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Primer

Executive function

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Executive functions are the high-level cognitive processes that facilitate new ways of behaving, and optimise one's approach to unfamiliar circumstances. As many situations in everyday life are not exactly the same as ones that we have encountered before, it follows that the operation of executive processes accompanies a very wide range of behaviours. But we particularly engage such processes when, for instance, we make a plan for the future, or voluntarily switch from one activity to another, or resist temptation; in other words, whenever we do many of the things that allow us to lead independent, purposeful lives. These processes are thought to be supported, at least in part, by structures within the frontal lobes of the brain. But they are understood far less comprehensively than some of the functions supported by other brain regions. Indeed, a review published as recently as 1996 described this domain as a "somewhat embarrassing zone of almost total ignorance" (Monsell, 1996). But cognitive neuroscience has recently made significant strides in characterising the nature of these processes, and their underlying brain mechanisms. This Primer surveys some of the theoretical frameworks commonly used for understanding executive functions, and their relationship with the frontal lobes.

Role of executive processes in the organisation of cognition

At the heart of most (but not all) theories of executive function is a distinction, or gradation, between routine (or 'automatic') and non-routine (or 'controlled') processing. Routine processing refers to mental operations that are well rehearsed or overlearned, for example reading out a word. By contrast, non-routine processing most commonly refers to mental operations that are used in situations when there is not a well-established stimulus-response association, or where a behavioural impasse has occurred (for example one notices an error, or realises that one is behaving in a sub-optimal fashion). The term 'executive functions' has become synonymous with those behaviours and abilities.

At an abstract level of processing, least tied to routine behaviour, are flexible representations of goals and intentions. Such 'higher-level' representations are often contrasted with 'lower-level' cognitive processes involved in analysing specific perceptual inputs (such as visual processing of stimuli such as 'BLUE') and generating specific motor outputs (such as vocal responses). According to most theories, executive function entails the modulation of lower-level processes by those at a higher level. Depending on our current goal, we are able to modulate lower-level perceptual-analysis and speech-output processes in order to produce appropriate behaviour. In different contexts we might ignore the word, read it out, or name its colour, even though we are presented with the same perceptual input in each case. Thus, executive functions allow us to behave flexibly, rather than being slaves to our environment and always behaving in a stereotyped manner when particular events occur. This equips us with the ability to adapt to novel, or changing, situations.

The modulation of various cognitive, perceptual, and motor processes according to abstract goals and intentions is commonly referred to as 'top-down control'. However, this should not imply a strict unidirectional influence from higher-level to lower-level processes. Instead, the role of executive function in cognition is probably more accurately considered in terms of continual interaction between higher- and lower-level processes. Higher-level processes are commonly triggered in everyday life by conflicts between representations or inputs at lower levels, for instance when something unexpected occurs or when behaviour does not have the usual consequences.

Paradigms in executive function research

Historically, a major obstacle to progress in research into executive function has been the difficulty of quantifying the processes supported by the human frontal lobes, a problem compounded by the variety of cognitive, social, and emotional changes that have been reported to occur as a consequence of damage to this region. Methodological and

technological advances over the last forty years, however, have established links between performance of certain paradigms which putatively make demands upon executive processes and the operation of prefrontal cortex, as assessed by human lesion studies, functional neuroimaging, and other methods (such as electrophysiology).

There are many such tasks that can be used in work on humans: the Wisconsin Card Sorting Test, the Tower of London test, the Trail-Making Test and the Hayling Sentence Completion Test, to name but a few. What these tasks generally have in common is that they require processing beyond the instantiation of a single set of well-learned or directly cued associations between stimuli and responses. This may be, for instance, because they require: overcoming the tendency to enact strong stimulus–response associations that are currently not relevant ('inhibition'); remembering and manipulating information over delay periods, especially in the face of interference ('working memory'); switching between two or more alternative stimulus–response mappings ('flexibility'); '(self-)initiation', because there is an absence of external cues to prompt behaviour; development of a novel strategy or approach ('strategy application'); or control of novel behavioural sequences over long periods of time ('multitasking' or 'prospective memory', for example).

Similar progress has been made in work on animals, except that in this case work has largely concentrated on tasks that have the first three characteristics. It is now clear that the dynamics of these types of paradigm are complex, and that many other brain regions are involved in their performance. Moreover, the prefrontal cortex, especially in humans, probably supports many abilities that have so far received scant attention (for example, aspects of social behaviour or creativity). But the development of these procedures has opened up the possibility of objective evaluation of what once seemed scientifically intractable. Consequently, the field is currently one of the fastest growing in cognitive neuroscience.

Theoretical accounts of executive function

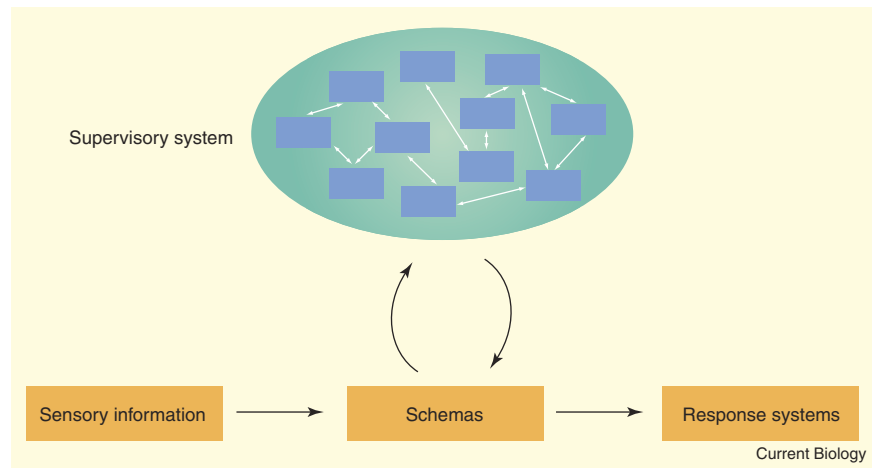Patients with frontal lobe damage may present with a wide range

Figure 1. The 'Supervisory System' model of executive functions.

According to this model, behaviour is controlled by schemas, which may appropriately be triggered by incoming perceptual information in routine situations; but in non-routine situations, the executive functions of the Supervisory System are called upon to modulate their level of activity. The Supervisory System is now thought to be composed of multiple, interacting, sub-systems. This illustration is based particularly on the framework put forward by Norman and Shallice (see Shallice, 1988). However, other frameworks, such as those presented by Duncan (2001) and Miller and Cohen (2001) have strong similarities.

of symptoms, which can occur in combination or singly. For this reason, many accounts of the organisation of the executive system have concentrated on finding principles that might explain, simultaneously, one or more of these symptoms. For instance, impulsivity and a failure to pursue goals over long periods of time are amongst the most common difficulties reported after frontal lobe damage. But, in other situations, frontal lobe damage can cause 'perseveration' (an inability to switch to a new behaviour when the previous one becomes inappropriate). How can these apparently contradictory patterns be reconciled?

Norman and Shallice put forward an influential framework for understanding executive function that can potentially account for both of these findings (Figure 1). According to this framework, behaviour is governed by sets of thought or action 'schemas'. A schema is a set of actions or cognitions that have become very closely associated through practice. These schemas can become activated in two distinct ways. First, they can be triggered by events in one's environment. For example, when driving, the schema to brake can be triggered by the sight of a red light (if you are an experienced driver). Environmental triggering of schemas can be sufficient to accomplish appropriate behaviour in routine

situations involving well-learned links between particular events in our environment and particular ways of behaving. However, in other situations, such as those involving novelty or where well-learned responses need to be inhibited, environmental triggering is inadequate and a second system is required to modulate the activity level of schemas. Norman and Shallice label this the 'supervisory system' and suggest that it is supported by the frontal lobes of the brain.

In some situations, environmental triggers lead to the activation of one schema, but an alternative schema needs to be selected. In these situations, damage to the supervisory system will make it more likely that the previously relevant schema, triggered by environmental events, will continue to be selected, leading to excessive behavioural rigidity. In other situations, where the task in hand is not strongly cued by environmental events, a reduction in supervisory input may lead to the triggering of inappropriate behaviour by salient objects in the environment, leading to excessive distractability. Thus, damage to the supervisory system could explain excessive rigidity, and also excessive distractibility, both of which have been reported to occur following damage to the frontal lobes.

Various other frameworks for understanding executive function

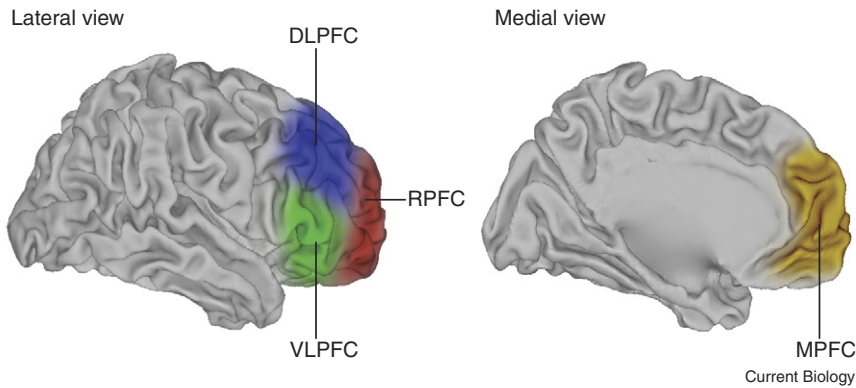Lateral view   Medial view

Current Biology

Figure 2. Gross architecture of human prefrontal cortex (PFC).

The lateral surface is split into a ventrolateral region (VLPFC), dorsolateral region (DLPFC) and rostral region (RPFC). The medial surface (MPFC) is illustrated as a single region, but recent studies indicate considerable anatomical and functional variation within this region as well.

have also been put forward. For instance, some theorists (John Duncan, for example) emphasise the malleability of high-level representations, which vary according to current task demands. This is consistent with observations from single-cell recording studies with awake, behaving monkeys. Whatever arbitrary task the monkey has been trained to perform, cells are typically found, particularly within the lateral prefrontal cortex, that respond selectively to task-relevant information. This indicates a remarkable ability of the prefrontal cortex to adapt its functions to the current task. Other theorists (Jordan Grafman, for example) emphasise that high-level representations need to be learned (governing, for example, the appropriate set of responses associated with temporally extended events such as visiting a restaurant). Despite these differences in emphasis, there is a great deal of consensus that executive function involves higher-level processes modulating lower-level ones according to current task demands, so that our behaviour is not always driven by immediate environmental triggers.

Can executive function be fractionated?

Executive function is an umbrella term, referring to those high-level processes that control and organise other mental processes. But can such processes be divided into distinct subprocesses — in other words, can the putative 'supervisory system' be fractionated? Two questions might be asked here. First, at a behavioural level, can the

different cognitive processes that come under the rubric of 'executive function' be separated? And second, can it be shown that different parts of the frontal lobes support distinct aspects of executive function? Although these questions were once controversial, it is now known that the answer to both is unequivocally yes.

Behavioural studies show that, although there are often significant positive correlations between participants' scores on various tests of executive function, there correlations tend to be rather low (typically $r < 0.4$) and often no higher than correlations with non-executive tests. Moreover, factor analysis reveals the presence of multiple distinct factors in scores derived from batteries of executive function tests. It therefore seems unlikely that executive function refers to a single, undifferentiated cognitive process. There are many other sources of supporting evidence. For instance, damage to different frontal lobe brain regions has differential effects on various executive function tests, and neuroimaging studies have shown that engagement of different aspects of executive function are accompanied by haemodynamic changes in different parts of the frontal lobes.

Executive function and the brain

The frontal lobes, and particularly the prefrontal cortex (PFC), are well-placed for a role in high-level modulation of lower-level processes supported by posterior brain regions. Along with rich interconnections within its subregions, the PFC sends and receives projections from virtually all major sensory and motor cortical

systems, with access to highly processed multi-modal sensory information represented in higher-order sensory regions. There are also strong interconnections between the PFC and subcortical structures, such as the basal ganglia. The PFC is thus well placed to integrate diverse, high-level representations, and to exert control over various brain systems.

It is now commonly accepted that patterns of activity within PFC represent current behavioural context and/or current goals and intentions, and that these representations can bias processing in posterior sensory and motor brain regions. However, the PFC is a very large region, with considerable variation in cytoarchitecture and connectivity. In what ways do the roles of different prefrontal regions differ?

Mapping function to structure

Determining the relative contributions of different frontal subregions to different executive functions is a highly complex matter, both theoretically and methodologically. On current evidence, however, one can make some preliminary suggestions. Figure 2 illustrates some of the major subdivisions of the human PFC, which may be divided into lateral and medial surfaces. On the lateral surface, the PFC may be further subdivided into ventrolateral, dorsolateral, and rostral regions. Although the medial PFC is depicted as a single area in Figure 2, there is now strong evidence that this part of PFC can also be subdivided both on cytoarchitectonic and functional grounds.

Ventrolateral PFC (VLPFC) is thought to be involved in comparatively simple tasks, such as short-term maintenance of information that cannot currently be perceived in 'working memory' (for example, memorising a phone number you have just been told, before keying the numbers into a telephone). It has also been proposed — although this is controversial — that different parts of the VLPFC are used to store different types of information (for example, the sound of a word versus its meaning). By contrast, dorsolateral PFC (DLPFC) has been most commonly implicated not so much in maintaining information that is no longer available in our environment, but in manipulating that information. For example, although DLPFC is probably not involved in processes such as remembering a

telephone number, it does seem to play a role in more difficult tasks, such as dialling the number in reverse order (rearranging the digits that we have just been told). DLPFC has also been suggested to be involved in complex functions such as making plans for the future.

A brain region with strong projections to and from the DLPFC is the anterior cingulate cortex (ACC), part of the medial PFC. One influential theory proposes that this brain region detects the need for control, for example where there is competition between two or more ways of behaving in a certain situation, both of which may be triggered by events in our environment, requiring top-down input to resolve the conflict. It is suggested that the ACC does not itself provide higher-level modulation of lower-level processes, but instead signals to DLPFC when such higher-level modulation is required. For example, in functional neuroimaging studies of the Stroop task, where participants must respond to the colour of the word rather than what it says, activity in ACC is greater for stimuli such as BLUE (where there is conflict between the two dimensions), compared with stimuli such as BLUE (which does not induce conflict between word-reading and colour-naming tendencies, and is therefore less dependent on higher-level control). This theory is attractive because it offers the beginnings of an explanation of how the PFC 'knows' when it is required to exert top-down control on other brain regions, and it has been implemented in explicit computational modelling studies. But it is controversial because, although it is consistent with much data from neuroimaging, patients with damage to the ACC often perform well on tasks that require the detection of conflict.

The largest, but most mysterious, sub-region of prefrontal cortex is the rostral PFC (RPFC). As a proportion of whole-brain volume, some have estimated the human RPFC to be twice as large as the corresponding region in the chimpanzee brain. Yet curiously, patients with damage restricted to the RPFC often perform well on standard neuropsychological tests, including 'classical' tests of executive function such as the Wisconsin card sorting test. Instead, patients with damage to this region seem to have particular difficulty in real-world 'multitasking'
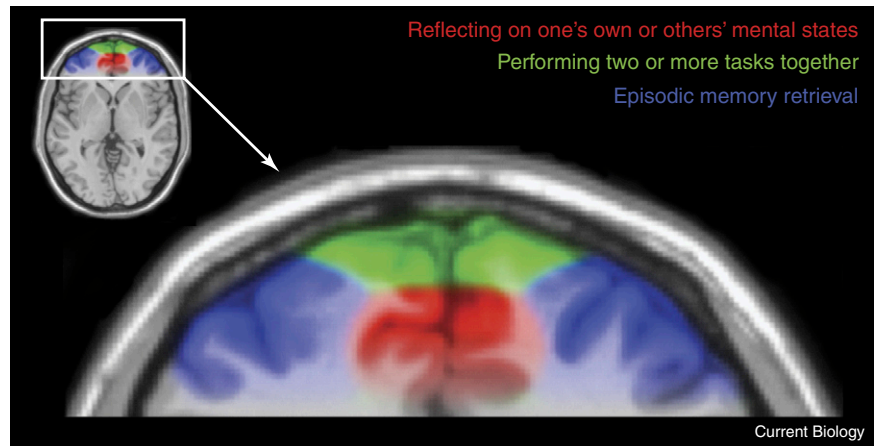

Figure 3. Functional specialisation within rostral prefrontal cortex (RPFC).
This illustration represents the results of a recent meta-analysis of functional neuroimaging studies reporting activation within RPFC. Until recently this was considered by many as a functionally homogenous region, but these results indicate that different parts tend to be activated, depending on which of these three categories of task was being performed. (Adapted from Gilbert, S.J., Spengler, S., Simons, J.S., Steele, J.D., Lawrie, S.M., Frith, C.D., and Burgess, P.W. (2006). Functional specialization within rostral prefrontal cortex (area 10): A meta-analysis. J. Cogn. Neurosci. 18, 932-48.)

situations, such as organising a shopping trip when there are few strict constraints — participants are relatively free to organise their behaviour however they like — but there are also multiple instructions to be remembered, rules to be followed, and potential distractions in the environment. Recent accounts have focused on the role of RPFC in the most high-level human abilities, such as combining two distinct cognitive operations in order to perform a single task, trying to work out what other people are thinking ('mentalising'), and reflecting on information we retrieve from long-term memory ('source memory', for example trying to work out when we last saw a person familiar to us). We recently put forward the unifying hypothesis that this brain region serves as a 'gateway' between cognitive processes directed towards current incoming perceptual information, versus information that we generate ourselves. We have also shown by a meta-analysis of functional neuroimaging results that there are distinct functions associated with different parts of the RPFC, with segregation especially between lateral versus medial regions, and between rostral versus caudal regions (Figure 3).

Conclusions
There is clearly much more to learn about the prefrontal cortex, and the executive functions it supports.

We are very far from having a full understanding of its functional architecture. For instance, although many distinctions have been reported between the functions of homologous regions in the left and right hemisphere, laterality effects are still relatively poorly understood. And relatively little is known of the functions of prefrontal cortex in explicit computational terms. In other words, we may know *that* a particular region of prefrontal cortex supports a particular ability, but not necessarily *how*. Nevertheless, recent research combining single-cell recording, neuroimaging, neuropsychological, computational modelling, and meta-analytic techniques has led to considerable advances in our understanding of executive function. In particular, we now have a much greater understanding of the ways in which executive functions can be split into various discrete processes, and the ways in which prefrontal cortex can be split into functionally discrete subregions, than we did ten years ago.

The next ten years are likely to bring advances even more rapid than the last. This is for at least three reasons. First, there has been increasing recent interest in the involvement of prefrontal cortex in human social cognition, and the ways in which this relates to tests of executive function. Second, there is strong evidence that psychiatric conditions such as schizophrenia

and developmental disorders such as autism involve disruption of executive function (in ways that may distinguish one group from another). Finally, it is known that prefrontal cortex matures relatively slowly, with some parts continuing to develop through adolescence and into adulthood. The consequences of this for fields such as education are only just beginning to be explored. Thus new developments in the field promise to transform the way that we understand the highest levels of human cognition, its disorders, and development.

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Type of threat influences postconflict allopreening in a social bird

Andrew N. Radford

In many social species, aggressive conflict between individuals in the same group (intragroup conflict) is often followed by increased allogrooming (when one individual grooms another) involving the protagonists and their relatives [1,2]. Although conflict between groups (intergroup conflict) is also common (see [3]), there has been little consideration of its impact on intragroup affiliative behaviour (see [4] for an exception). Moreover, there has been no investigation of whether the different threat posed by different rival groups (for example, neighbours and strangers [5]) influences the level of subsequent affiliative behaviour. Experiments using playbacks to simulate territorial intrusions by green woodhoopoes (*Phoeniculus purpureus*), reported here, show that intragroup allopreening — the avian equivalent of allogrooming — increases significantly in response to strange groups, but not neighbouring groups, and that the increase is due to more allopreening of subordinate helpers by the dominant pair. This is the first experimental evidence for an influence of intergroup conflict on intragroup affiliative behaviour, and lends support to the recent idea that intragroup cooperation should increase most when the intergroup threat is highest [6].

Green woodhoopoes provide an ideal opportunity to investigate how the type of threat posed by rival groups influences intragroup affiliative behaviour. First, allopreening is a common and easily scored affiliative behaviour [7]. Second, groups frequently engage in obvious territorial contests, which involve the combined cackling of adult group members ('rallies') [3], and allopreening increases following these contests (my unpublished data). Third, green woodhoopoes can discriminate between rivals using group-specific

signatures in their rallies [8], and they respond more rapidly to the playback of strangers than neighbours [8]. Neighbours may be viewed as less threatening because on winning a contest they only invade the loser's territory temporarily to forage and examine roost holes [9], but no changes in territory boundaries result [10]. In contrast, a strange group may take over the owner's territory permanently if successful in a contest [11].

I recorded allopreening events in the hour before and after simulated intrusions into the territories of 12 groups. Each group received two playback trials: one of a rally from a neighbouring group; the other of a rally from a strange group of the same size and sex ratio as the neighbouring group. I noted the identity of the individual donating and receiving each bout of allopreening, and also whether the bout focused on the head (which cannot be reached by the recipient itself) or the rest of the body (see Supplemental data available on-line with this issue for further details).

Intragroup allopreening rates increased significantly in the hour following simulated intrusions by strange groups, but not those by neighbours (Figure 1A). There was no significant increase in head allopreening, but body allopreening did increase significantly (Figure 1B), supporting the idea that the former serves a primarily hygienic function, while the latter fulfils a social function [7]. The increase in body allopreening following the playback of a strange group resulted from a significant increase in allopreening donation by the dominant pair (Figure 1C) to subordinate helpers (Figure 1D).

Intragroup allopreening may have increased to reduce stress [1], although there is no evidence that third-party affiliation has this effect [2]. And if stress reduction was important, the dominant pair might have been expected to receive, rather than donate, more allopreening, as they have the most to lose (a breeding position, as well as a territory) if a strange group defeats them. Alternatively, the dominant pair might have been attempting to improve affiliative relationships in the group and enhance social cohesion [12], thus maximising the likelihood that subordinate helpers participate in the next contest; relative group size is a key factor determining the outcome