THE PREFRONTAL CORTEX AND COGNITIVE CONTROL

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One of the enduring mysteries of brain function concerns the process of cognitive control. How does complex and seemingly wilful behaviour emerge from interactions between millions of neurons? This has long been suspected to depend on the prefrontal cortex — the neocortex at the anterior end of the brain — but now we are beginning to uncover its neural basis. Nearly all intended behaviour is learned and so depends on a cognitive system that can acquire and implement the 'rules of the game' needed to achieve a given goal in a given situation. Studies indicate that the prefrontal cortex is central in this process. It provides an infrastructure for synthesizing a diverse range of information that lays the foundation for the complex forms of behaviour observed in primates.

TOP-DOWN
Brain signals that convey knowledge derived from prior experience rather than sensory stimulation.

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Humans and other animals can do more than reflexively react to sensory information that is immediate and salient. We engage in complex and extended behaviours geared towards often far-removed goals. To do so, we have evolved mechanisms that can override or augment reflexive and habitual reactions in order to orchestrate behaviour in accord with our intentions. These mechanisms are commonly referred to as 'cognitive' in nature and their function is to control lower-level sensory, memory and/or motor operations for a common purpose. So cognitive control is essential for what we recognize as intelligent behaviour.

Insight into the neural mechanisms for cognitive control may come from what is arguably their most important feature: they are sculpted by experience. Virtually all intended behaviours are learned and so depend on a cognitive system that can acquire the rules of the game — what goals are available and what means can be used to achieve these goals[1–4]. Take, for example, dining in a restaurant. We are not born knowing that this can be a rewarding experience or how to act in this situation. Instead, our experiences arm us with expectations about the important sensory information deserving our attention (for example, the wine list), typical events, appropriate actions and expected consequences (for example, paying the bill). This knowledge allows diverse brain processes to be orchestrated along a common internal theme. So a key function of the neural circuitry mediating cognitive control is to extract the goal-relevant features of our experiences for use in future circumstances. It has been proposed that the prefrontal cortex — a neocortical region that finds its greatest elaboration in humans — is centrally involved in this process[4–8].

The prefrontal cortex (PFC) (FIG. 1) is an interconnected set of neocortical areas that have a unique, but overlapping, pattern of connectivity with virtually all sensory neocortical and motor systems and a wide range of subcortical structures[9–12]. This provides an ideal infrastructure for synthesizing the diverse range of information needed for complex behaviour. The PFC also has widespread projections back to these systems that may allow it to exert a 'TOP-DOWN' influence on a wide range of brain processes[9–12]. Indeed, the effects of PFC damage are most apparent when cognitive control is most needed — when the knowledge about a given situation must be used to select the appropriate goal-directed actions (BOX 1).

Here I review recent neurophisiological studies in monkeys that have explored the neural basis of cognitive control. They indicate that a major function of the PFC is to extract information about the regularities across experiences and so impart rules that can be used to guide thought and action[8,13–15].

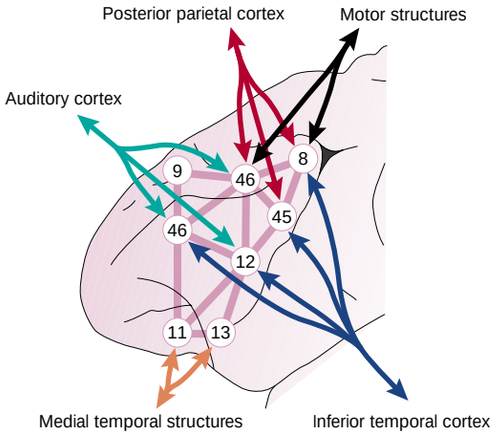


Figure 1 | **Integrative anatomy of the macaque monkey prefrontal cortex.** Numbers refer to sub-regions within prefrontal cotex as defined by Brodmann. Different PFC subregions have unique, but overlapping, patterns of connections with other brain regions. For example, the more posterior and dorsal portions of the lateral PFC are more heavily interconnected with cortical areas that emphasize processing of visuospatial and motor information. Ventral and anterior lateral regions are more heavily interconnected with cortical areas that emphasize information about visual form and stimulus identity. The ventral (orbitofrontal) PFC is more associated with subcortical structures that process 'internal' information such as homeostasis. Above and beyond this regional emphasis, however, there is also multimodal convergence. Many PFC areas receive converging inputs from at least two sensory modalities[94,95] and there are ample interconnections between different PFC areas (illustrated by the purple lines) that could bring together results from a wide range of brain processes. For simplicity, this figure only shows a subset of PFC areas and a subset of their connections. Areas on the medial surface are not shown or discussed in this review.

GOAL-DIRECTED BEHAVIOUR
Behaviour directed toward attainment of a future state (for example, obtaining a graduate degree).

INTERNAL STATES
Brain information not directly related to a sensory input or motor output; for example, homeostatic information such as hunger, thirst or other motivational influences.

TASK CONTINGENCIES
The logical structure of a given task (for example, if the light is green, cross the street).

LIMBIC STRUCTURES
A collection of subcortical structures important for processing memory and emotional information. Prominent structures include the hippocampus and amygdala.

MULTIMODAL RESPONSES
Neural activity elicited by more than one sensory modality.

SACCADE
A rapid, ballistic eye movement from one point of gaze to another.

Associations, conjunctions and rules

GOAL-DIRECTED BEHAVIOUR requires predictions about events, INTERNAL STATES and actions that are likely to achieve a goal. But to make these predictions, we need to form associations between their internal representations[16]. A neural ensemble of a task, then, might be composed of neurons whose activity reflects learned associative relationships between these goal-relevant elements, that is, the TASK CONTINGENCIES (BOX 2). Prefrontal neurons do have this property — they show conjunctive tuning for learned associations between cues, voluntary actions and rewards. Prefrontal neurons even show tuning for complex, behaviour-guiding rules. So they may help form neuron ensembles that represent the regularities across experiences that describe the principles needed to achieve a particular goal in a particular situation.

For example, the lateral PFC is directly interconnected with higher-order sensory and motor cortex, and indirectly connected (through the ventromedial PFC) with LIMBIC STRUCTURES that process 'internal' information such as reward[9–12]. The neural activity in the lateral PFC reflects this — many of its neurons show MULTIMODAL RESPONSES[17–22]. Furthermore, the lateral PFC is critical for normal learning of arbitrary associations between sensory cues, rewards and voluntary actions[23–27].

Many lateral PFC neurons reflect these learned associations[18,28,29]. For example, Watanabe used a set of tasks in which visual and auditory cues signalled, on different trials, whether reward would or would not be delivered[18,28]. Most lateral PFC neurons were found to reflect the association between a cue and reward. A given neuron might be activated by a cue, but only when it signalled 'reward'. In contrast, another neuron might be activated only by a cue that signalled 'no reward'. Similarly, we trained monkeys to associate, in different blocks of trials, each of two cue objects with a SACCADE to the right or left[29], and found that the activity of 44% of lateral PFC neurons reflected associations between objects and the saccades they instructed (FIG. 2). Other neurons had activity that reflected the cues or the saccades alone, but they were fewer in number. Fuster and colleagues[30] have also shown that PFC neurons can reflect learned associations between visual and auditory stimuli.

Striking examples of experience-dependent neural plasticity come from Bichot and Schall's studies of the frontal eye fields, part of Brodmann's area 8 that is important for voluntary shifts of gaze. Normally, neurons in this area fire selectively to saccade targets appearing in certain visual field locations. However, when monkeys were trained to search for a target defined by a particular visual attribute (for example, red), the neurons in the frontal eye fields acquired sensitivity to that attribute[31]. Bichot and Schall[32] trained monkeys to search for a different target every day and found that neurons not only discriminated the current target, but also distracting stimuli that had been a target on the previous day, relative to stimuli that had been targets even earlier. Monkeys were also more likely to make errors in choosing that distracting stimulus. It was as if the previous day's experience left an impression in the brain that influenced neural activity and task performance.

But monkeys and humans do more than remember simple contingencies. They can discern the regularities across them to extract general principles or rules. This is reflected in PFC activity as well. White and Wise[21] found that the activity of up to half of PFC neurons depended on whether the monkey was guiding its behaviour by a spatial rule (a cue's location indicated where the target would appear) or an associative rule (the identity of the cue indicated the target's location). Hoshi *et al.*[33] found that many PFC neurons were modulated by which rule (matching shape or location) the monkey was currently using. We have also observed lateral prefrontal neurons with rule-dependent activity (BOX 3)[34,35]. These neurons could correspond to the 'rule-coding' units in the models of Dehaene and Changeux[13,36].

So PFC neurons convey information about the formal demands of tasks, a possible foundation for the complex forms of behaviour of primates. The mechanisms that guide the formation of these representations are discussed in the next section.

Reward signals and rule representations

If PFC neural ensembles reflect goal-relevant information, their construction is probably guided by reward.

Box 1 | Behavioural effects of prefrontal cortex damage

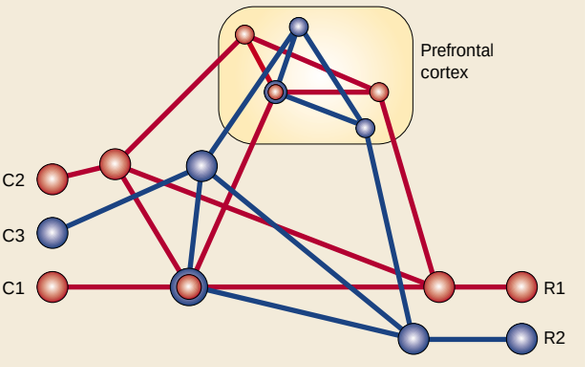
Humans with prefrontal damage can seem strikingly normal upon superficial examination. They can carry on a conversation, often have normal IQ scores and can perform familiar routines without difficulty. However, despite their good performance on standard neuropsychological tests of perceptual, memory and motor skills, their ability to organize their lives is profoundly impaired. They are impulsive and irresponsible and consequently can have trouble holding a job, remaining married and so on. Careful testing has revealed that the behaviour of humans and monkeys with prefrontal damage can be described as stimulus-bound. Their behaviour is captured by salient sensory cues that reflexively elicit strongly associated actions. They are unable to override these impulses to engage in behaviours that depend on knowledge of a goal and the means to achieve it, that is, behaviours that are weakly established, complex, changing, or that must be extended over time[4,7,10,11,86]. For example, consider a classic test of prefrontal impairment, the Wisconsin Card Sorting Task. Subjects are instructed to sort cards according to the shape, colour or number of symbols appearing on them. They start with one rule (for example, colour) and, once that is acquired, the experimenter changes the rule (for example, shape) without telling the subject. Rules are acquired and changed until all the cards have been sorted using all possible rules. Normal people have little difficulty with this task. In contrast, people with prefrontal damage can learn the first rule but then they are unable to escape it: they make a great deal of errors because they lapse back to the earlier rule[91]. The ability of monkeys with PFC lesions to perform an analogue of this task is also impaired[92]. Shallice and Burgess described patients with damage to the frontal lobes who are able to execute simple routines in which clear sensory cues could elicit a familiar action (for example, 'buy a loaf of bread')[93]. However, they were unable to carry out an errand that involved organizing a series of such routines. They would, for example, enter shops that were irrelevant to the errand. In these cases, the basic elements of behaviour are intact but it seems that they are missing the flexibility to shift between different rules and so override PREPOTENT RESPONSES to persist toward a goal. Here, I suggest that the PFC allows for this flexibility by dynamically establishing task-relevant neural pathways in other brain systems (BOX 2).

Reward information does have a pervasive influence on PFC activity — activity in the lateral PFC and ventromedial PFC conveys the identity and size of expected rewards[18,28,37–39]. A major source of reward-related signals may be the dopamine-mediated innervation of the PFC from a group of cells situated in the ventral tegmental area(VTA) of the midbrain.

VTA neurons have properties that are ideal for providing a signal that guides acquisition of goal-relevant information. Initially, they give a burst of activity to unpredicted rewards[40,41]. With experience, they become activated by cues that predict reward and not by the rewards themselves[42]. These neural responses that have been transferred to the cues also wane with further training, perhaps because they transfer to environmental cues that are earlier predictors of reward[43]. VTA neurons are also inhibited when an expected reward is withheld[44]. This codes the degree to which a reward, or a cue that predicts reward, is surprising. As the aim of the organism is to predict the means to achieve reward, this 'prediction error' indicates when the associative learning that underlies this ability should occur[45].

The resulting dopamine influx into the PFC could affect plasticity through several plausible mechanisms. For example, dopamine could augment NMDA (*N*-methyl-D-aspartate) receptor-mediated glutamatergic transmission, which has been directly implicated in plasticity[46]. Dopamine may also help augment and sustain PFC activity[47,48], allowing activity-dependent plasticity mechanisms to work.

Box 2 | A suggested role for the prefrontal cortex in cognitive control



The figure shows processing units representing cues such as sensory inputs, current motivational state, memories and so on (C1, C2 and C3); units representing two voluntary actions (for example, 'responses' R1 and R2); and internal or 'hidden' units representing intervening stages of processing. The PFC is shown as being connected to the hidden units because it is interconnected with higher-order 'association' and premotor cortices, not with primary sensory or motor cortices. A situation in which the PFC seems particularly important is pictured here: when the same cue (C1) could lead to one or another response (R1 or R2) depending on some other item of information (C2 or C3). For example, if the phone rings (C1) and you are at home (C2), you answer it (that is, C1…R1). But if the phone rings (C1) and you are a guest in someone else's home (C3), you do not (C1…R2). During learning, reward signals may strengthen the connections between PFC neurons that process the information that leads to reward, resulting in a pattern of activity that reflects the pattern of associations between goal-relevant information that is unique to each situation (that is, the task contingencies). Once established, a subset of the information (for example, C1 and C2) can activate the entire representation (for example, the constellation of PFC 'units' shown in red), including information about the appropriate response (for example, R1). Bias signals from the PFC task representations may then select task-relevant neural pathways in other brain systems (for example, C1–R1). A different set of cues (C1 and C3) would activate a different PFC representation (shown in blue) and, consequently, a different pattern of bias signals selects a different set of neural pathways (C1–R2). By providing a bias signal to the intermediate (hidden) units, the PFC favours the pathways in the posterior neocortex and other brain areas that are appropriate for the task. So task-relevant pathways can be dynamically and flexibly established because they depend on the current pattern of PFC activity. A loss of flexibility is a hallmark of PFC damage (BOX 1).

PREPOTENT RESPONSES
Reflexive actions, either innate or well established through a great deal of experience.

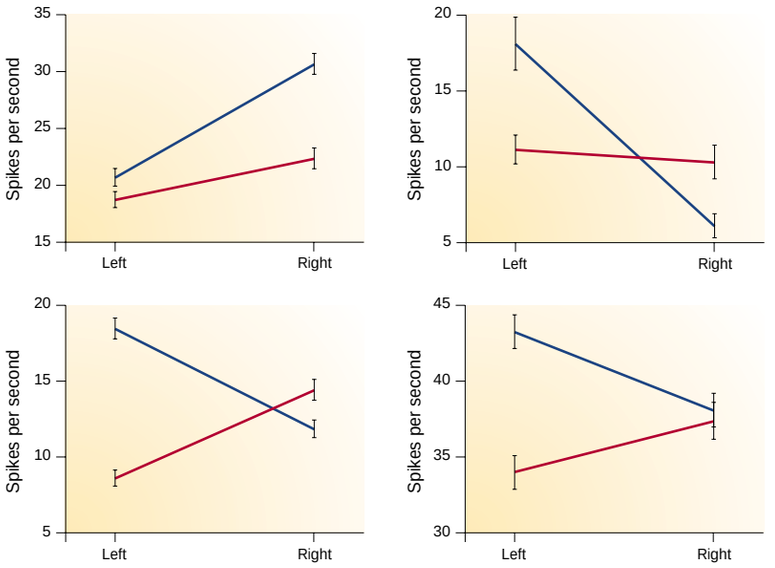


Figure 2 | **Conjunctive tuning in the prefrontal cortex.** The activity of four single PFC neurons when each of two objects instructed either a saccade to the right or a saccade to the left on different trials. The lines connect the average values obtained when a given object cued one or the other saccade. The error bars show the standard error of the mean. Note that in each case, the neuron's activity depends on both the cue object and the saccade direction and that the tuning is nonlinear or conjunctive. That is, the level of activity to a given combination of object and saccade cannot be predicted from the neuron's response to the other combinations. (Adapted from REF. 29.)

PFC activity elicited by a transient event can be sustained for many seconds[19,20,49–53]. This allows PFC neurons to form associations between events separated in time[29,30]. When the dopamine influx reaches the PFC, it could strengthen connections — associative links — between neurons that were activated by the event that elicited the midbrain dopamine burst and the event that preceded it. Iteration of this process could drive the progressively earlier generation of the dopamine signal from the VTA neurons[54]. During learning, as dopamine arrives progressively earlier, more and more information could be linked into an increasingly multivariate PFC representation that will ultimately describe the constellation of goal-relevant task features.

A possible neural correlate of this phenomenon was observed[29] in an experiment in which we recorded neural activity from the lateral PFC of monkeys learning associations between each of two cue objects and each of two saccadic eye movements. As the monkeys learned, neural activity reflecting the forthcoming saccadic response appeared progressively earlier in the trial (FIG. 3). The initiation of saccade-related activity shifted with learning, from just before the execution of the saccade (and acquisition of reward) to an earlier point in time, nearly coincident with the cue that instructed the response that led to reward acquisition.

Keeping to a task

The capacity for PFC neurons to sustain activity is important not only for learning, but also for persisting towards goals. One of the classic signs of PFC damage is increased distractibility: subjects seem unable to focus on a task when other, irrelevant events compete for their attention[55] (BOX 1). This may reflect the loss of mechanisms for maintaining goal-relevant information, a process known as 'WORKING MEMORY'. This has been explored in a variety of neurophysiological studies in monkeys[19,20,49–53].

Many cortical areas seem to have some sort of short-term buffering ability. What sets working memory apart as being more 'cognitive' is that it can retain information over potentially distracting events. PFC neurons do have this ability. For example, when monkeys are required to sustain the memory of a sample object across a delay period filled with visual distractors that each require attention and processing, sustained activity within the PFC acts to maintain the sample memory[52]. In contrast, sustained activity in extrastriate visual areas seems to be more easily disrupted by the presence of distractors — following presentation of a distractor, neural activity in the INFERIOR TEMPORAL CORTEX and POSTERIOR PARIETAL CORTEX no longer reflected the sample object that the monkey was retaining in memory[52,56,57].

How does the PFC 'latch' onto goal-relevant information and maintain it without disruption? Several models have been suggested[48,58–61]. They typically use a form of a gating signal that instructs the network when to maintain a given activity state. Dopamine influx into the PFC may again be involved. Its neuromodulatory effects could strengthen current representations, protecting them against interference from disruption by irrelevant, distracting information until another dopamine influx reinforces another representation[48,59,61].

Bias signals and top-down control

The ability to sustain task information is of little use unless the PFC can somehow use it to control processing in other brain systems. PFC activity could exert a top-down influence by providing an excitatory signal that biases processing in other brain systems towards task-relevant information. To understand how this might work, consider selective visual attention. In the visual system, neurons processing different aspects of the visual scene compete with each other for activation. This is thought to be important for enhancing contrast and separating objects from the background. The neurons that 'win' the competition and remain active are those that incur a higher level of activity. The biased competition model proposes that visual attention exploits this circuitry[62]. In voluntary shifts of attention a competitive advantage is conferred by excitatory signals (thought to originate from the PFC) that represent the 'to be attended' stimulus. These excitatory signals enhance the activity of neurons in the visual cortex that process that stimulus and, by virtue of the mutual inhibition, suppress activity of neurons processing other stimuli. This idea of excitatory bias signals that resolve local competition can be extended from visual attention to cognitive control in general[8,63].

Several studies have indicated that the PFC exerts a top-down influence over other neocortical regions. Deactivation of the lateral PFC attenuates the activity of extrastriate neurons to a behaviourally relevant cue[64,65]. Tomita *et al.*[66] showed that top-down signals originating

WORKING MEMORY
The representation of items held in consciousness during experiences or after retrieval of memories. Short-lasting and associated with active rehearsal or manipulation of information.

INFERIOR TEMPORAL CORTEX
A neocortical region responsible for high-level analysis of form information.

POSTERIOR PARIETAL CORTEX
A region of the visual cortex thought to be involved in visuospatial, visuomotor and attentional processes.

Box 3 | Task-dependent activity in the lateral prefrontal cortex

We trained monkeys to alternate between tasks that used the same cues and responses but three different rules: matching (delayed matching to sample), associative (conditional visuomotor) and spatial (spatial delayed response)[34]. The first two tasks shared common cue stimuli, but differed in how these cues were used to guide behaviour, whereas the latter two used different cues to instruct the same behaviour. All three required the same motor responses. The associative task required the monkeys to associate a foveally presented cue stimulus with a saccade either to the right or left. The cue–response pairings were reversed within each session in order not to confound the influence of cue stimulus and response direction on neural activity. The object task used the same cue stimuli as the associative task; however, in this case the monkeys needed only to remember the identity of the cue and then saccade to the test object that matched it. Conversely, the spatial task used small spots of light to explicitly cue a saccade to the right or left and so required the monkeys to simply remember the response direction. We found that over half of lateral PFC neurons were task-dependent. A given neuron might be activated by a cue object during one task (for example, the associative task), but be unresponsive when the same cue appeared under identical sensory conditions during another task (for example, the object task). Also, the baseline activity of many neurons varied with the task — a given neuron might consistently show higher baseline activity whenever the monkey performed the object task, for example. These results indicate that PFC neurons do not simply code a stimulus or forthcoming action. Rather, they also convey their behavioural context, the pattern of associated information that is unique to a particular task.

from the PFC are required to activate (recall) a long-term memory stored in the inferior temporal cortex.

Other suggestive evidence comes from Miller and Desimone's[52,56,67] investigation into the respective roles of the PFC and inferior temporal cortex in working memory. Monkeys were trained to hold a sample object 'in mind' while they viewed a sequence of objects. They were required to respond when the sample was repeated and to ignore other irrelevant object repetitions. As noted above, sustained activity in the prefrontal, but not inferior temporal, cortex maintained the sample memory across intervening stimuli[52,56]. However, many inferior temporal neurons showed an enhancement of their neural responses to the sample repetition but not to irrelevant repetitions[52,67]. This indicated that sustained activity to the sample in the PFC might have enhanced responses to its repetition in the inferior temporal cortex[52].

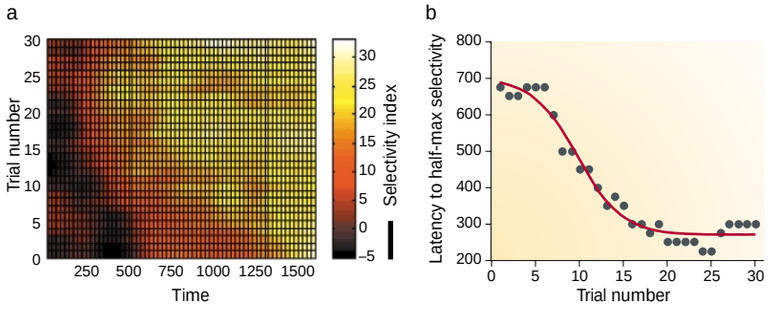


Figure 3 | **Change in latency of response-related activity with learning. a** | The average degree of saccade-direction selective activity for 64 lateral PFC neurons is shown in this surface plot. Directional selectivity appeared earlier (further to the left) with increasing trial number. Each individual box represents the average selectivity index for 25 ms of one trial. The trials are aligned on the initiation of the saccadic eye movement and include the cue and delay intervals. The black bar in the lower right corner illustrates the average standard error of the mean for all the data points. **b** | The time at which half of the maximal selectivity was reached within each trial is plotted along with the fitting sigmoid function. Note that the largest change in latency occurred for trials 5–15, which is exactly when the monkeys were learning the associations. (Adapted from REF. 29.)

Because task representations in the PFC include disparate information, the excitatory signals from this area could be involved in selecting particular sensory inputs (attention), memories (recall) or motor outputs (response selection). By simultaneously biasing processing in different brain systems towards a common 'theme' (the task), the PFC can select the neural pathways needed to perform the task (BOX 2).

Practice and automaticity

The PFC may have a key role in task acquisition, but it is unlikely to be the long-term repository of all task information. Plasticity is evident throughout the neocortex, even early in sensory processing[68–70]. As task-relevant neural pathways in other brain systems are repeatedly selected by PFC bias signals, activity-dependent plasticity mechanisms could strengthen and establish them independently of the PFC. When this happens, the PFC may become less involved and the task less taxing on our limited cognitive resources; that is, its performance becomes automatic. Indeed, PFC damage often impairs new learning while sparing well-practised tasks[71], and neuroimaging and neurophysiological studies have found greater PFC activation during initial learning with weaker activity to familiar stimuli or during performance of well-practised tasks[29,72–75]. An example is an experiment in which monkeys were required to learn to associate each of two novel cue objects with a saccade to the right or left[29]. They also performed this task with well-practised object–saccade associations — two highly familiar cue objects that were used throughout months of training and whose associations with saccades had therefore been well established. The average activity across the entire population of 254 lateral prefrontal neurons studied in this experiment is shown in FIG. 4. Novel objects that required new associative learning elicited, on average, more activity than the familiar objects for which the associations were already well learned. Weaker responses to familiar stimuli are not unique to the PFC: neurons in the inferior temporal cortex also show this property[76–79].

The PFC may remain critical for implementing task information, particularly in situations when familiar behaviours need to be flexibly combined into a coherent sequence. In addition, the PFC is required to activate long-term visual memories stored in the temporal lobe[66,80]. The PFC could retain links to stored representations that allow it to bring visual memories and other task knowledge 'online' when needed.

Indeed, the PFC does not work alone. It is interconnected with other structures that make unique contributions to cognition. For example, the hippocampus seems to bind stimuli into long-term memories of specific episodes[81]: it has neurons that show conjunctive tuning for the co-occurrence of sensory features[82] (see Eichenbaum, this issue). In contrast, I suggest that the PFC represents not specific episodes but the regularities across them that describe task rules. Furthermore, the PFC engenders flexibility. Unlike the hippocampus, which seems to consolidate 'permanent' connections in the neocortex, the PFC

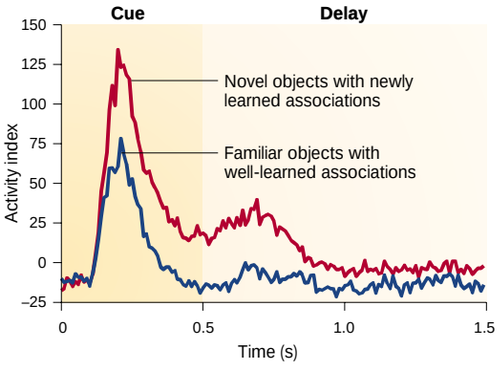


Figure 4 | **Stimulus familiarity and prefrontal neurons.** Plot of the normalized activity of 254 prefrontal neurons in trials in which unusual objects were used (red) versus trials that used highly familiar objects (blue). Activity was normalized by expressing it as a percentage change over average baseline firing rate during the inter-trial interval (not pictured). The shaded area represents the time of cue presentation. The bin width was 10 ms.

dynamically selects among existing pathways. The BASAL GANGLIA and CEREBELLUM are important structures for automating behavioural and cognitive routines, particularly their timing[7,83,84]. Mechanisms that determine when to exert control are also critical and this may depend on the ANTERIOR CINGULATE CORTEX[85].

Conclusions

One of the brain's great mysteries is cognitive control. How does the brain produce behaviour that seems organized and wilful? Here, I have reviewed evidence that cognitive control stems from patterns of activity in the PFC that represent goals and the means to achieve them. Bias signals are provided to other brain structures that can flexibly guide the flow of activity along task-relevant neural pathways, so establishing appropriate mappings between inputs, internal states and outputs needed to perform a given task.

This account of PFC function complements other theories. Goldman-Rakic and colleagues have emphasized the role of the PFC in holding sensory information online temporarily through sustained activity[10]. This is important because sensory events are often fleeting, but we must frequently wait to make a decision or a response based on them. Here, I have extended and modified this idea to include not just recent sensory inputs, but also task contingencies and rules. Such information must be maintained until the goal at hand is achieved. Maintenance of information is also critical because learning rules typically involves forming associations between disparate events separated in time. Fuster[30,86] has emphasized the importance of the PFC in temporal integration and this idea is central to the model I have proposed here. Petrides and Owen have explored the role of the PFC in the monitoring and manipulation of information held 'in mind', an important cognitive faculty[87,88]. The ability of the PFC to flexibly form associations in accord with a current goal may be the neural implementation of this capacity.

PFC organization could provide important clues to PFC function. One possibility is that different PFC regions conduct qualitatively different operations[87–89]. Other possibilities include organization on the basis of stimulus dimension[90]. These schemes are not mutually exclusive. The model proposed here does not address this issue directly, but it does make related claims. I have suggested that the PFC is involved in representing acquired relationships between various pieces of information, a function essential for intelligent behaviour. This allows for the possibility of a relative regional emphasis of certain stimulus domains or processes, but it also indicates that disparate information cannot be divided into separate PFC modules. Also, the functions I have ascribed to the PFC indicate that learning will be important in the formation of its representations, and hence in its organization.

In conclusion, I intended to convey here a general view of the type of mechanisms that might underlie the role of the PFC in cognitive control. Virtually all complex behaviour involves constructing relationships between diverse, arbitrary pieces of information that have no intrinsic connection. Insight into the role of the PFC in cognition can surely be gained from a better understanding of this process.

BASAL GANGLIA
A collection of interconnected subcortical structures reciprocally connected to the prefrontal cortex.

CEREBELLUM
A structure overlying the pons that is important for sensorimotor coordination.

ANTERIOR CINGULATE CORTEX
A structure lying close to, and connected with, the prefrontal cortex, which is involved in error detection.

Links

ENCYCLOPEDIA OF LIFE SCIENCES Neural activity and the development of brain circuits | Learning and memory | Dopamine

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