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Prefrontal function and cognitive control: from action to language

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The prefrontal function has evolved to control adaptive behavior beyond basic associative and reinforcement learning processes. Here we review core principles governing the prefrontal architecture of inferential and hierarchical processes controlling the formation, storage and recollection of flexible task-sets regulating human adaptive behavior. We outline three key principles of this functional architecture: inferential temporal control, task-set creation based on probabilistic marginalization processes over inferred latent states and, two nested abstract levels of action chunking. These principles may help to understand the role of the prefrontal function in the evolution of the human faculty of language.

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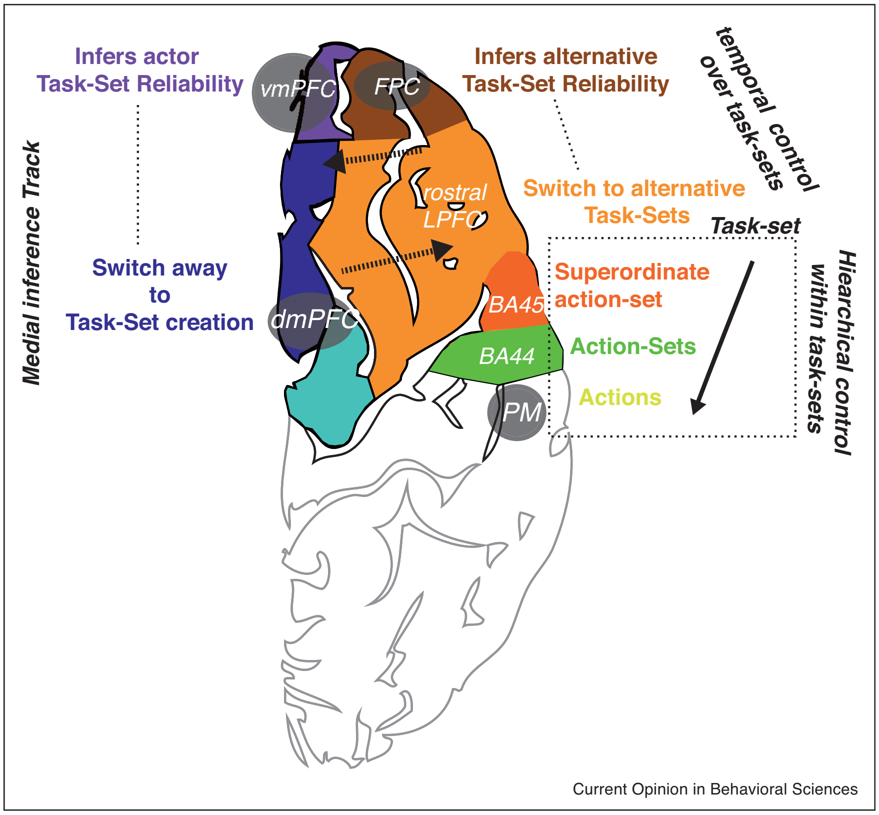
Introduction

Cognitive control refers to mental processes that evolve as regulating adaptive behavior beyond basic reinforcement and associative learning processes [1•]. Cognitive control is a cardinal function of the prefrontal cortex (PFC) [2]. The PFC appears in mammals as comprising the orbitofrontal and anterior cingulate cortex [3] develops in primates with the emergence of lateral PFC [4] and further evolves in humans mainly as follow: the apparition of the (lateral) polar PFC essentially connected to other PFC regions and a temporal-prefrontal connectivity that decreases in the anterior cingulate cortex but increases in the caudal lateral PFC (corresponding in the right hemisphere to Broca's area) [5,6•]. Cognitive control overcomes a key limitation of reinforcement and associative learning processes, whereby adaptation occurs by erasing previously learned contingencies, thereby preventing from building and recollecting a long-term repertoire of behaviors and thoughts usually referred as task-sets [7]. Cognitive control thus enables arbitrating between (1) staying with the ongoing task-set and adjusting it to external contingencies through reinforcement learning, (2) switching to a previously learned task-set stored in long-term memory, (3) exploring and learning new task-sets [8]. In everyday uncertain environments featuring both recurrent and new situations, optimally arbitrating between these options is a computationally intractable problem [1•]. The PFC thus comprises a complex system of inferential and hierarchical control processes approximating the optimal adaptive solution for guiding adaptive behavior in uncertain, changing and open-ended environments, corresponding typically to our social life. The architecture of control processes in the PFC presumably plays a central role in shaping higher cognition including judgment, reasoning, planning and language. We outline here a theoretical framework we proposed [1•] to describe this architecture and its possible involvement in language processing.

Task-sets as instantiations of external states

In open-ended environments featuring an unlimited range of situations/dimensions, a physical device cannot have a comprehensive parametric representation of the external world and consequently, of associated behaviors. Instead, one needs to constantly be able to create new behavioral strategies as new discrete entities, when new external states are detected. Such discrete entities instantiating the various external states the agent has identified so far are referred to as *task-sets*. Task-sets are large-scale frames linking together several internal models implemented in multiple cortical regions and invoked together to drive behavior. Each task-set comprises internal models stored in posterior associative and premotor regions (collectively named the *selective* model) generating behavioral responses to stimuli [9,10]. Each task-set also comprises internal models learning external contingencies and predicting action outcomes given responses to stimuli (collectively named the *prospective* model). Recent empirical evidence suggests that prospective models, at least those bearing upon reward-valued outcomes, are primary implemented in the ventromedial PFC [11–13]. The *actor* is the task-set driving ongoing behavior and which internal models adjust to current external contingencies typically through reinforcement and associative learning, while previously learned task-sets form a repertoire stored in long-term memory [14].

Figure 1



Prefrontal cortex and cognitive control. Schematic view of the architecture of inferential and hierarchical control processes governing human adaptive behavior. *Abbreviations*: PM, premotor cortex; dmPFC, dorsomedial prefrontal cortex; LPFC, lateral prefrontal cortex; vmPFC, ventromedial prefrontal cortex; FPC, polar lateral prefrontal cortex; BA 44, 45, Broadman's areas 44, 45. See text for explanation.

Cognitive control as inferences over time

The actor prospective model serves two key functions: (1) emulating the learning of selective models without overtly acting by mentally generating action outcomes, a process named model-based (reinforcement) learning, which may occur in the background even when the person is overtly acting [15,16]; (2) most importantly, inferring from actual action outcomes whether the current external state remains the same or equivalently, whether the current actor still remains applicable to the situation. This inference is based on probabilistic beliefs that constantly measures actor reliability in predicting actual action outcomes compared to chance level and updated through the Bayes rules according to the actor prospective model. While the actor is deemed reliable (reliability compared to chance level > 0.5), the actor remains the same. Otherwise, a new actor is created as a mixture of task sets stored in long-term memory. The new actor typically starts as deemed unreliable but through learning, will subsequently become reliable. In that event, the new actor is consolidated in long-term memory as a new task-set and may subsequently be replaced when it becomes unreliable again. Empirical results provide evidence that the ventromedial PFC monitors actor reliability [17] notably in relation with subjective confidence judgments [18], the dorsal ACC along with the dorsal striatum controls when to switch away from the ongoing actor by detecting when it becomes unreliable [17,19–21], and the ventral striatum signals when a newly formed actor becomes reliable [17]. These monitoring and control processes involving the medial PFC-striatum loop circuit constitute a basic, consistent form of cognitive control presumably present in all mammals [1•] (Figure 1). Note that in this control system, the more frequently an external state reoccurs, the more the long-term memory contains task-sets created for instantiating this state. Consequently, as these task-sets comprise similar internal models, new actors will more often resemble these task-sets. This control system is thus limited in building actor task-sets as a mixture of previously learned selective and prospective models, weighted by the frequency of the associated external states.

To overcome this limitation, task-sets comprise an additional internal model named *contextual* model that learns contextual cues predicting task-set reliability [1•,14]. Contextual models serve two functions: (1) updating actor reliability according to the occurrence of contextual cues, which proactively enables switching away from current actors and creating new actors before acting (i.e. proactively); (2) weighting the contribution of memorized task-sets to actor creation according to contextual cues. Actor creation thus consists in optimally building new internal models (selective, prospective and contextual models) by probabilistically marginalizing over stored task-sets (*or* over previously inferred external states): namely, mixing previously learned task-sets weighted by contextual cues with respect to associated contextual models [1•,14]. As a result, when the same contextual cues re-occur, actor creation becomes equivalent to recollecting the 'exact' task-sets previously learned in that context. The actor is then maintained over time and possibly adjusted while deemed reliable, even in the absence of contextual cues having contributed to its creation. This notion of control, also termed episodic or temporal control, has been identified in the rostral lateral PFC in both monkeys and humans (typically Broadman areas 9/46) [22–25,26•]. As the lateral PFC appears in primates, episodic/temporal control is likely to have emerged in primates [1•] and endows them with the additional ability to proactively build actor task sets from long-term memory that match the context in which the individual is acting.

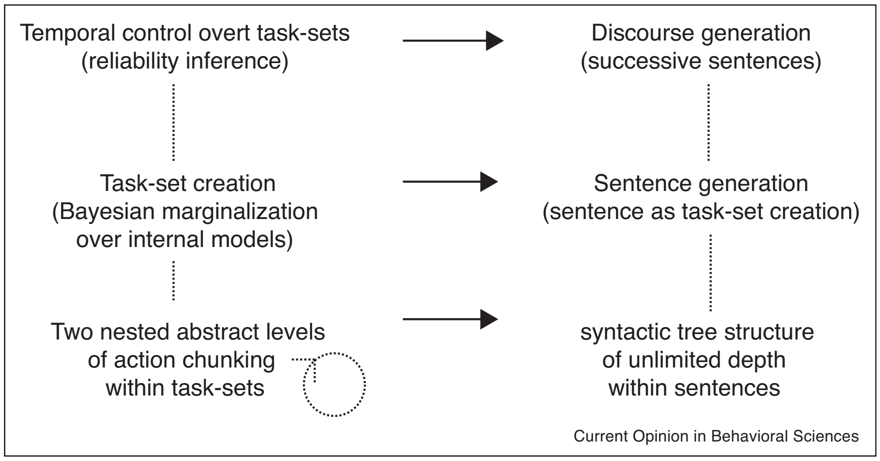
Cognitive control as counterfactual inferences

The control system described above and involving the ventromedial PFC, ACC and rostral-lateral PFC is based on inferring the actor reliability only. Studies provide evidence that unlike monkeys, humans are able to monitor in parallel the reliability of a few task-sets, typically two-three task-sets, in addition to the actor [14,17,27•]. Evidence was that these additional task-sets are monitored based on action outcomes produced by the actor. Those make no contributions to behavior and are termed counterfactual task-sets [14]. This inferentiel buffer corresponds to the notion of capacity-limited working memory [28,29]. Previous studies [14,17] further show that when the actor is deemed unreliable and one counterfactual task-set becomes reliable, the latter becomes the actor yielding to the notion of task-switching. When the actor and all counterfactual task-sets are deemed unreliable, a new actor is created from long-term memory as described above. When one counterfactual task-set become reliable, while the newly created actor still remains unreliable, the latter is disbanded and the former becomes the actor. In the converse case, the newly created actor is consolidated in long-term memory as described above, possibly yielding the counterfactual task-set the least recently used as actor to be removed from the inferential buffer, whenever its capacity-limit is reached. This additional control system enables to directly switch to pending task-sets when they appear to be more applicable to the situation than the ongoing actor. It also enables hypothesis-testing bearing upon actor creation against previously reliable task-sets. fMRI studies [17,30–33] provide evidence that in contrast to the actor, counterfactual task-sets are monitored in the polar-lateral PFC (lateral Brodmann area 10), within the sub-region which has apparently no homologs in monkeys [5,6•]. Consistently also, the polar-lateral PFC is critically involved in ordering online multiple task-sets in behavioral sequences in the absence of overt/external cues [34]. Finally, while the dorsal ACC is involved in switching away from the actor when it becomes unreliable for creating a new actor (see above), the lateral PFC posterior to the polar PFC is involved in recollecting a counterfactual task-set as actor when it becomes reliable [17] (Figure 1).

Cognitive control as hierarchical organization of behavior

Task-set control organizes behavior into temporal frames over which external contingencies are deemed stable. This temporal form of control primary involves dorsomedial (ACC) and ventromedial PFC along with rostral-lateral and polar-lateral PFC. Actor task-sets are created, selected or retrieved through monitoring task-set reliability over time. The actor task-set then provides a consistent set of flexible internal models driving behavior over temporal episodes. Empirical evidence further suggests that within the actor task-set, selective models mapping stimuli onto actions spontaneously develop as hierarchical rather than flat mappings favoring the generalization of subordinate sensorimotor mappings to new combinations of sensory attributes, even when there is no immediate behavioral advantages in forming these representations [35–37]. In the presence of stimuli mixing multiple dimensions, one dimension is mapped onto motor responses and forms sensorimotor associations whereas the other dimension is preferentially mapped onto this set of sensorimotor associations, referred to as *action sets*. Such hierarchical structures enable selecting action sets according to additional cues. Neuroimaging studies provide evidence that this hierarchical control involves the caudal-lateral PFC (Broca's area and its right homolog). While the premotor cortex is engaged in selecting response to stimuli, the caudal-lateral PFC is involved in learning and selecting action sets (sensorimotor mappings or action sequences) according to additional cues [9,10,22,25,26•,35,38•,39,40–43]. Effective connectivity analyses measuring information flows across lateral PFC further confirm that task-sets in rostral-lateral PFC regions control the selection of action sets in caudal-lateral PFC, which in turn control the selection of sensorimotor associations in the premotor cortex [22,25,26•,44], thereby reflecting a top-down hierarchy of selection processes within task-sets from rostral-lateral to caudal-lateral PFC and premotor cortex. Neuroimaging studies further supports the idea that within task sets, hierarchical selective models driving action selection according to cues comprise at least two hierarchical levels within the caudal lateral PFC: (1) a lower level corresponding to action sets and involving posterior caudal-

Figure 2



Cognitive control and language. Proposed correspondence between cognitive control processes and generation of language structures.

lateral PFC regions (typically BA 44); (*2*) a higher level corresponding to sets of action sets involving anterior caudal-lateral PFC (typically BA 45) [38•] (Figure 1).

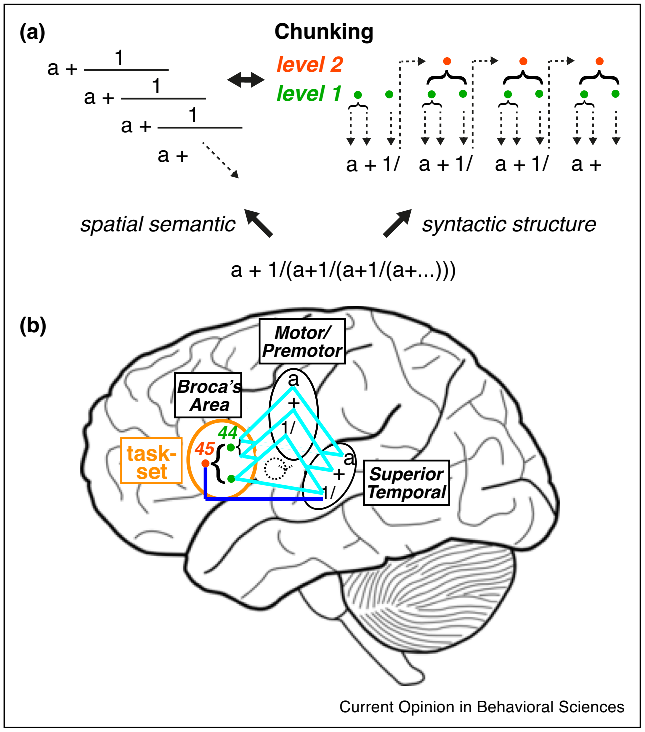
Cognitive control and language

As concluding remarks, we propose here three key principles of cognitive control that may help to understand the involvement of prefrontal function in language (Figure 2). Language production is certainly the most advanced example of hierarchically organized behavior. As any behaviors, first, speech primary unfolds over time as a sequence of sentences, each forming a consistent temporal episode of words hierarchically organized according to syntactic rules. In that sense, sentences may be viewed as task-sets comprising hierarchically organized selective models. Thus, speech can be viewed as a series of task-sets, which sequential production is based on inferential processes involving as mentioned above, ventromedial PFC and dorsal ACC along with rostral-lateral and polar-lateral PFC monitoring their successive reliability, that is, to which extent each task-set/sentence is applicable to the ongoing discourse situation. Neuroimaging studies confirm that these PFC regions are involved in discourse generation (review in [45]).

Second, sentence generation may be viewed as actor creation, which was shown for actions to primary involve the caudal PFC (i.e. Broca's area and its right homolog) and premotor cortex bilaterally [17]. Consistently, neuroimaging studies reveal the central role of Broca's area in sentence generation (review in [45]). As indicated above, critically, actor creation and more specifically, the creation of new selective models consists in the complex, Bayesian optimal process of mixing previously stored selective models weighted by contextual cues according to associated contextual models. Mathematically, this operation is able to generate any selective models within the high-dimensional space comprising all combinations of previously learned selective models and consequently, might account for sentence generation. By contrast, for poorly learned non-native languages, processing complex multi-utterance sentences was found to involve rostral-lateral and polar-lateral PFC [46]. In this case, sentence processing might simply require generating successive utterances as independent task-sets and consequently involving anterior PFC regions.

Third, Broca's area and its right homolog implement selective models controlling action selection through *two nested, abstract levels of chunking* [38•]. Mathematically, such a two-level abstract chunking structure is sufficient to generate nested tree structures of unlimited depth, providing that through a loop circuit, low-level chunks may instantiate high-level chunks in a backward manner (Figure 3a). Such nested tree structures are considered as the fundamental characteristics of the human faculty of language [47]. The increased connectivity between posterior language areas (superior temporal cortex) and Broca's area in humans compared to monkeys [6•] might constitute this loop circuit (Figure 3b) and consequently, serve to generate such nested tree-structures accounting for the evolution of language. Recent studies provide some preliminary support to this view, as Broca's area was found to be causally engaged in processing nested-tree structures [48•]. Beside production, language comprehension requires decoding the syntactic structure of sentences. This is a highly automatized process, at least for the native language, which also engages Broca's area [46,48•]. As shown in Figure 3, the same two-nested levels of abstract chunking that operate in Broca's area in connection with the superior temporal cortex may also be used to decode syntactic structures and as a task-set creation process, map complex sentences onto their semantic representation. In this view, the same neural

Figure 3



Tree-structures and two-level abstract chunking. **(a)** An example showing a recursive tree-structure of unlimited depth (left panel). The right panel shows how this tree-structure can be generated or decoded using only two nested levels of abstract chunking and a backward loop from the lower to higher level. Actually, the right panel represents the formal syntactic structure of linear formulae (i.e. sentence) $a + 1/(a + 1/(a + 1/(a + \ldots)))$, which allows mapping the linear formulae onto the spatial semantic representation shown in the left panel. **(b)** Putative neural circuits in the cortex generating or decoding the tree-structure shown in a as a single task-set (schematic diagram with approximate localizations). Cyan and blue lines represent (bidirectional) connections. The superior temporal cortex and motor/premotor cortex encodes auditory and motor representations of the tree content (*a*, +, 1/). Broca's area including BA 44 and BA 45 implements the two nested levels of abstract chunking. The blue line highlights the backward frontal-temporal loop circuit from the lower to higher level. The motor/premotor cortex is involved in production (generation) rather than comprehension (decoding).

circuit corresponding to the execution of a single task-set is engaged in sentence production and comprehension with the activation and inactivation of motor outputs, respectively.

Finally, it is worth noting that the proposed model describes the prefrontal function and its involvement in language at the algorithmic level. The underlying neuronal mechanisms are poorly understood. This certainly constitutes a major challenge for future research, as neuronal recordings in animals might remain poorly informative about the evolution of uniquely human functions like language or counterfactual reasoning.

Conflict of interest statement

Nothing declared.

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