1) a peripheral system comprising premotor/caudal PFC regions and orbitofrontal regions involved in the selection of actions based on perceptual cues and reward values, respectively, and embedded in behavioral sets associated with external contingencies inferred as being stable; (2) a core system comprising ventromedial, dorsomedial, lateral and polar PFC regions involved in superordinate probabilistic reasoning for arbitrating online between exploiting/adjusting previously learned behavioral sets and exploring/creating new ones for efficient adaptive behavior in variable and open-ended environments.

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The prefrontal cortex is often described as subserving decision-making and executive control. Decision-making research focuses on the PFC function in action selection according to perceptual cues and reward values [1,2]. Executive control research focuses on the PFC function in learning and switching between behavioral rules or sets that guide action [1,3–10]. These two lines of research have often been carried out independently. Here we review recent findings and outline a theoretical framework unifying these two conceptual approaches of PFC function.

From simple decisions to task sets

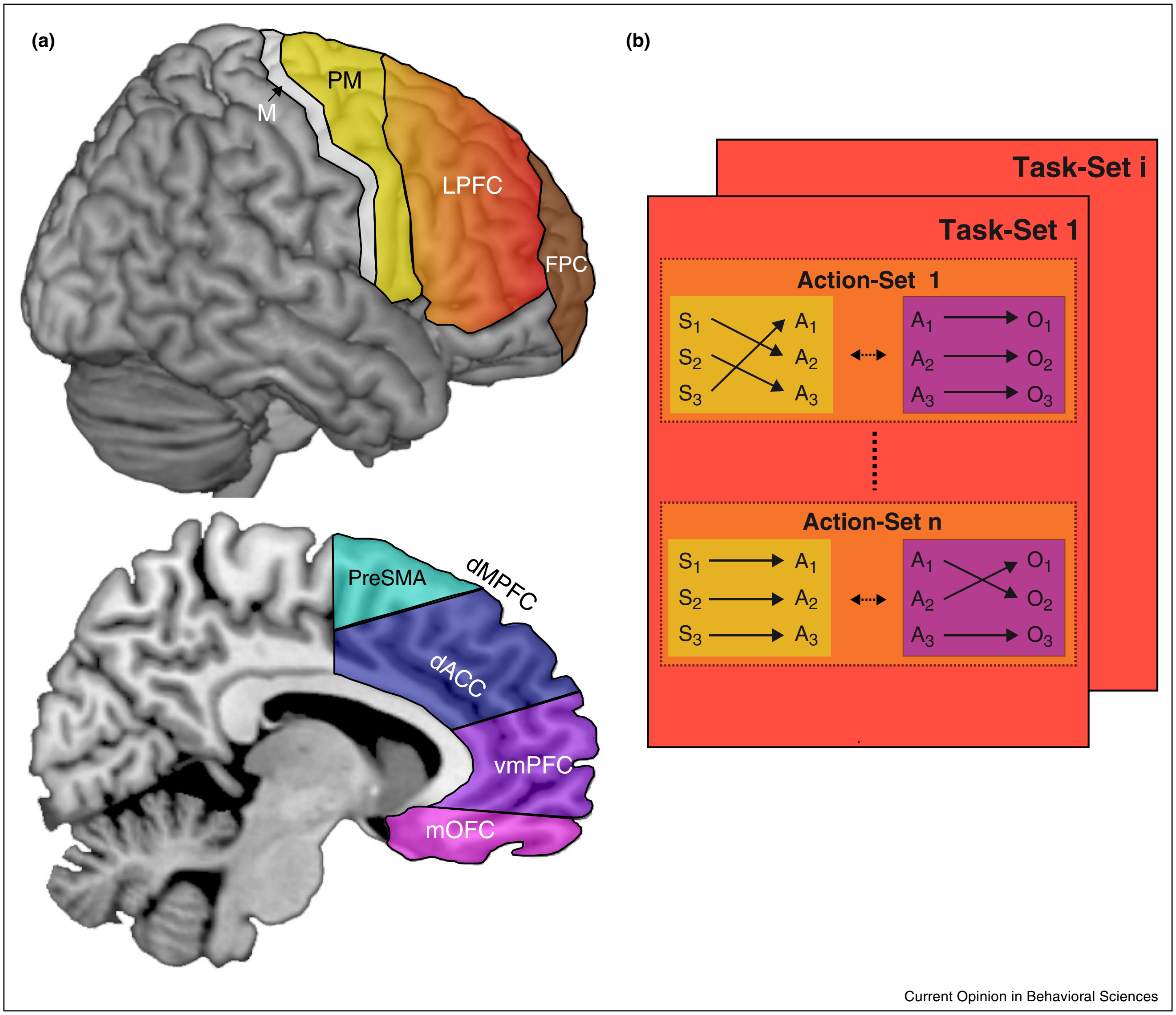
There is converging evidence that the computation of expected rewards driving action selection primarily involves the ventromedial PFC (vmPFC) [11–13]. The vmPFC, especially its ventral portion (often referred to as the medial orbitofrontal cortex), enables to convert distinct subjective reward scales into a 'common currency' scale for allowing value comparison [14–17] that drives selection. Reward values are generally associated with action outcomes rather than actions per se. Consistently, the vmPFC is involved in predicting action outcomes [18–21,22•], suggesting that the vmPFC encodes action-outcome associations for selecting actions according to reward values. By contrast, selecting actions according to perceptual cues involves the lateral premotor cortex [9,23–25]. However, when expected rewards and perceptual cues are not linked to specific actions, decisions are presumably made between more abstract action sets that may subsequently guide the selection of specific actions according to stimuli. In such situations, consistently, both reward-based and cue-based decisions engage the lateral prefrontal cortex (lPFC) [26,27], which subserves cognitive control, that is, the formation and selection of such action sets [3,9,23,24,28–32]. Importantly, abstract action sets spontaneously develop for controlling action selection even when their formation provides no immediate behavioral advantages [28,29]. Thus, lPFC activations often reported in simple choice tasks suggest that whenever possible, subjects build abstract action sets and primarily choose between these sets for subsequently selecting simple actions, especially in sequential decision tasks facilitating the formation of stable sets across trials.

Abstract action sets thus comprise multiple stimulus-action and (stimulus)-action-outcome associations, which are learned and continuously adjusted online for maximizing rewards. Computational modeling suggest that stimulus-action and (stimulus)-action-outcome associations are learned and adjusted through reinforcement and statistical learning respectively [33•,34], while abstract action sets emerge through probabilistic clustering processes [29]. Collectively, these flexible representations invoked together for driving action selection while the same external situation perpetuates, constitute a consistent behavioral strategy also referred to as a *task set* (Figure 1).

Task sets and adaptive behavior

Task sets are critical executive units for efficient adaptive behavior in everyday environments featuring external situations that often change and may reoccur periodically

Figure 1



Prefrontal cortex and structures of executive representations. **(A)** The frontal lobes comprise the premotor (PM), lateral prefrontal (lPFC) and frontopolar (FPC) regions on the lateral side (top); on the medial side (bottom), the dorsomedial (dmPFC including the pre-SMA and dACC), the ventromedial (vmPFC) and orbitofrontal (mOFC) regions. **(B)** Task-sets are temporal abstraction including action sets which in turn comprise stimulus-action and action-outcome associations. Color matches across panels and illustrates the anatomical mapping of these executive representations.

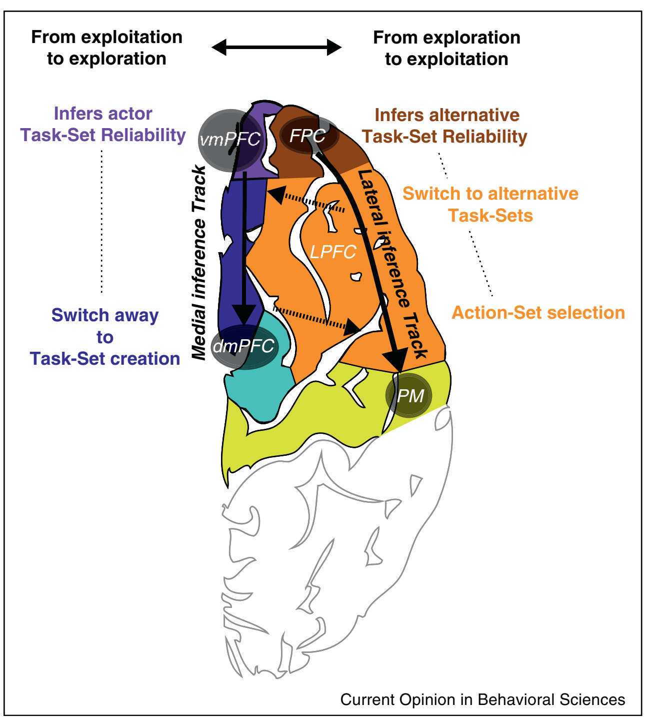
and where new situations may always arise. Task sets are formed and stored as mentally instantiating external situations for possibly exploiting them when these situations reoccur [33•]. This adaptive capacity requires *continuously* arbitrating between exploiting/adjusting previously learned task sets vs. exploring/creating new ones. The PFC has likely evolved to make this arbitration online [35•]. The arbitration however is a complex probabilistic reasoning problem, which optimal solution is actually computationally intractable [33•]. Accordingly, we recently proposed that the core PFC executive system comprising the ventromedial, dorsomedial, lateral and frontopolar PFC regions has primarily evolved as implementing an approximate algorithmic solution to this problem [35•]: the solution especially assumes that the executive system infers online the *absolute reliability* of the current task set driving ongoing behavior (i.e. the *actor* task set): this quantity measures the probability that given external evidence, this task set is still applicable to the situation or equivalently, that the situation remains unchanged (considering that the range of external situation is potentially infinite). The concept of absolute reliability generalizes the notion of expected/unexpected uncertainty [36] to open-ended environments and is related to the psychological notion of metacognition and confidence [37].

The medial PFC: from exploitation to exploration

We noted above that task sets comprise a forward model predicting action outcomes, and the vmPFC is likely to encode the forward model of the actor task set. fMRI studies further reveal that in reversal learning tasks, vmPFC activations vary with the probability that the current situation remains unchanged according to actual action outcomes [18]. Moreover, we recently observed that in conditions inducing subjects to build multiple task sets according to actual action outcomes, vmPFC activations (along with perigenual anterior cingulate activations) specifically correlate with the absolute reliability of the actor task set [38••]. These results provide evidence that the vmPFC is specifically involved in inferring the actor task-set reliability according to the consistency between expected and actual action outcomes. In agreement with this hypothesis, vmPFC activations were also found to predict subjects' confidence in making simple reward-based decisions [37] (Figure 2).

The notion of absolute reliability implies that task sets are inferred as being either reliable (i.e. more likely applicable than non-applicable to the current situation) or unreliable (the converse) [33•]. When the actor task set passes from the reliable to unreliable status, the current external situation has likely changed. Modeling and behavioral results show that in that event, subjects switch away from exploiting/adjusting the current actor set and start exploring by forming a new actor set built upon the collection of task sets stored in long-term memory [33,38••]. fMRI results show that unlike the vmPFC, the dorsomedial PFC (dmPFC) comprising the dorsal anterior cingulate cortex (dACC) and the pre-supplementary motor area (pre-SMA) responds specifically to this algorithmic transition [38••]. Consistently, neuronal recordings confirm that when animals switch from exploitation to exploration behaviors, neuronal ensembles in the dmPFC exhibit abrupt activity resetting [31,40••,41••]. Additional fMRI results in humans suggest that in foraging tasks, the dmPFC monitors the opportunity to switch from exploitation to exploration [42]. Altogether, these findings suggest that while the vmPFC infers the actor absolute reliability from action outcomes, the dmPFC monitors the actor absolute reliability not only for regulating actor adjustments [39•] but especially for detecting when the actor task set *becomes* unreliable and enforcing the switch from exploitation to exploration. This discrete, non-parametric transition consists of inhibiting the ongoing actor task set for creating a new actor task set driving behavior. According to electrophysiological recordings [43–45], the dACC may enforce the transition at the set level, while the pre-SMA may be involved in inhibiting its executive elements, that is, action sets and related stimulus-action associations.

Figure 2



The PFC core executive system and probabilistic reasoning driving adaptive behavior. See text for details.

From a normative viewpoint, creating a new task set consists of mixing the task sets stored in long-term memory according to current external evidence and task-set internal models [33•,35•]: the new task set optimally reuses previous learned situations for driving behavior, when the actor task set becomes unreliable. Current empirical findings suggest that this creation process involves the caudal LPFC and premotor cortex along with basal ganglia [23,38••]. Newly created task sets driving behavior is initially inferred as being unreliable but through learning (see above), may subsequently become reliable. fMRI results show the latter event elicits ventral striatal along with premotor and caudal LPFC activations. These activations presumably reflect the consolidation of newly created task sets in long-term memory when they become reliable [38••]. Exploration behaviors thus consist of creating and learning new task sets and perpetuate until the medial PFC infers these new task sets as becoming reliable.

The lateral PFC: from exploration to exploitation

Behavioral results suggest that humans can infer the absolute reliability of three or four task sets concurrently [33•,38••]: the current actor along with two or three alternative task sets. The latter correspond to task sets previously inferred as being reliable and used as actor but no longer reliable. When subjects switch into exploration as described above, the former actor typically remains monitored as an alternative task set (which may be subsequently retrieved, see below). Several fMRI studies have pointed out the role of the lateral frontopolar PFC (FPC) in exploration [46–49]. Other fMRI studies show that the FPC is involved in holding on and monitoring alternative courses of action [19,20,50]. Recent results indicate that consistently, FPC activations more specifically correlate with the absolute reliability of two concurrent alternative task sets [38••]. The FPC thus appears to keep track and infer the absolute reliability of a few alternative task sets, which notably occur during exploration periods (Figure 2).

Such alternative task sets make no contribution to ongoing behavior but may be subsequently retrieved for driving behavior [33•,38••]: As two task sets cannot be judged as being reliable simultaneously, any alternative task set becoming reliable is retrieved and replaces the current actor task set. This retrieval process enables the organism to switch out of exploration periods by rejecting newly created task sets. The retrieval process also enables exploration periods to be skipped by directly switching to an alternative task set, when the ongoing actor task set becomes unreliable. fMRI data show that consistent with its critical role in task-switching [12,24,51], the lPFC detects when one alternative task-set become reliable [38••]: the lPFC presumably initiates the retrieval process that propagates from middle to caudal lPFC regions [38••].

PFC functional architecture and adaptive behavior

Altogether, these recent findings suggest that the PFC comprises two parallel inferential tracks (Figure 2): (1) a medial track from the vmPFC to dmPFC arbitrating between exploiting/adjusting the current task set driving behavior vs. exploring/creating new task sets from long-term memory. While the vmPFC infers the reliability of the current actor task set in predicting action outcomes, the dmPFC detects when this task set *becomes unreliable* for inhibiting it and switching into exploration; (2) a lateral track from the FPC to lPFC arbitrating between exploring/learning new task sets vs. exploiting alternative task sets recently used as actor. While the FPC infers the reliability of these alternative task sets in predicting current action outcomes, the lPFC detects when one *becomes reliable* for retrieving it as actor. The lateral track thus enables to avoid switching or perseverating in exploration periods, when alternative behavioral strategies are judged as applicable to the current situation. Recent MRI-based anatomical studies [52,53,54•] reveal that the human FPC region considered here has no equivalent in non-human primates, suggesting that this adaptive faculty based on counterfactual inferences is unique to humans.

Our review outlines a theoretical framework, whereby simple choices primarily involve a 'peripheral' PFC system including the lateral premotor and medial orbitofrontal cortex. The latter drives the selection of motor responses in direct association with stimuli and expected rewards, respectively. The caudal lPFC has the capacity to abstract multiple stimulus-response and response-outcome associations into action sets. The caudal lPFC thus enables to collectively select multiple associations according to external cues and expected outcomes for carrying out behavioral plans. Action sets are associated with external situations perceived as featuring *stable* contingencies over time and mentally instantiated as discrete task sets. Task sets comprise action sets and constitute a temporal abstraction level aiming at efficient adaptive behavior in everyday environments where external situations change and may reoccur periodically, and new situations may always arise. Accordingly, the ventromedial, dorsomedial, mid-lateral and frontopolar PFC form the core executive system inferring online the possible changes of situations and arbitrating between (1) adjusting and exploiting the current task set driving ongoing behavior, (2) switching to alternative task sets and (3) exploring/creating new ones.

Concluding remarks

The notion of exploration is central to the framework outline here and consists of the *deliberative, reversible decision* to create a new task set. In contrast to the *online* reinforcement learning of task sets, task set creation is an *offline*, computationally costly process resetting the actor task set. The new actor task set is formed as the mixture of task sets stored in long-term memory based on external evidence according to task sets' internal models of external contingencies [35•]. Interestingly, the offline creation vs. online learning of task sets corresponds to the theoretical distinction between model-based and model-free learning, respectively [34,56]. In model-based learning, indeed, action values are inferred from internal models of external contingencies while in model-free learning, action values are learned by interacting with the environment through reinforcement learning. A usual view is that both model-based and model-free reinforcement learning methods operate online concurrently, so that the continuous mixture of model-based and model-free action values drives behavior [34,56]. In the present view, however, task set creation occurs at specific time points when the actor task set that adjusts through reinforcement learning is inferred as becoming unreliable (and the alternative monitored task sets remain unreliable). Following its creation, the new actor task set is subsequently adjusted through reinforcement learning, so that the task sets driving behavior derives from intermittent, offline model-based creation that progressively and increasingly incorporates online model-free learning. Both views account for empirical data suggesting that adaptive behavior forms a mixture of model-based and model-free adaptive processes [55]. The two views however differ in the way the two adaptive processes are combined over time. Disentangling these two theoretical views and understanding how the brain builds new task sets from those stored in long-term memory thus appear as central issues for future research.

Conflict of interest

Nothing declared.

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