

An information theoretical approach to prefrontal executive function

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The prefrontal cortex subserves executive control – that is, the ability to select actions or thoughts in relation to internal goals. Here, we propose a theory that draws upon concepts from information theory to describe the architecture of executive control in the lateral prefrontal cortex. Supported by evidence from brain imaging in human subjects, the model proposes that action selection is guided by hierarchically ordered control signals, processed in a network of brain regions organized along the anterior–posterior axis of the lateral prefrontal cortex. The theory clarifies how executive control can operate as a unitary function, despite the requirement that information be integrated across multiple distinct, functionally specialized prefrontal regions.

Introduction

'Executive' functions enable higher mammals to select actions on the basis of internal plans and goals, rather than merely responding to the exigencies of the local stimulus environment. The executive system is synonymous with the functioning of the prefrontal cortex (PFC), the cortical zone lying anterior to the premotor cortex along the lateral surface of the frontal lobes. Despite the pivotal role of this region in guiding behavior, we still know remarkably little about how it is functionally organized. In part, this is because many current theories of PFC function remain largely descriptive, simply attributing to the frontal lobes those 'higher' functions that are assumed not to be processed in peripheral sensory and motor systems [1]. In particular, although most researchers agree that the PFC is not an undifferentiated processing engine, current theories have failed to describe how it can simultaneously be fractionated into specialized subsystems and yet enable functional integration within and between these modules and sensory association areas (Box 1). Here, we briefly present a model that draws upon concepts from information theory [2] to describe how executive function can be subdivided into hierarchically ordered control processes, each responsible for selecting an action on the basis of information that is successively more remote in time [3]. Concurrently, we summarize data from functional neuroimaging experiments indicating that these control processes map onto a network of brain regions lying along the rostrocaudal axis of the lateral PFC and premotor cortex, and describe connectivity analyses revealing

functional integration within this network. Our theory thus offers an account of both functional fractionation and functional integration in the lateral PFC that is consistent with findings from a wide range of subdomains within the cognitive neurosciences, including working memory, attentional control, episodic memory retrieval, task switching and prospective memory.

Quantifying executive control

We begin with the notion that even the most complex executive functions can be decomposed into simple routines for selecting actions (or thoughts), and that the demand of executive control can be measured as the amount of information required for action selection. According to information theory [4], the total amount of information $H(a)$ required for selecting an action a when a stimulus s occurs is the sum of two terms (Box 2, Equation 1): (i) the 'mutual' information $I(s,a)$ between stimulus s and action a (i.e. the amount of information conveyed by stimulus s and involved in selecting action a); and (ii) that remaining portion of information $Q(a|s)$ (the 'conditional' information) required for selecting action a but which is unrelated to stimulus s . High values of $I(s,a)$ are obtained when stimulus s frequently triggers action a : for example, a ringing telephone might provoke you to lift it from the receiver. The quantity $Q(a|s)$ corresponds to the controlled processes, characteristic of executive function, which must be engaged when the stimulus-related information $I(s,a)$ is not sufficient to explain the action selection. For example, to let the telephone ring unanswered, one must deploy control processes (to inhibit the prepotent response of lifting the receiver), and the quantity $Q(a|s)$ is an index of the demand of these processes. Accordingly, we refer to $I(s,a)$ as 'sensorimotor control', and $Q(a|s)$ as 'cognitive control'. This distinction between sensorimotor and cognitive control processes complements extant theories dissociating external, stimulus-driven and internal, control-driven modes of behavior [5].

Fractionating cognitive control: contextual versus episodic control

The novel contribution of our information-theoretical model lies in the fractionation of cognitive control itself, according to the temporal framing of actions and events involved in selection. Drawing upon important work from primate neurophysiology and functional imaging [6–8], we argue that control signals that guide behavior can be further subdivided into those related to the immediate context in which

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Box 1. Classical theories of executive function

Our model owes much to classical theories of the functional organization of the PFC, which, for the purposes of a brief review, we class into two groups: those that emphasize the processing of cross-temporal contingencies (i.e. filling in the gap between perception and action) and those that focus on top-down attentional control (i.e. the modulation of processing in peripheral systems on the basis of current plans or goals).

Group 1. Temporal theories

- Several researchers have argued that the primary function of the frontal lobes is the active maintenance of information in working memory, consistent with the finding that PFC neurons are tonically active in a delay period bridging stimulus presentation and a subsequent test. Drawing upon observed dissociations between the dorsal and ventral aspect of the lateral PFC, researchers have argued that the PFC is patterned according to the type of information maintained (e.g. spatial versus verbal [46]), or contains discrete areas for ‘maintenance’ and ‘manipulation’ of information [27].
- Related theories propose that the PFC is responsible for the representation of complexes linking perception with action [17,18], ranging from higher-order plans represented in more anterior regions to simple codes for controlling skilled movement in the premotor cortex.

Group 2. Top-down theories

- Shallice [47] was among the first to argue that the PFC is a top-down attentional ‘supervisor’, biasing competition among internal routines for action on the basis of current goals.
- Passingham [21] agrees that ‘attention to action’ is a key function of the PFC and emphasizes how more anterior PFC regions exert control over posterior regions, including the premotor cortex.
- In a currently influential variant of this view, Miller and Cohen [6] have proposed that ‘cognitive control’ is the cardinal function of the PFC, responsible for contextually modulating activity levels in peripheral centers for sensory perception and motor preparation, through long-range corticocortical connections.

However, whereas theories in group 1 provide a good account of functional specialization within the PFC, they do not describe how information is functionally integrated within the PFC and beyond. By contrast, the theories in group 2 tend to assume that the PFC is monolithically devoted to control processes. Despite the convincing account offered of functional integration between the PFC and other association areas, these models have done much less to advance our understanding of functional fractionation within the PFC.

the stimulus occurs (contextual control) and those related to past events. Context can provide important information for guiding action selection. For example, imagine that the telephone rings when you are visiting a friend; you might be less likely to reply than if you were in your own house. By defining a new set of contextual signals, c , the information-theoretical approach enables a simple formalization of this further fractionation of cognitive control, in which $Q(a|s)$, in turn, is equal to the sum of two control terms: $I(c,a|s)$, corresponding to contextual control, and the remainder $Q(a|s,c)$, corresponding to those control signals related to past events (Box 2, Equation 2). We refer to this second quantity $Q(a|s,c)$ as ‘episodic control’, and argue that it comprises signals for guiding action selection which are attributable to a past event instigating a temporal ‘episode’ in which a new set of rules apply. To continue with the same example: you are at a friend’s house but your friend is busy; your friend asks you to answer the telephone if it rings. Your friend’s instruction defines a new episode with its own ‘episodic’ control signals (or rules), which have to be

Box 2. Information theory and executive control

According to information theory [4], the total amount of information $H(a)$ required for selecting an action a among alternative actions with relative frequency or probability $p(a)$ is given by:

$$H(a) = -\log_2 p(a)$$

Thus, if $p(a) = 1$ then $H(a) = 0$ (i.e. action a is the only possible action, and no information processing is required in order for a to be selected). Conversely, when $p(a)$ is close to zero, there is only a small probability that a will be selected by chance, and so more information processing must have occurred if a is selected over other possible actions. Consider now a stimulus s . Processing stimulus s might provide some information for selecting action a , which is given by the mutual information $I(s,a)$ between s and a :

$$I(s,a) = \log_2 [p(s,a) / p(a)p(s)]$$

where $p(s)$ is the probability that s occurs and $p(s,a)$ the joint probability that s occurs and that a is selected. If s and a are unrelated, then $p(s,a) = p(a)p(s)$ and $I(s,a) = 0$: stimulus s conveys no information for selecting action a . If stimulus s invariably triggers action a (i.e. the probability of selecting a given that s $p(a|s) = p(s,a)/p(s) = 1$) then $I(s,a) = H(a)$: stimulus s conveys all the information required for selecting action a (i.e. action a is an automatic response to stimulus s). Accordingly, we refer to mutual information $I(s,a)$ as sensorimotor control on action a . Then, consider the following quantity, usually referred to as the conditional information:

$$Q(a|s) = H(a) - I(s,a) \quad (\text{Eqn 1})$$

$$= -\log_2 p(a|s)$$

The quantity $Q(a|s)$ corresponds to the psychological notion of cognitive control: it measures the information required for selecting action a beyond sensorimotor control, varying from zero when action a is an automatic response to stimulus s , and increasing as action a becomes less predicted by stimulus s . Furthermore, total information $H(a)$ for selecting a is the sum of sensorimotor control $I(s,a)$ and cognitive control $Q(a|s)$ (Figure 1). A key feature of cognitive control is that it can be similarly broken down into two further terms, as follows:

$$Q(a|s) = I(c,a|s) + Q(a|s,c) \quad (\text{Eqn 2})$$

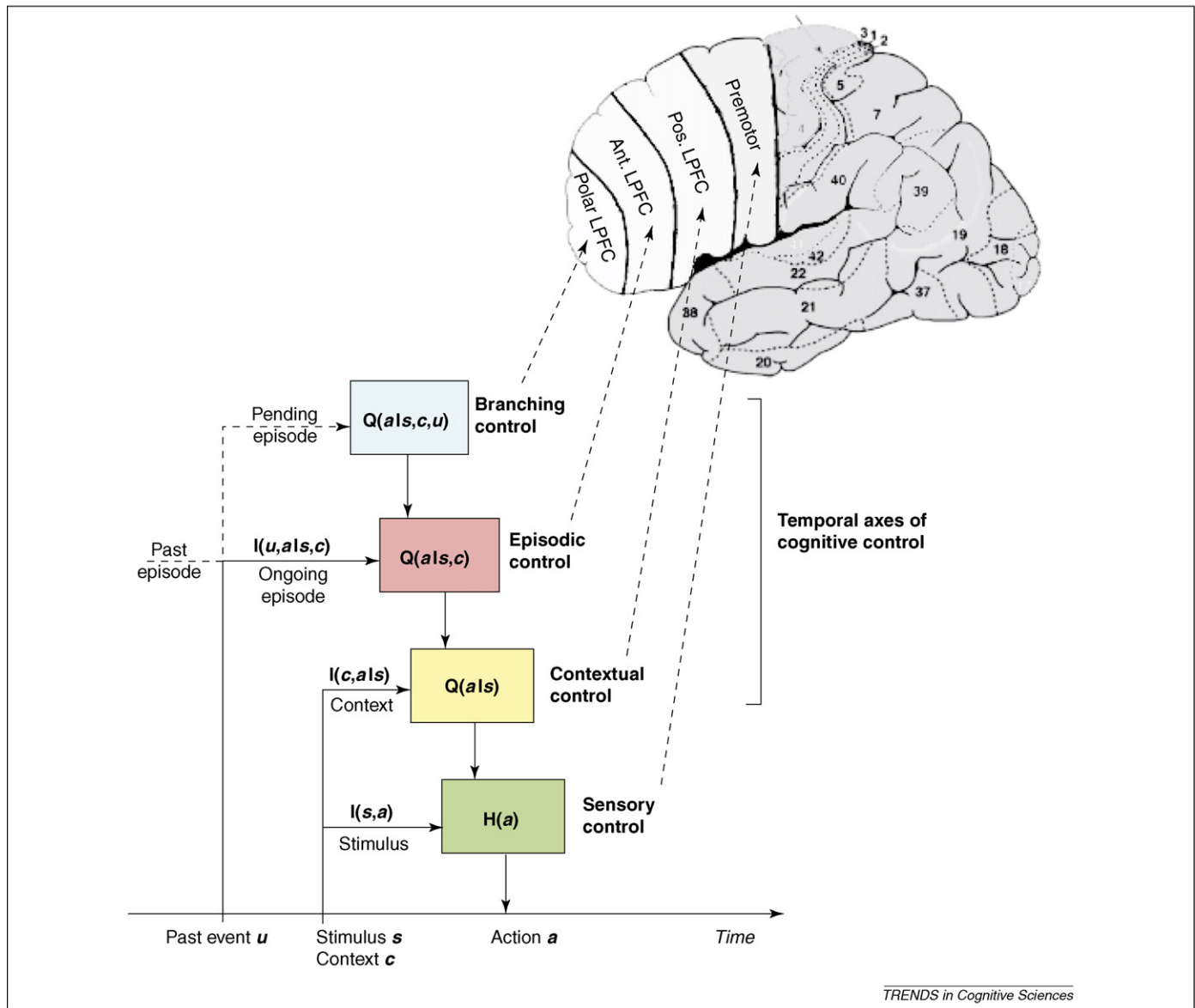
The first term, $I(c,a|s)$, measures the information conveyed by additional signals c , independent of stimulus s and involved in selecting a . The first term is referred to as contextual control, where c belongs to the immediate perceptual context in which the stimulus occurs. The second term is then the remaining information conveyed by past events and can again be broken down into two terms as follows:

$$Q(a|s,c) = I(u,a|s,c) + Q(a|s,c,u) \quad (\text{Eqn 3})$$

where $I(u,a|s,c)$ and $Q(a|s,c,u)$ measure the information conveyed by past events following and preceding the past event u , respectively. If event u has fully specified the ongoing behavioral episode (i.e. selecting actions after u has been independent of events preceding u), then the first term is referred to as episodic control. Then, $Q(a|s,c,u)$, referred to as branching control, measures the demand of control to revert back to the information belonging to the behavioral episode preceding u and required for selecting the current action a [3,9].

integrated with those owing to sensorimotor and contextual control in the service of action selection.

If executive function can be fractionated into sensorimotor, contextual and episodic control, as suggested by the information-theoretic model, then we would expect these processes to be associated with distinct regions of the PFC (Figure 1). Koechlin *et al.* [9] tested this hypothesis using a task in which subjects performed simple color and letter judgments, which remained constant over all experimental blocks or varied from block to block, or even from



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Figure 1. Model overview. Cognitive control operates according to three nested levels of control processes (contextual, episodic and branching) implemented from posterior to polar prefrontal regions. $H(a)$ measures the total amount of control information required for selecting action A and processed in the premotor cortex. $H(a)$ is the sum of two control terms: bottom-up information conveyed by a stimulus S [$I(s,a)$, sensorimotor control] and the remaining top-down information conveyed by the posterior lateral PFC (Pos. LPFC), and measuring cognitive control. Cognitive control, in turn, is the sum of two control terms: bottom-up information conveyed by the context c in which stimulus s occurs [$I(c,a|s)$, contextual control]; and the top-down remaining information $Q(a|s,c)$ processed in the anterior LPFC (Ant. LPFC). Finally, this latter control term is the sum of bottom-up information conveyed by a past event u [$I(u,a|s,c)$, episodic control] and the remaining top-down information processed in the polar LPFC (branching control). Branching control is related to the information conveyed by events preceding u and maintained in a pending state until completion of the ongoing episode.

trial to trial, depending upon the immediate context in which stimuli appeared (Figure 2). Concurrent functional magnetic resonance imaging (fMRI) revealed that these control processes were implemented in a hierarchically ordered fashion along the anterior–posterior axis of the lateral PFC (Figure 3a–c). Activity in the more anterior portion of the dorsolateral PFC [$y = +32$, Brodmann's Area (BA) 46] varied with the amount of episodic information $Q(a|s,c)$ that was required to select the correct response; activity in the posterior dorsolateral PFC ($y = +8$, BA 44/45) varied with $Q(a|s)$, the sum of contextual and episodic information; and activity in the premotor cortex ($y = -8$, BA 6) varied with $H(a)$, the total sum of sensorimotor, contextual and episodic information. Moreover, behavioral

data suggested that sensorimotor, contextual and episodic factors were found to make independent contributions to reaction time, as predicted by the model. These data led Koechlin *et al.* to conclude that episodic, contextual and sensorimotor control are implemented in these three frontal regions, respectively.

Fractionating cognitive control: episodic versus branching control

In a final hierarchical stage proposed by the model, episodic control $Q(a|s,c)$ is itself further subdivisible into the sum of two control terms. Let us define the instruction cue related to any past event (e.g. your friend's request that you pick up the telephone if it rings) as a control signal u .

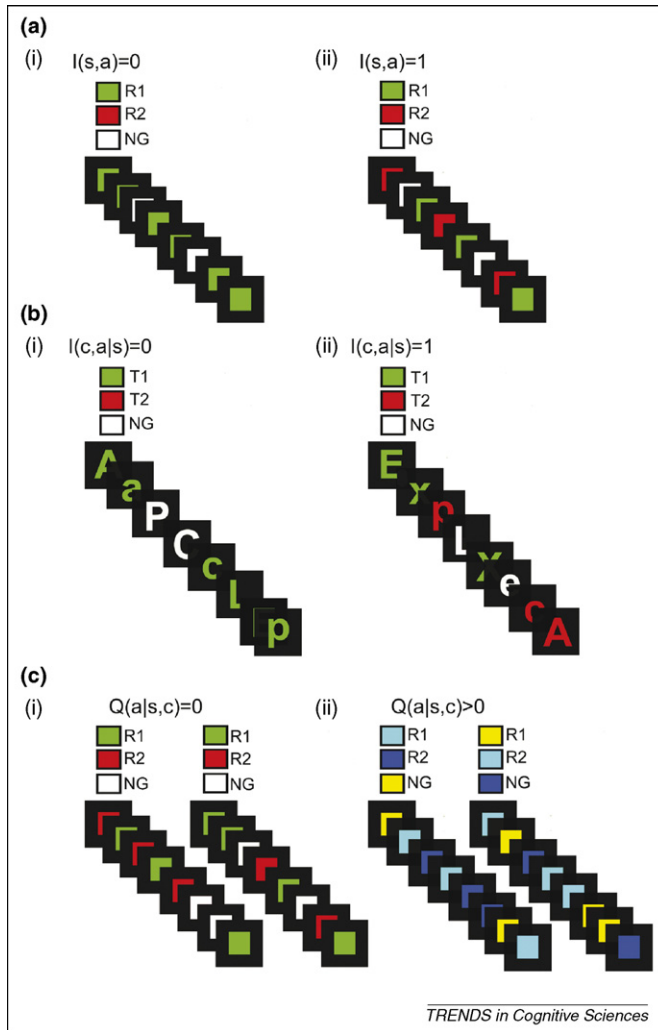


Figure 2. Description of the color and letter tasks used by Koechlin *et al.* [9]. Subjects made speeded responses to colored shapes or letters, or withheld a response to a no-go stimulus, on the basis of an instruction cue, which initiated each block. (a) Sensorimotor control was manipulated by varying the number of different responses required within a single block. In (i), sensorimotor control is low because the same response is required on every trial [R1 = response 1 (e.g. left hand); R2 = response 2; NG = no go]. However, in (ii), the subject is required to select left and right responses on the basis of the color of the stimulus. (b) Contextual control was manipulated by requiring subjects to make either vowel or consonant, or upper case or lower case letter judgments, the task being determined by the color of the letter [T1 = task 1 (e.g. vowel or consonant); T2 = response 2; NG = no go]. Where contextual control was low (i), the task remained the same across the entire block; in high contextual control blocks (ii), the task changed from trial to trial. Note that sensorimotor control is equal in both of these conditions because in both tasks, both responses (R1 and R2) are possible. (c) Episodic control was manipulated by varying the contingencies linking the instruction cues and the task. Throughout both letter and shape tasks, when the response- or task-relevant colors were red, green or white, the same color always denoted the same response (for example, green was always 'respond left', and white was always no-go (i)). However, when the colors were blue, yellow and cyan, the response demanded by each color varied on a block-by-block basis (ii).

Episodic control can thus be said to be composed of control owing to that signal and subsequent ones $I(u,a|s,c)$ plus control owing to signals that precede it $Q(a|s,c,u)$ (Box 2, Equation 3). Accordingly, we consider ongoing behavior to be composed of multiple successive temporal frames or episodes, each of which contains a different set of rules for governing behavior. Although an instruction cue u signaling the onset of a new episode carries important informational value for action selection within that episode, information from episodes preceding the current one might also provide

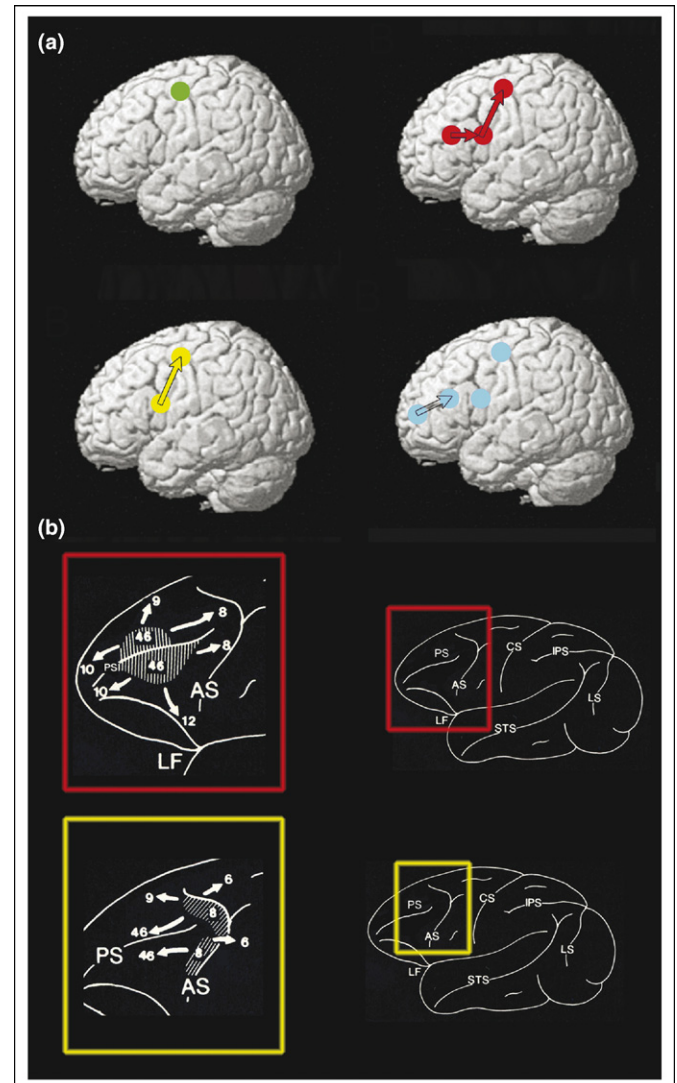


Figure 3. Prefrontal and premotor regions associated with sensorimotor, contextual and episodic control, and branching. (a) Disks rendered onto a standard brain mark the peak coordinates of the PFC networks associated with sensorimotor (green), contextual (yellow) and episodic (red) control, and branching (cyan) for the left hemispheres only. Right hemisphere data were similar. Filled arrows indicate observed functional connectivity, tested through structural equation modeling, observed within each network. Unfilled arrows signal functional connectivity predicted by the model but as yet untested [9,14]. (b) Intrinsic connections between prefrontal and premotor regions in the monkey PFC. Solid arrows indicate projections that were identified experimentally. Numbers indicate BA. This connectivity pattern supports an anteroposterior functional organization of lateral PFC regions. Note the parallel with functional activations shown in (a). Modified, with permission, from Ref. [48].

signals that carry over to guide behavior. To extend our example yet further, consider the following scenario: you are at your friend's house, and he is working, so he asks you to answer the telephone if it rings (instruction cue u_1). Subsequently, however, your friend tells you that he will soon be expecting an important call, and wants to answer it himself. The episode defined by the signal u_1 is thus placed in a pending state; a new episode, u_2 , in which you are not required to answer the telephone if it rings, is initiated. Importantly, however, once the expected call has been taken, you revert to the original episode, and u_1 once again governs action selection. This type of behavior, which we call 'branching', is the basis of all behaviors requiring simultaneous engagement in multiple tasks, and is one of the

ways by which humans overcome the serial constraint on behavior, whereby only one task can be centrally processed at any one time [10–13]. Accordingly, branching control enables a task or a behavioral episode to be interrupted and temporarily maintained in a pending state while another is being performed, and/or to revert back to a pending task or episode following completion of the ongoing one.

Koechlin *et al.* [14,15] investigated the neural correlates of branching, using a paradigm requiring subjects temporarily to suspend the performance of an ongoing letter-matching task in favor of a secondary task. Relative to control conditions, which captured the delay period and task-switching elements, in addition to increased relational complexity (but not the branching element) of this task, the active maintenance of information from the pending task was associated with activity in yet more anterior PFC regions, in the frontopolar cortex corresponding to lateral BA 10 (Figure 3d). This suggests that during execution of the current episode *u*, the most anterior portions of the PFC maintain (in a distractor-resistant fashion) pending information from a yet more temporally distant episode, enabling this information to be flexibly retrieved when this episode is re-instantiated [16].

The cascade model

Collectively, these data depict a hierarchically ordered executive system lying along the anterior–posterior axis of the lateral PFC (Figure 1), with control signals owing to events which occurred in the more and more distant past arising from successively more anterior cortical regions. At the apex of the hierarchy, the most rostral parts of the lateral PFC subserve in branching control, the arbitration among several past cues for action selection during multiple task performance; subsequently, anterior dorsolateral PFC regions additionally vary with episodic control, whereby a discrete past event defines a new set of rules for action selection; the posterior dorsolateral PFC additionally varies with contextual control, whereby the immediate environment provides a contextual signal to guide action selection; and the premotor cortex, at the base of the hierarchy, integrates all these signals with those from the stimulus itself (sensorimotor control) to decide how to act. Information thus flows in a ‘cascade’ from anterior to posterior regions, with multiple control signals owing to temporally distinct events arriving from the PFC to govern response selection within the premotor cortex.

Direct evidence for this cascade of information was offered by structural equation modeling of the fMRI time series taken from the PFC [9]. As predicted by the model, only episodic control was associated with coupling between the anterior and posterior PFC, whereas connectivity between the posterior PFC and premotor cortex increased in both episodic and contextual control conditions (Figure 3). Sensorimotor control did not affect the flow of information between frontal processing stages. This ‘cascade’ of neural information from anterior to posterior regions thus offers an account both of how the PFC is functionally fractionated and how integration of neural information occurs within this hierarchical system.

The cascade model also garners support from a broad range of theoretical and empirical work from outside of the

authors’ laboratory. Notably, several elements from extant theories of executive function have been incorporated into this model, and in particular those of Fuster [17] and Grafman [18], who first emphasized the principles of ‘functional proximity’, whereby higher levels of control are predicted to involve more anterior prefrontal regions, and ‘subsidiarity’, whereby higher levels of the hierarchy are only recruited when lower levels do not provide enough information to control action selection. Thus, in the cascade model, a situation that can be addressed with recourse to habitual sensorimotor associations (such as when the telephone rings in the familiar context of one’s own home) does not require the activation of PFC regions subserving contextual or episodic control, a notion supported by neuropsychological data describing the behavior of patients with prefrontal lesions [19]. However, when higher regions are recruited proactively, their signals can bias and overrule prepotent sensorimotor associations or task sets, to optimize controlled action selection. Similarly, when conflict arises because of multiple, incongruent sensorimotor associations, higher regions are recruited reactively, and their top-down signals achieve selection between these multiple conflicting representations.

Evidence supporting the cascade model

The cascade model is supported by a wide variety of evidence from neuroimaging studies in humans, and single-unit and lesion studies in non-human primates. First, a considerably body of empirical work has established that response selection relies on the premotor cortex [6,20,21], with single neurons in macaque premotor regions coding for one of several possible sensorimotor associations. In addition to human neuroimaging studies, single-unit recordings also support the notion that contextual control is the province of the dorsolateral PFC. For example, neurons in the posterior dorsolateral PFC have been shown to code for the conjunction between a stimulus and a variety of contexts, including task set [22], spatial location [23] and category membership [24]. Moreover, monkeys with lesions involving the posterior part of the dorsolateral PFC are impaired at selecting responses that are guided by contextual signals [25]. Together, these studies argue for a dissociation between the premotor and the dorsolateral PFCs which is echoed by the fractionation of action selection into sensorimotor and contextual control in the cascade model.

Consistent with the notion that the anterior portion of the PFC maintains the rules for action selection across a behavioral episode (episodic control), evidence from lesion studies in monkeys has revealed that BA 46, rather than those in more posterior PFC regions (BA 8 and BA 45), seems to be crucial for action selection based on maintaining or monitoring information conveyed by past events [26,27]. Other brain imaging studies have also emphasized that cognitive control owing to past information tonically activates more anterior PFC regions, whereas selection owing to more immediate information activates the posterior PFC [7,16,28,29], consistent with the dissociation between episodic and contextual control proposed by the cascade model. In the ventrolateral PFC, more anterior regions have been shown to subserve controlled retrieval, and more posterior regions to support postretrieval selection mechanisms [30], a view

compatible with the model described here. Finally, a wealth of other data indicates that episodic retrieval [31], prospective memory [32] and subgoaling [33] recruit the rostral PFC, supporting a role in arbitrating among multiple task-sets during branching for the most rostral regions at the apex of the cascade hierarchy [34].

It is worth noting that the cascade model makes no claims about possible functional segregations between the ventral and dorsal sectors of the lateral PFC. Accordingly, the model is *a priori* consistent with previously proposed ventrodorsal segregations based on the modality of processed information, particularly within posterior PFC regions (e.g. spatial versus verbal or object) [35]. However, because, in the cascade model, higher control information is combined with lower control information through top-down interactions for selecting actions, such functional segregations might be more subtle and depend on the crossmodality of higher and lower control signals. This idea is supported by recent neuroimaging results [36] and by single-unit studies in monkeys showing neurons in both dorsal and ventral PFC regions that code for locations, objects or both, depending on what information is crucial for behavioral control [23,37,38].

It remains to be described how the associations underlying selection processes (i.e. 'selection rules') at each level of the cascade model are acquired in the first place. One possibility is that neurons gradually adapt their response fields according to the recently active episodic, contextual signals or sensorimotor associations in respective hierarchical regions [39]. However, the essence of the cascade model is to represent and process context- or episode-dependent associations rather than to form new associations by altering those previously learned. Thus, higher control levels might be actively engaged during the learning of new lower-level associations to link them to new environmental contexts or behavioral episodes, and, concomitantly, inhibit and protect prepotent, previously learned associations. This is a complex computational issue that is beyond the scope of the current discussion, and that speaks to the nature of long-term representation in the PFC, and it is likely to be an important topic for future research.

Importantly, the hierarchical organization of cognitive control described herein corresponds to the integration of temporally more distant events in action selection rather than to the processing of more complex selection rules [9,15]. In confirmation of this hypothesis, it was recently found that action selection in structured behavioral plans of increasing complexity was confined to premotor and posterior PFC regions, specifically in Broca's area and its right homolog [40]. This finding is consistent with the respective role of premotor and posterior PFC regions in sensory and contextual control, given that the two types of control essentially operate according to immediate sensory signals but at distinct hierarchical levels of action representation (sensorimotor associations versus consistent sets of sensorimotor associations). Thus, contextual control can be further considered as a set of selection processes operating along hierarchical structures of action plans, possibly including those of human language [40,41].

In summary, thus, the cascade model provides a conceptual framework for understanding functional fractionation and functional integration within the lateral

Box 3. Questions for future research

- *Quantification of prefrontal executive function.* Our information-theoretic approach further provides quantitative laws to describe the gradual engagement of the different forms of cognitive control and related prefrontal regions. Experimental evidence supporting such quantitative laws was essentially obtained for episodic control [9]. It remains to be demonstrated that the predicted quantitative laws hold for the other levels of cognitive control.
- *Top-down versus bottom-up processing in the lateral PFC.* Classical theories of executive control, in addition to the cascade model, emphasize the role of top-down interactions within the PFC. However, corticocortical interactions within the lateral PFC are reciprocal (Figure 3), raising the issue of the function of bottom-up projections. A related question is to understand how higher control levels are recruited during action selection. Given that, in the cascade model, the engagement of higher control levels might be conditional to the inability of lower control levels to complete action selection alone, bottom-up projections might participate in the recruitment of higher control levels in action selection.
- *Functional segregation between posterior associative and prefrontal regions.* The lateral PFC is strongly connected to posterior associative brain regions in the parietal and temporal lobes. Because prefrontal and posterior associative regions are most often coactivated, an important issue is to clarify the functional segregation between these brain sectors. A related problem is the nature of long-term representations in prefrontal compared with posterior regions.
- *Functional limit of executive control.* According to the cascade model, the apex of the prefrontal executive system is implemented in the most anterior prefrontal regions and corresponds to control processes underlying multitasking and the temporary maintenance of pending behavioral episodes. An important open question is the identification of the capacity limits of this control level because it will reveal an upper processing bound on the prefrontal executive system, and intrinsic limitations underlying human higher cognition such as reasoning and planning.

PFC. This model offers a quantitative approach to understanding the function of the PFC, moving beyond the phenomenological terms, such as 'goals', 'intentions' or 'tasks', which are typically used to describe executive processes. Overall, our main argument is that it is the temporal structure of events involved in action selection that determines the functional organization of the lateral PFC, and that defines the crucial building blocks for executive function. However, many questions remain unanswered. Here, we have focused exclusively on the lateral PFC; an important goal for future research will be to determine how the cognitive architecture of the lateral PFC interacts with other sectors of the PFC, and in particular with the medial PFC, which has been implicated in monitoring and evaluating ongoing actions [42,43], and the orbitofrontal cortex involved in coding subjective values of stimuli and associated actions learned from experience [44,45]. Finally, the cascade model provides a possible framework to address several other unresolved issues regarding the prefrontal function (Box 3).

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