Architecture of central executive functions in the human prefrontal cortex

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The prefrontal cortex subserves executive control, i.e. the ability to select actions and to organize behavior in relation to internal drives and subjective preferences, ranging from the simplest behaviors, like choosing an apple or a pear in a fruit basket, to the most complex ones like deciding the next move in a game of chess. Whether simple or complex, decisions to act emerge from the combination of *preferences* (e.g. I prefer apples), *drives* (e.g. I want an apple) and *choices* (e.g. I choose the apple). Empirical studies suggests that broadly speaking, preferences, drives and choices are respectively processed in the ventral, medial and lateral sector of the frontal lobes [1]. The lateral sector, and especially the portion lying anterior to the premotor cortex, the so-called lateral prefrontal cortex, is the brain region that evolved the most recently in hominids and is involved in action selection, when action choices are context-dependent, a function usually referred to as cognitive control [2] .

Here, we briefly present a model based on our recent brain imaging results describing the functional organization of the lateral prefrontal cortex underlying cognitive control [3]. According to our model and in agreement with empirical data [4,5], cognitive control is subserved by a system of lateral prefrontal regions forming a cascade of top-down selection processes operating along the caudo-rostral axis from the premotor cortex to the most anterior region of the frontal lobes, the so-called frontopolar cortex. In this system, the premotor cortex is involved in selecting actions in response to stimuli (sensorimotor control), while posterior lateral prefrontal regions are involved in selecting premotor representations (stimulus-response associations) according to the immediate context of action, i.e. with respect to contextual signals accompanying stimulus occurrences (contextual control). More anterior prefrontal regions, in turn, are involved in selecting posterior prefrontal representations according to the temporal/behavioral episode in which the subject is acting, i.e. with respect to the occurrence of past events (episodic control). Finally, frontopolar regions are involved in re-instantiating in the anterior prefrontal regions a previously suspended behavioral episode upon completion of the ongoing one (branching control). In this system, more anterior/higher regions are only engaged in order to alter or disambiguate action selection in more posterior/lower regions on the basis of temporally more distant information. Thus, as confirmed by experimental results, cognitive control is organized from posterior to polar prefrontal regions according to the temporal rather hierarchical structure of representations involved in action selection. Conversely, we experimentally showed that posterior prefrontal regions subserving contextual control form a confined multistage sub-system involved in action selection according to the hierarchical rather than the temporal structure of action plans, suggesting a fundamental segregation between the prefrontal systems involved in the temporal and hierarchical organization of behavior [6].

Thus, the lateral prefrontal regions are involved in selecting and maintaining action selection rules (i.e. task-sets) according to the immediate context and/or the ongoing temporal episode in which the person is acting. This lateral prefrontal system was shown to obey a serial principle, which allows only a single task-set to govern action selection at any one time[7]. The apex of this lateral prefrontal system corresponds to the frontopolar cortex which overcomes this serial constraint by enabling the joint consideration of multiple task-sets. Experimental data that we and others collected [5] [8] depicts an anterior prefrontal system in which lateral prefrontal regions select and maintain the task-set governing ongoing action, while the frontopolar cortex enables previously selected task-sets to be maintained in a *pending* state for subsequent, automatic retrieval and execution upon completion of the ongoing one. This process called "cognitive branching", forms a domain-general core function at the basis of the behaviors and mental activities requiring simultaneous engagement in multiple tasks that are not serially organized into a single, pre-established superordinate plan.

It remains to understand how the frontopolar cortex "decides" to place an ongoing task into a pending state and to later revert back to it. This is a key theoretical issue because in contrast to lateral prefrontal regions, the frontopolar cortex is not under the control of higher brain centers. Based on recent experimental results [9], we proposed that with no supervisory optimization, cognitive branching between two concurrent behavioral options occurs in the frontopolar cortex, when reward expectations associated with each option (or expected penalties if not executed) are large enough so that it would be too costly or risky to simply abandon one. In that event, comparing the rewards expected from executing each option immediately will determine which option is placed in a pending state (the less rewarding one) and which one is selected for guiding immediate behavior (the more rewarding one). We elaborated a minimal neurocomputational model showing how the frontopolar cortex may mechanistically implement reward-based cognitive branching with no supervisory optimization through interactions with neighboring prefrontal regions coding for expected future rewards, namely the medial and orbital prefrontal regions [10].

A key model prediction is that the capacity of the frontopolar cortex cannot exceed the processing of a single pending task at any one time: According to the model, the frontopolar cortex can process only a single pending task-set at any one time. In particular, the model especially predicts that the frontopolar cortex is unable to recursively perform cognitive branching, i.e. resuming a primary and secondary pending task after completion of a third task, because interferences supervene between the two pending tasks. Thus, our model support the idea that the prefrontal executive system lacks the computational power to perform recursive cognitive branching, and consequently to control recursive tree-searches in the exploration of deep branching sets of future possible situations underlying reasoning, problem-solving or complex decision-making. This further suggests that the property of recursion, which plays a prominent role in human language, is an intrinsic attribute of a linguistic coding system rather than a domain-general property of behavioral control and that complex reasoning and planning, like exploring and switching in and out deep decision-trees, may only be achievable when such structures are mapped using linguistic coding systems. Nevertheless, the capacity-limited frontopolar function may have simply endowed humans with two key adaptive advantages: on the one hand, an ability to pursue long-term behavioral plans while able to respond to concomitant environmental demands, in physical or social environments; on the other hand, to explore any potential gain from the interposition of new task-sets within ongoing behavioral routines or from the contingent recombination of previously established behavioral plans as in genetic recombination mechanisms

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