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Task Set and Prefrontal Cortex

Katsuyuki Sakai

Department of Cognitive Neuroscience, Graduate School of Medicine, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0033, Japan; email: ksakai@m.u-tokyo.ac.jp

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Key Words

task rule, task switch, conflict, functional brain imaging, single-unit recording

Abstract

A task set is a configuration of cognitive processes that is actively maintained for subsequent task performance. Single-unit and brain-imaging studies have identified the neural correlates for task sets in the prefrontal cortex. Here I examine whether the neural data obtained thus far are sufficient to explain the behaviors that have been illustrated within the conceptual framework of task sets. I first discuss the selectivity of neural activity in representing a specific task. I then discuss the competitions between neural representations of task sets during task switch. Finally I discuss how, in neural terms, a task set is implemented to facilitate task performance. The processes of representing, updating, and implementing task sets occur in parallel at multiple levels of brain organization. Neural accounts of task sets demonstrate that the brain determines our thoughts and behaviors.

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this prospectively configured task in an abstract form. When subjects are then asked to perform another task, they have to establish a new task set in a form distinct from the previous one. The stimulus set and response set are the same between the two tasks, but the rules of association between the stimuli and responses differ. For example, subjects judge whether a visually presented digit is even or odd in one task, and in the other, they judge whether the digit is larger or smaller than five. Thus a task set has to be specific in the sense that it represents a rule of a specific task to be performed. However, a task set is nonspecific in the sense that it can be applied to any stimulus as long as it belongs to a task-relevant stimulus set.

A number of behavioral experiments have provided conceptual frameworks to explain how the task sets are established (Meiran et al. 2000, Monsell 2003). Neurophysiological experiments have also identified the neural correlates of the cognitive components associated with task sets (Bunge & Wallis 2007). The aim of this review is not just to provide a list of brain areas with labels of psychological terminologies, but to examine whether the neural data obtained thus far are sufficient to explain the behaviors that have been explained within the framework of task sets. By focusing on the data obtained from the prefrontal cortex, I discuss the neural mechanisms involved in representing, updating, and implementing task sets. I specifically highlight the differences in the inferences that one can draw from single-unit recording studies on monkeys and brain-imaging studies on human subjects.

INTRODUCTION

In cognitive neuroscience studies, investigators usually begin experiments by giving task instructions to the subjects. The subjects heed the instructions and prepare for the experiment. The subjects may remember the instructions by verbally rehearsing them, but after practice for several trials, the task information is maintained as a configuration of perceptual, attentional, mnemonic, and motor processes necessary to perform the task. A “task set” refers to

REPRESENTATION OF TASK SET

Rule-Specific Neural Activity

A task set is a psychological construct. Therefore, a fundamental question is whether such a construct exists in the brain. The neural correlates of a task set are considered to be the neural activity specific to the rule of a particular task. The activity should be independent of the task items (hereafter, called targets) that the

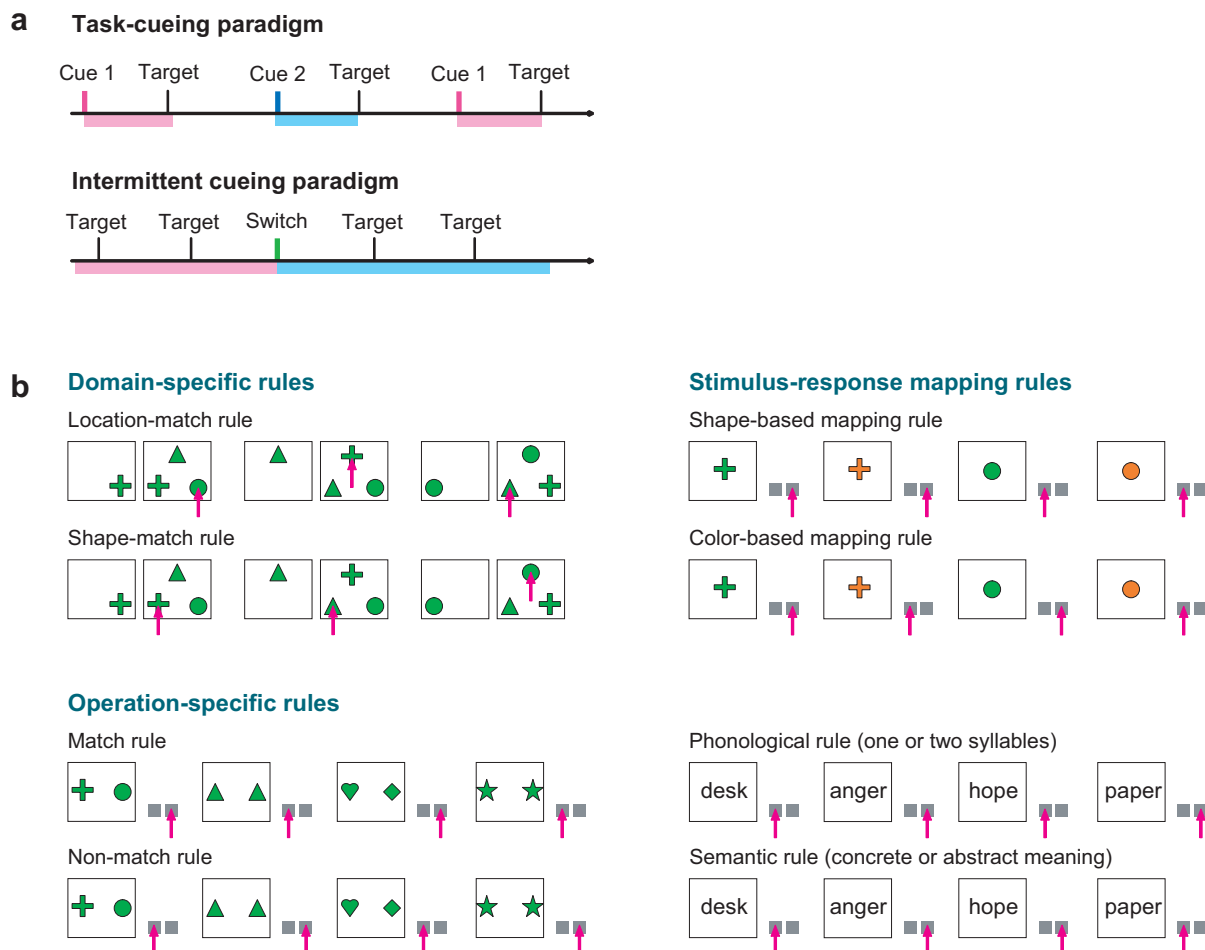


Figure 1

Task paradigms used to study task sets. (*a*) In a task cuing paradigm, a cue specifies the task to be performed for each trial and subjects process the task item (target) accordingly. In an intermittent cuing paradigm, subjects perform one task over a block of trials and, after a switch cue, change to another task. The horizontal bars (pink and blue) indicate the activity associated with task sets that are maintained during the cue-target interval or during a block of trials. (*b*) Examples of tasks that are compared in a study. The tasks can differ in terms of the sensory domains of the task, the association between the stimulus and response (stimulus-response mapping), and cognitive operations such as comparative and linguistic operations. Pink arrows indicate correct responses.

subjects are to process using the rule. Also the task set activity should be independent of task cues as long as they instruct the same task.

To identify the rule-specific neural activity, a task-cueing paradigm has been used: For each trial, a cue instructing the to-be-performed task is presented, followed by a target. The neural correlates of a task set can be identified as the sustained neural activity during the cue-target interval in a particular task

(Figure 1*a*). Another paradigm is an intermittent cuing paradigm, in which subjects perform one task for a block of trials and then switch to another task on the basis of a switching cue or feedback. In this setting the neural correlates of a task set can be identified as neural activity that is sustained across trials of a particular task block.

Recent studies have identified activity of a single neuron that satisfies these criteria. Also

GO-NOGO task: a special case of a stimulus-response mapping in which a stimulus is associated with making a response (go) or not responding (no-go)

DLPFC: dorsolateral prefrontal cortex

VLPFC: ventrolateral prefrontal cortex

Stimulus-response (SR) mapping: a paradigm in which subjects respond to each stimulus in a particular set with a prespecified response

several imaging studies have successfully identified the rule-specific regional activity. In these studies, neural activity is compared between tasks that differ in a particular aspect of the cognitive processes, such as sensory domains of the tasks, rules of specific associations between a target and a response, and rules of cognitive operations applied to the targets (**Figure 1b**).

I first examine the spatial distribution of the rule-specific neural activity within the prefrontal cortex. The prefrontal cortex is known to be constituted with multiple areas that differ in terms of cytoarchitectures and anatomical connections with other areas (Petrides & Pandya 1999, 2002) (**Figure 2**). Each of these prefrontal areas has its unique functional fingerprint, that is, a unique pattern of the degree of involvement across tasks (Passingham et al. 2002). The question here is how the represen-

tations of rules that differ in a particular cognitive component are associated with the regional segregation within the prefrontal cortex.

Domain-Specific Rules

Single-unit studies have shown a difference in the distribution of rule-specific neurons when tasks are compared that differ in terms of the sensory domain of the task. For example, neurons that are active on a motion-based GO-NOGO task were found in the dorsolateral prefrontal cortex (DLPFC), whereas neurons that are active on a color-based GO-NOGO task were found in the ventrolateral prefrontal cortex (VLPFC) (Sakagami & Tsutsui 1999). In another study, neurons that are active in a location-match task were found in the more posterior part of the principal sulcus region relative to neurons that are active in a shape-match task (Hoshi et al. 2000). However, inactivation of this posterior region did not affect the performance of the location-match task, whereas inactivation of the more anterior region caused an increase in the number of errors for both the location- and the shape-matching tasks. Thus the difference in the distribution of task-specific neurons may not be clear when the functional relevance of these neurons is examined. The difference may also depend on whether the task rules are associated with specific features of the target items, as in a fixed stimulus-response mapping (SR mapping) task, or with sensory domains of the target items regardless of their specific visual features.

Human brain-imaging studies have also shown that task rules are represented in different prefrontal regions depending on the sensory domain of the task. The posterior part of the DLPFC and VLPFC is active during the cue-target interval for a location and a letter memory task, respectively (Sakai & Passingham 2003). Representations of different SR-mapping rules have also been associated with activation in different prefrontal regions when the rules are associated with different stimulus features. For example Yeung et al. (2006) found that, in addition to the feature-specific

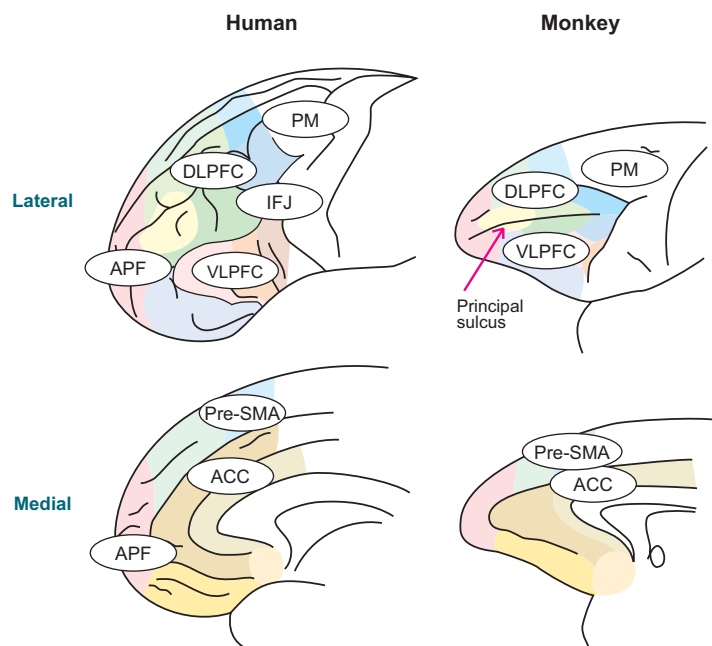


Figure 2

Schematic drawings of the lateral (*top*) and medial (*bottom*) prefrontal and other frontal regions in human and monkey. Regions defined by colors are Brodmann's areas based on Petrides & Pandya (1999). ACC, anterior cingulate cortex; APF, anterior prefrontal cortex; DLPFC, dorsolateral prefrontal cortex; IFJ, inferior frontal junction; PM, premotor cortex; Pre-SMA, presupplementary motor area; VLPFC, ventrolateral prefrontal cortex.

extrastriate areas, the right VLPFC was active when subjects responded on the basis of the gender of a face, whereas the left VLPFC was active when subjects responded on the basis of the number of syllables in a word.

These studies suggest that tasks that differ in the sensory domains are represented in different posterior prefrontal regions. However, the activation in these areas may simply reflect attentional sets for different sensory domains rather than task sets for different SR mapping rules (see sidebar on Attentional Set). More convincing evidence for the neural correlates of a task set can be obtained by comparing tasks that differ in terms of the way subjects process the same task items, i.e., operations of the task.

Operation-Specific Rules

Judgment of whether the sample and test objects are the same requires comparative operations between the two objects. This object-match task can be thought of as an abstract task because the task is not based on associations between specific stimuli and responses. The type of comparative operations differs in match vs. nonmatch tasks. Cognitive operations also differ in object-match vs. object-response association tasks. Single-unit studies have shown that there exist neurons that are active in a specific cognitive operation, and the spatial distribution of these neurons within the prefrontal cortex does not differ depending on the type of operations (Asaad et al. 2000, White & Wise 1999, Wallis et al. 2001) (**Figure 3a**). These operation-specific neurons have been found in the extensive prefrontal regions including the DLPFC, VLPFC, and orbitofrontal cortex.

Neurons representing different strategies are also represented by single-neuron activity within the same region in the DLPFC (Genovesio et al. 2005). Strategies are like special kinds of abstract rules that are acquired on the basis of past task performance history. In this study monkeys were trained to make a saccade to the left, right, or upward direction in response to a visual object. The monkeys could not learn any fixed SR mappings

ATTENTIONAL SET

We can respond to a stimulus faster when we have advanced knowledge about the features of the stimulus or the types of the movement we are to make. Such facilitation of behavior depends on the ability to represent the advanced information prior to the onset of the stimulus or movement. An attentional set is a definition of the representations of the advanced information involved in selecting task-relevant stimuli and responses (Corbetta & Shulman 2002). An attentional set is mediated by the sustained activity in the dorsal fronto-parietal network prior to the onset of the stimulus or movement. The network sends top-down signals to regions specifically involved in the actual processing of sensory features or in execution of the movements and facilitates neural processing in those regions. A task set reviewed in this article is regarded as an extension of an attentional set because it refers to representations of advanced information about the to-be-performed task.

because the response suggested by the same stimulus can differ depending on the previous trial. Instead the monkeys adopted freely between repeat-stay and change-shift strategies; that is, if the object repeated from a previous, successful trial, the monkeys repeated the response, and if the object changed, the monkeys shifted to a different response. In addition to the strategy-specific neurons, neurons in the same region in the DLPFC also represented fixed SR mapping rules that the monkeys learned during different sessions. The result suggests that task rules at different levels of abstraction, namely, exemplar-based fixed SR mappings and abstract response strategies, are represented by separate sets of neurons within the DLPFC.

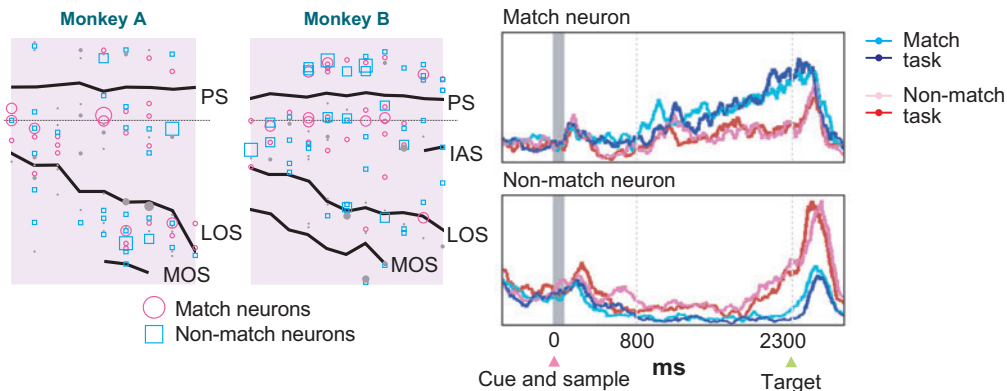
By contrast, using brain imaging on human subjects, it is difficult to distinguish among different task operations. The conventional analysis of brain imaging such as functional magnetic resonance imaging (fMRI) is to compare, for each voxel of several millimeters, the magnetic resonance (MR) signals between task conditions, but neurons representing different operation-specific rules are likely to coexist within the same voxel.

fMRI: functional magnetic resonance imaging

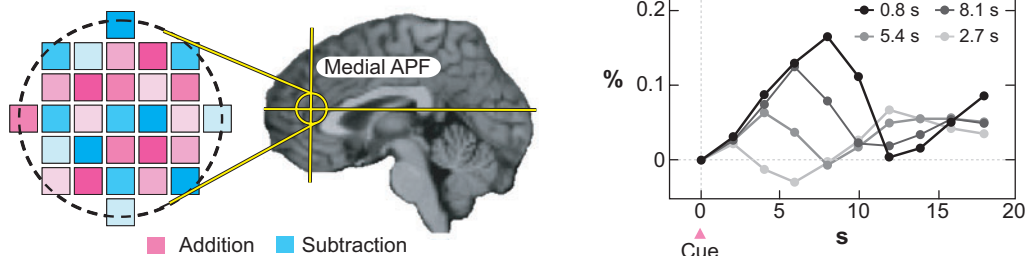
A recent study, instead, used a multi-voxel pattern of the MR signals to distinguish between the two arithmetic operation rules (Haynes et al. 2007). Human subjects were

asked to choose between addition and subtraction and then, after a delay, were shown two digits to which they were to apply the selected arithmetic operation. The medial and

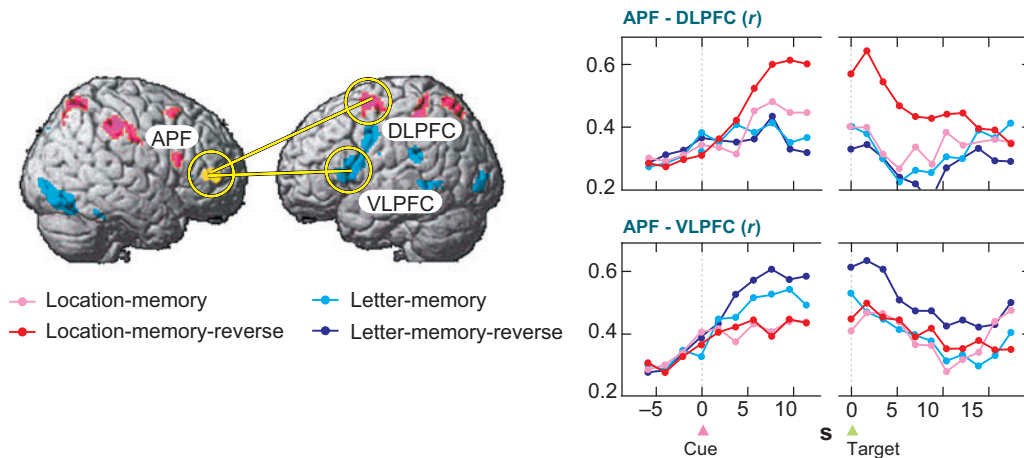
a Rule-specific activity of a single neuron



b Rule-specific pattern of multi-voxel MR signals



c Rule-specific pattern of inter-regional interactions



lateral part of the anterior prefrontal cortex (APF) showed sustained activity before the actual arithmetic calculation. Conventional voxel-based comparison of the MR signals failed to distinguish between addition and subtraction, but the spatial pattern of the MR signals across multiple voxels within these prefrontal regions successfully distinguished between the arithmetic operations before the subjects actually performed the calculation (**Figure 3b**). The signal pattern may reflect slight differences in the proportion of addition and subtraction neurons across voxels. Although the precise neural mechanism of coding arithmetic operations remains open, this new analysis technique allows us to overcome the limitation of the spatial resolution of functional brain imaging and opens up the possibility to decode abstract human thought.

Imaging studies have also shown that the pattern of interregional interaction changes according to the rule of the upcoming task. The correlation of activity between the lateral APF and posterior DLPFC was higher when subjects were cued to remember a sequence of locations in reverse order, whereas the correlation between the same region in the APF and posterior

VLPFC was higher when subjects were cued to remember a sequence of letters in reverse order (Sakai & Passingham 2003) (**Figure 3c**). The results suggest that the strength of functional connectivity changes depending on the requirement to perform a reversal operation on the sequence of remembered items. The changes were observed before the presentation of targets, that is, before the reversal operation was actually performed. The interregional interactions observed in this study reflect a preparatory process to perform a specific cognitive operation. Another study showed that the lateral APF interacted with the ventral premotor cortex (PM) and anterior VLPFC when subjects were cued to perform phonological judgment and semantic judgment for a visually presented word, respectively (Sakai & Passingham 2006). These interregional interactions reflect preparation for specific linguistic operations. Different sets of neurons within the APF may project to posterior frontal regions that are specifically involved in different tasks, and selective activation of each set of the APF neurons results in the rule-specific patterns of interregional interaction (see sidebar on Task Set for Memory Retrieval).

APF: anterior prefrontal cortex

PM: premotor cortex

Figure 3

(a) Rule-specific activity of a single neuron. *Left:* Neurons that are preferentially active in match task and nonmatch task are distributed in the same region of the prefrontal cortex in monkeys. IAS, inferior arcuate sulcus; LOS, lateral orbital sulcus; MOS, medial orbital sulcus; PS, principal sulcus. *Right:* Time course of activity of a match-selective neuron and a nonmatch-selective neuron. The neurons show a selective activity increase for the preferred task before a target is presented. Plots shown in dark and light *pink* and *blue* indicate trials in which different cues are used to instruct the same task. The original figures are kindly provided by J. Wallis based on Wallis et al. (2001). (b) Rule-specific pattern of multi-voxel signals. *Middle:* The medial part of the anterior prefrontal cortex (APF), as indicated by *yellow cross hairs* and a *circle*, is active when human subjects select between addition and subtraction. *Right:* The duration of the activation in the APF expands and contracts according to the length of the cue-target interval, indicating sustained activation. Adapted with permission from Haynes et al. (2007). *Left:* The magnetic resonance signals across multiple voxels in this region show a spatial pattern specific to whether the subjects intend to perform addition or subtraction as in the schematic drawing. The squares in *pink* and *blue* indicate voxels within the medial APF that are active in addition and subtraction, respectively. The lightness of the color indicates the strength of selectivity to a preferred task rule. The consistency of the signals' spatial patterns is confirmed across experimental sessions. (c) Rule-specific pattern of interregional interactions. *Left:* The anterior prefrontal cortex (APF), dorsolateral prefrontal cortex (DLPFC), and ventrolateral prefrontal cortex (VLPFC) are active when subjects are cued to perform a location and letter memory task. *Right:* Time course of the correlation coefficients (r) of magnetic resonance signals between the APF and the DLPFC (*top*) and between the APF and the VLPFC (*bottom*). The correlation of the signals between the APF and the DLPFC is significantly higher when human subjects remember a sequence of locations in reverse order. By contrast, the correlation of the signals between the APF and VLPFC is significantly higher when human subjects remember a sequence of letters in reverse order. The selective increase of correlation coefficients is observed during the cue-target interval as well as during task execution. Adapted with permission from Sakai & Passingham (2003).

TASK SET FOR MEMORY RETRIEVAL

Neural activity during preparation for memory retrieval differs depending on the kinds of information to be retrieved. Duzel et al. (1999) observed a sustained change of event-related potential in the right fronto-polar cortex during the cue-target interval of an episodic memory task irrespective of whether verbal or nonverbal items were used for the memory test, but the activity was not observed in a semantic task. This activity reflects retrieval mode, which refers to a tonically maintained cognitive set for episodic memory retrieval (Rugg & Wilding 2000). The sustained preparatory activity in the frontal region also differs within the episodic memory domain depending on the kinds of information to be retrieved, known as retrieval orientation (Herron & Wilding 2006). Retrieval mode and retrieval orientation can be considered as task sets for memory retrieval.

Hierarchical Organization of Rule Representations

Imaging studies suggest a rostro-caudal gradient within the prefrontal cortex in representing task sets according to the level of the abstractness of the task rule. When tasks with different sensory domains are compared, posterior prefrontal areas show differential activation depending on the task (Sakai & Passingham 2003). When tasks with different cognitive operations are compared, the amount of activation in these posterior areas does not differ significantly, but the interaction pattern with the anterior prefrontal area differs significantly. The multi-voxel signal pattern within a region also represents abstract arithmetic operations more strongly in the anterior prefrontal regions than in the posterior prefrontal regions (Haynes et al. 2007).

However, a regional difference in rule representation has rarely been demonstrated in single-unit studies. In single-unit recording, one can sample only two or three neurons in one electrode track, which is separated from another track by 1 or 2 mm, and regional difference is examined by comparing the number of rule-selective neurons across coronal sections of the brain or across regions defined by gross anatomical landmarks. Therefore, regional dif-

ference may be underestimated in single-unit studies. The advantage of a single-unit study is that it can clarify the local neural mechanisms of the rules represented at different levels of abstraction, which is the topic of future studies.

In addition to regions that show rule-specific activation, other regions are commonly involved in different task sets. Dosenbach et al. (2006) asked 183 subjects to perform 10 tasks that involve various kinds of cognitive processing, and they found that the anterior cingulate cortex (ACC) and anterior insula/operculum showed sustained activation during the cue-target interval as well as during the task performance, consistently across all these tasks. These results suggest a hierarchical organization of task set representation, in which ACC and anterior insula/operculum constitute a core task set system and play roles in regulating task-specific representations in the posterior frontal and other association areas. Whether these core areas contain multiple sets of task-specific neurons or whether the neurons in these areas are highly adaptive such that they can code different rules depending on experimental contexts are open issues.

Rule Selectivity

The rule specificity of neural activity is relative rather than absolute. In single-unit studies, the strength of rule selectivity has been estimated using receiver-operating characteristic (ROC) values, which are equivalent to the probability that an independent observer could identify the task condition solely on the basis of the neuron's firing rate. For example, in comparison between match and nonmatch tasks, the mean ROC value for the entire population of prefrontal neurons recorded, which include neurons nonspecific to the task condition, was 0.54 during the cue-target interval (Wallis & Miller 2003). This ROC value suggests that the task rules can be predicted on the basis of the neurons' firing rate with a probability significantly larger than chance, but at first glance the value seems to be very small. In fact, only 5% of the neurons exceeded the ROC value of

ACC: anterior cingulate cortex

ROC: receiver-operating characteristic

0.70. Because the monkeys actually performed a particular task, the ROC value should ideally be 1.0. The ROC value for the repeat-stay and change-shift strategies was higher than this, at 0.60, and the proportion of neurons exceeding the ROC value of 0.70 was ~20% (Genovesio et al. 2005). Rather surprisingly, the predictability of task rules can be higher in human brain imaging. In Haynes et al. (2007), the predictability of the intended arithmetic operators was 0.71 when multi-voxel pattern of the MR signals was examined in the medial APF.

However, a limitation exists in the inference that we can make regarding the rule specificity of the neural activity. Because rule specificity has been examined by comparing only two or three tasks in one experiment, whether the rule specificity can be generalized outside the context of that experiment remains to be determined. This is especially the case in experiments using monkeys because in most cases they had been trained only for the two tasks examined in the experiment. Also, because the neural coding is known to be adaptive depending on the experimental context (Duncan 2001), the neurons may be tuned to discriminate between the two tasks examined in a particular experiment; however, the same neurons can also be active for a completely different task when the monkeys were trained on a different task set. In fact, selectivity of neural coding for categorical sensory information changes depending on the task requirement (Freedman et al. 2002). Also, in single-unit studies, neurons are categorically classified as belonging to one task or the other on the basis of arbitrary chosen statistical threshold. In reality, however, the rule specificity of neurons changes gradually as indicated by the different ROC values across neurons. To what extent the categorical coding of task rules is part of a default mechanism of the brain based on its anatomical connectivity patterns remains an open issue.

Orthogonality of Rules

Another open issue is the orthogonality of the rules that are compared in a study. Rules are

considered orthogonal when subjects switched between two SR mapping rules where the same stimulus can produce the same or a different response. However, in SR mapping reversal, the same stimulus always produces a different response, and subjects can use one rule as a default and perform the other task by first performing the default task and then selecting an alternative response: The rules are not orthogonal. Pro- and antisaccade tasks and match and nonmatch tasks are also nonorthogonal rule sets.

When match and nonmatch tasks were tested in human subjects, APF activity increased when subjects prepared to perform a nonmatch task compared with when they prepared for a match task (Bunge et al. 2003). The subjects may have coded the match task as a default and conceptualized the nonmatch task as the reverse of the match. The APF activity can be indicative of the reversing operation. By contrast, in single-unit studies on monkeys, investigators saw no indication of such default strategies in terms of both behavior and neural activity (Wallis et al. 2001). It may not be surprising, however, to find that different sets of neurons code either a match or a nonmatch rule because one rule is the reverse of the other.

Buschman et al. (2006) recently trained monkeys to perform logical OR, AND, and XOR operations on visual images associated with go or no-go responses. The advantage of this paradigm is that each abstract task rule is orthogonal to the other. The study also gives researchers an opportunity to investigate the neural mechanisms involved in the representation of hierarchically organized rules because the XOR rule is, in theory, built on AND and OR rules. The behavioral data were consistent with hierarchical rule organization.

TASK SET UPDATING

Building Up a Task Set

To adopt a task set is to select, link, and configure the elements of cognitive processes necessary to accomplish the task (Rogers & Monsell 1995). Thus establishing a task set is time

consuming because it requires higher-order neural interactions between regions in the prefrontal and posterior association cortices that represent the elements of the task (Rougier et al. 2005). Preparation effect indicates the time required to establish a task set. However, merely showing a benefit of longer cue-target intervals is not sufficient to demonstrate that a task set has been established during this period because faster performance on trials with a long cue-target interval may be due to facilitation of processes nonspecific to the task, such as interpretation of task cues or general readiness for the presentation of targets. One must show the task-specific benefit of increased preparation time independently of task cues (Stoet & Snyder 2003) (**Figure 4a**).

The differential effect of preparation time across tasks is associated with the complexity of the neural mechanisms involved in representing the task rules. When human subjects performed phonological or semantic judgment for a visually presented word, reaction time (RT) on trials with a 300-ms preparation time increased compared with those with longer preparation times (Sakai & Passingham 2006). By contrast the RT of the case judgment was shorter than these and did not differ significantly between trials with preparation times of 300 ms and those

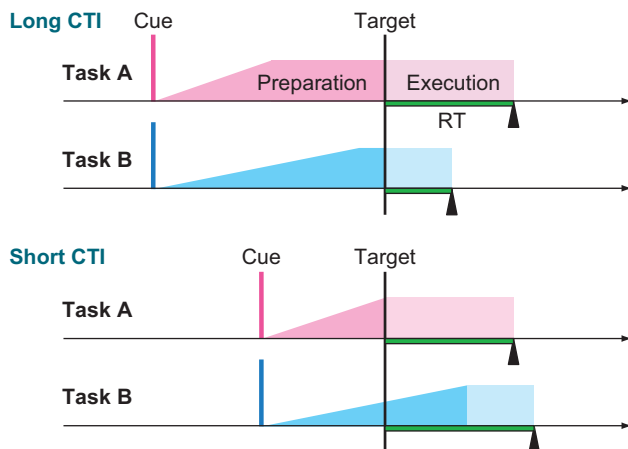
with longer preparation times. These behavioral data suggest an extra element of cognitive processes involved in preparation for phonological and semantic tasks compared with case judgment tasks, which may be the transformation of visually presented words into phonological and conceptual codes. Correspondingly APF activity was sustained during the preparation period as well as during the task performance in the phonological and semantic tasks but not in the case judgment task (**Figure 5a**). A 300-ms preparation time may be too short to recruit the APF, and on these trials, establishing the task set was carried over after the presentation of a target, thereby increasing RT (**Figure 4a**).

In single-unit recording studies, task establishment can be shown as an increment of task-selective activity. When monkeys were cued to perform a match or nonmatch task, the ROC value of the rule-selective prefrontal neurons gradually increased and exceeded 0.60 at 415 ms after the presentation of a task cue (Wallis & Miller 2003). This ROC value can be used to examine the order of recruitment of rule-selective neurons across brain areas. The ROC value in the PM exceeded 0.60 at 280 ms, significantly earlier than that in the prefrontal cortex (Muhammad et al. 2006, Wallis & Miller

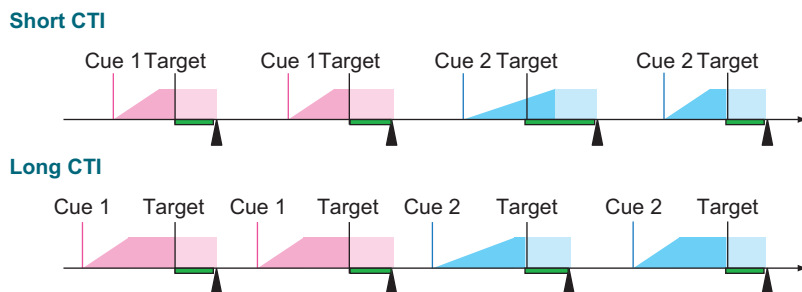
Figure 4

Schemes to explain behavioral phenomenon associated with task switching. (*a*) Preparation effect. *Top*: On trials with long cue-target intervals (CTI), the process of preparation for both task A and B, indicated by the slope of the colored bars, is complete during the CTI. The difference in reaction time (RT) reflects the difference in the time involved in task execution between the two tasks, as indicated by light color shading. On trials with short CTI, the preparation for task A is complete during the CTI, and there is no change in the RT compared with that on long CTI trials, whereas the preparation for task B is incomplete during the CTI, and the remaining preparatory process is carried over after target presentation, thus resulting in an increase in the RT. (*b*) Switch cost. When subjects switch between two tasks (*pink and blue*), the establishment of a new task takes time, as indicated by the longer slope on the first trial after a task switch. On trials with long CTI, this effect is eliminated because the preparation of a new task is complete during the CTI. (*c*) Residual cost. Even with ample preparation time, there still remains a cost in switching from one task to the other. This may be due to an interference effect from a previous task set (*green arrow*, the residual of a previous task is indicated in *pink*), which causes an increase in target processing. (*d*) Mixing cost. The RT is longer on repeat trials in a mixed task block (the first, second, and fourth trials in the upper panel) than on trials in a single task block (all trials in the lower panel). This finding is likely due to the extra time needed to select between two tasks or due to an interference effect from an irrelevant task. Still to be determined is whether both of the two tasks, or neither of them (not shown), are simultaneously represented during the intertrial interval (*green arrows*).

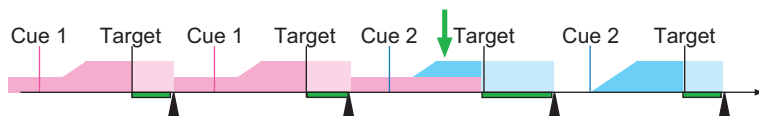
a Task-specific preparation effect



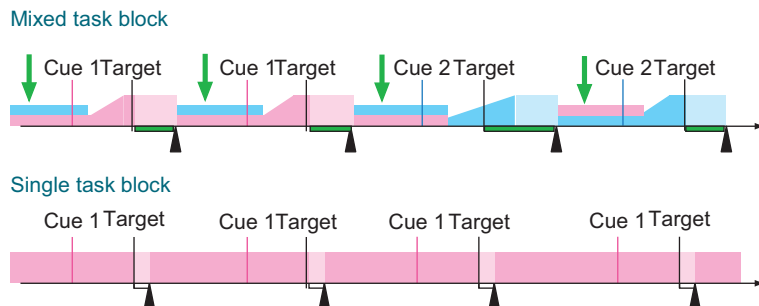
b Switch cost and preparation effect



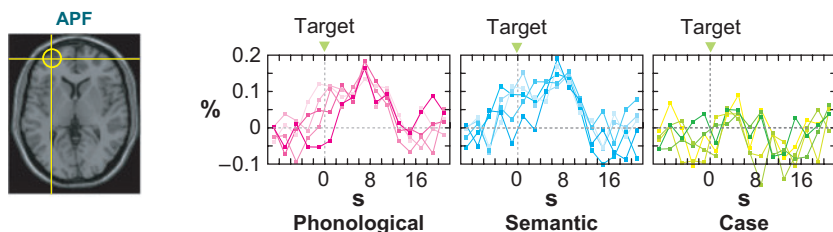
c Residual cost



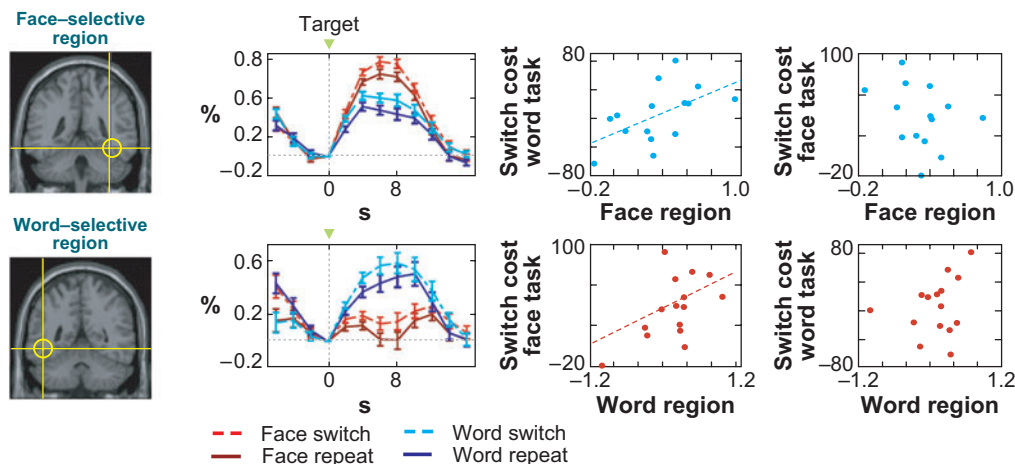
d Mixing cost



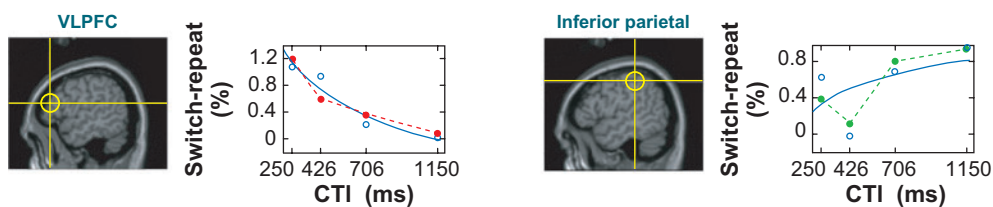
a Rule-specific activity of a single neuron



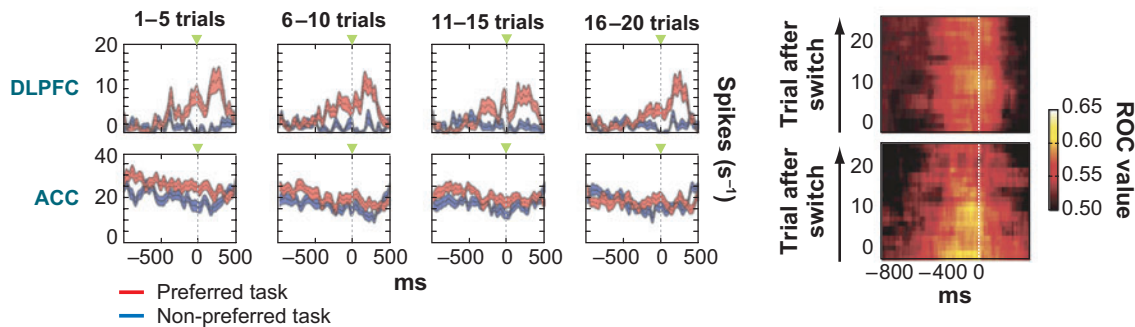
b Activity associated with irrelevant task



c Activity associated with conceptual and response conflict



d Neuronal activity changes after task switch



2003). It should be noted, however, that the time needed to establish a task set may change depending on the cue-target interval especially when a fixed interval is used, as in these studies. Also ROC values show only the discriminability between the two tasks tested in an experiment and do not provide the estimate of the time at which a particular task set is established outside the context of the experiment.

The time needed to establish task sets may also be one of the components that produce switch costs, which reflect the difference in performance between trials immediately after a task switch and trials that repeat the same task (**Figure 4b**). The switch costs are larger when switching between tasks with high rule complexity than when switching between tasks with low rule complexity (Rubinstein et al. 2001). Increasing costs when switching between complex tasks reflect increased demand for setting up these tasks, which requires incorporation of extra cognitive elements. The degree of stimulus discriminability or task difficulty did not affect the switch cost, suggesting dissociation between task set establishment and actual processing of task items.

Interference from a Previous Task Set

Switching costs cannot be eliminated completely even when ample preparation time of more than 1 s is allowed to configure a new task set. This residual cost supports the notion that a previous task set may interfere with the present task set (Allport et al. 1994, Meiran 1996; but see Rogers & Monsell 1995 for other accounts) (**Figure 4c**).

In neural terms, the residual effect of a previous task set is shown as a neural activity increase in areas involved in the previously relevant, now irrelevant task. Yeung et al. (2006) used overlapping face and word stimuli and asked human subjects to switch between face-based and word-based SR mapping tasks. Face-selective and word-selective areas in the extrastriate cortex were more active on trials immediately after task switch than on task repetition trials, regardless of whether the task currently performed was a face task or a word task (**Figure 5b**). The behavioral switch cost was positively correlated with the differential activity between switch and repeat trials in areas representing currently irrelevant stimulus feature. The

Figure 5

(a) Task-specific preparatory activity observed in the APF (*yellow cross hairs and a circle on the left*). *Right panels*: When human subjects are cued to perform a phonological or semantic judgment task, the APF shows sustained activation during the cue-target interval (CTI). The five levels of the lightness in color shading of the plots indicate trials with CTI of 0.3, 2, 4, 6, and 8 s. Note significant activation occurs before target presentation on trials with long CTIs. The APF does not show significant activation when subjects perform a visual case judgment task (*rightmost panel*). Based on data from Sakai & Passingham (2006). (b) Activity associated with an irrelevant task in task switching. When human subjects switched between stimulus-response mapping tasks on the basis of a face and a word in the stimulus, the face-selective and word-selective regions in the extrastriate cortex (*yellow cross hairs and a circle on the left panel*) were more active on trials immediately after task switch than on repetition trials, regardless of whether the task currently performed was a preferred or nonpreferred task for that area (*second panel from the left*). The switch cost in reaction time was positively correlated with activity in these regions when the task currently performed was a nonpreferred task for that region (*third panel from the left*) but was not significantly correlated when the task was a preferred task (*right*). Adapted with permission from Yeung et al. (2006). (c) Activity associated with conflicts at a conceptual level and response level during task switch. *Left*: The activation in the VLPFC changes depending on the CTI (*circles in blue; a curved line in blue is a fitted line*), consistent with a model estimate of conceptual conflict (*filled circles and dotted lines in red*). *Right*: The activation in the inferior parietal cortex changes depending on the CTI (*circles in blue, a curved line in blue is a fitted line*), consistent with a model estimate of cumulative response conflict (*filled circles and dotted lines in green*). The plots are adapted with permission from Badre & Wagner (2006). (d) Activity of single neurons during task switching. *Left four panels*: Activity of a single neuron in the prefrontal cortex (*top*) and ACC (*bottom*) when monkeys switched between pro- and antisaccade tasks. Activity during performance of the neurons' preferred (*red*) and nonpreferred task (*blue*) is shown in four five-trial sub-blocks after the task switch. *Right*: The change in the receiver-operating characteristics (ROC) values for a population of prefrontal and ACC neurons. Trials are sorted from bottom to top after the task switch, and time zero on the abscissa indicates the target presentation. In the ACC, the ROC values increase earlier and higher on trials immediately after the task switch, but on the following trials the onset becomes later and the peak becomes lower. The ROC values in the DLPFC remain unchanged after the task switch. Adapted with permission from Johnston et al. (2007).

Incongruent trials: a trial in which a stimulus is associated with different responses depending on the task rules

Pre-SMA: presupplementary motor area

IFJ: inferior frontal junction

Stroop task: tests a subject's ability to counter interference, such as naming the color of a visually presented word indicating a different color

correlation between the switch cost and the activity in areas representing a currently relevant stimulus feature was not significant. The results are consistent with the idea that switch costs are due to the interference from a previous task set.

The interference effect of a previous task endures several trials after a task switch (Wylie & Allport 2000). Consistent with this finding, an imaging study demonstrated that the APF activity increased on the third trial after a cognitive set shift in a Wisconsin card sorting task when the trial was incongruent with the previous set compared with when it was congruent (Konishi et al. 2005). The APF activity did not differ between the first trial on the set shift and task repeat trials. By contrast, the VLPFC activity was higher on set shift trials than on repeat trials and also on the later incongruent trials than on congruent trials. These results suggest that at least two separate mechanisms are involved in inhibition of a previous task set depending on temporal contexts.

Conflict Between Task Sets

Task switching is the process of selecting between the two competing task sets. Because a task set is a configuration of perceptual, attentional, mnemonic, and motor processes, the conflict can occur at various stages of cognitive processes depending on the differences between the two tasks, which could be associated with activation in different brain areas. When subjects switch between two tasks during which the same stimulus can produce a different response, conflicts occur at the response-selection stage, which has been associated with an increase in activation in the presupplementary motor area (pre-SMA) and possibly in the ACC in humans (Crone et al. 2006; Liston et al. 2006). By contrast the activity in the posterior parietal cortex and DLPFC was higher when the irrelevant stimulus dimension was salient, suggesting that these regions are sensitive to the conflict at a stimulus representation stage (Liston et al. 2006).

Compared with conflicts at stimulus- and response-processing stages, conflicts at a con-

ceptual rule-processing stage occur regardless of the overlap among stimuli and among responses. Badre & Wagner (2006) used a three-layer connectionist model, in which task item, rule, and response layers are reciprocally connected. Activation in the human left VLPFC paralleled the model estimate of conceptual conflicts, whereas activation in the left inferior parietal cortex paralleled the model estimate of response conflict (**Figure 5c**).

Aside from these studies above, several studies have been conducted to identify the brain regions responsible for monitoring and resolving conflicts at different cognitive processing stages, but the results are far from clear (Barber & Carter 2005, Bunge 2004). Because neurons representing targets, responses, and rules coexist within the same regions, the stimulus processing, response selection, and task-set reconfiguration may take place in parallel across multiple brain regions, and the clear-cut regional segregation may be merely a product of statistical threshold.

In contrast with the areas associated with a conflict at a specific cognitive processing stage, a specific region in the posterior part of the VLPFC, termed the inferior frontal junction (IFJ), is involved in updating task representations regardless of the specific task features (Brass et al. 2005). The IFJ was more active on switch trials than on repeat trials in a task-switching paradigm, more active on incongruent trials than on congruent trials in Stroop tasks, and also more active in verbal working memory tasks that require updating of memory than in target-detection tasks.

One of the controversial topics is the area involved in monitoring response conflicts. One idea is that the ACC plays a role in this process (Botvinick et al. 2001, Ridderinkhof et al. 2004). In particular, the ACC is involved in anticipatory preparation of conflicts that may arise among incompatible SR mappings. Imaging studies also suggest that activation in the ACC engages regulatory processes in the lateral prefrontal cortex. Other studies are inconsistent with this idea (Rushworth et al. 2005). Single-unit studies have shown that neurons in

the pre-SMA, but not in the ACC, are more active in conflicting situations. Several imaging studies also support the pre-SMA's role in conflict resolution, especially at a response-selection stage.

Evidence for Inhibition

A mechanism may exist that actively suppresses a previous task set (Allport et al. 1994). However, it is difficult to demonstrate that a neuron or brain region that is active on switch trials inhibits irrelevant task sets rather than facilitating a relevant task set. One way is to demonstrate that a region active on task switch trials is also active when inhibition alone should occur. The same region in the right VLPFC was active on set-shifting trials in a Wisconsin card sorting task and on no-go trials in a GO-NOGO task (Konishi et al. 1999). Patient studies consistently demonstrate that the right VLPFC inhibits irrelevant task sets and motor responses (Aron et al. 2004, Mayr et al. 2006). By contrast, the left VLPFC plays a role in endogenous control of establishing task sets regardless of switch or repeat.

Single-unit evidence for previous task set inhibition has been obtained from the pre-SMA. When monkeys performed a color-based selection of a saccade target, neurons in the pre-SMA showed phasic activity on trials after the color of a to-be-selected target changed (Isoda & Hikosaka 2007). When the same neurons were tested on a GO-NOGO task, the onset of the neural discharge was earlier for the neurons preferentially active on no-go trials than those active on go trials. The pre-SMA may have enabled the task switching by first suppressing automatic responses using a previous task set and then boosting a controlled response using a newly established task set.

Change in Task Representation after Task Switch

In imaging studies, frontal regions including the ACC, pre-SMA, and VLPFC have often been labeled as sites for general control mechanisms,

COGNITIVE CONTROL

Cognitive control guides thought and behavior in accordance with internally generated goals or plans (Miller & Cohen 2001). The prefrontal cortex may play a key role in cognitive control by maintaining the activity patterns that represent goals and rules and, by sending bias signals to the rest of the brain, establish the pathways for neural processing of environmental stimuli according to the requirements of the task and intention.

whereas posterior regions have been labeled as targets for the control. Here the absence of task-specific activity in the frontal regions has been taken to indicate their involvement in the general control mechanism (see sidebar on Cognitive Control).

However, a recent single-unit recording study showed that the ACC, which has been regarded as the key area for cognitive control, also contains rule-specific neurons. Switching between two tasks was associated with a change in the strength and onset of rule-selective neuronal activity rather than with the recruitment of switch-selective neurons (Johnston et al. 2007) (**Figure 5d**). In this study, monkeys performed a pro- or antisaccade task for a block of 30 trials and then switched to another task on the basis of feedback. The rule selectivity of ACC neurons increased on trials immediately after switching tasks and then decreased on subsequent task repetition trials. By contrast, the rule selectivity of prefrontal neurons remained unchanged between switch and repetition trials. On trials immediately after the switch, the rule selectivity in the ACC also appeared earlier than that in the DLPFC, but on subsequent repetition trials, it appeared later than that of the DLPFC. The switch-related increase in the ROC value observed in this study may be due to using feedback as the signal to switch between tasks. The ROC value may decrease on switch trials in a task-cuing paradigm as a result of residual neural activity reflecting the rule of a previous task.

As discussed above, the distinction between controlling and controlled regions is becoming

increasingly more obscure. The updating of a task set may be a self-regulatory mechanism emerging from interactions and competitions among rule representations. A regional difference in the strength and onset of representations for the to-be-performed task may provide clues to examine the mechanism of cognitive control.

Holding Multiple Task Sets

When subjects switch between two tasks, they are slower to respond even on task repetition trials compared with when they perform only one task. Mixing costs, which represent the difference in performance between task repeat trials in a mixed task block and trials in a single task block, reflect the demand to select among the task rules (**Figure 4d**). One idea is that, for each trial, subjects return to a neutral state immediately after executing a task, and establishing a task set is necessary even on task repetition trials. In fact, the same region in the VLPFC was active on switch and repetition trials in a mixed task block when the frequencies of the switch and stay trials were similar. Another possibility suggests that the two task sets are maintained with equal strength on each trial, and a target item activates the processing pathways for both tasks in parallel. According to this account, the mixing costs reflect competitions at the response-selection stage (Gilbert & Shallice 2002). Consistent with this idea, multiple motor sets are represented simultaneously in the PM during motor preparation (Cisek 2006).

The mixing costs were associated with activation in the lateral APF. An increase in APF activity was sustained throughout a mixed task block compared with a single task block, and larger activation in this area was associated with faster response in a mixed task block but not in a single task block (Braver et al. 2003). Consistent with this area's role in keeping multiple task sets at a relatively high level of activation, the APF was also active in a branching task, where subjects maintain an intention to perform a secondary task while continuously performing a baseline task (Koechlin et al. 1999).

TASK SET IMPLEMENTATION

Task Set Activity Facilitates Task Performance

The benefit of establishing a task set is facilitation of subsequent task performance, as shown in the preparation effect. Imaging studies have shown that higher activation during the pretask period is associated with faster performance. When subjects were cued to perform semantic judgment tasks, the VLPFC activity during the cue-target interval was larger on faster response trials, regardless of whether these were switch or repeat trials in a mixed task block or trials in a single task block (Braver et al. 2003). The APF also showed larger pretask activity on faster trials, but this correlation was observed on switch and repeat trials in a mixed task block but not on trials in a single task block. The results suggest that separate brain areas are involved in facilitating task performance depending on whether subjects perform multiple tasks or a single task. Another study showed that larger pretask APF activity was associated with a faster response on phonological and semantic tasks but not on a visual case judgment task (Sakai & Passingham 2006). These results indicate that the task set activity in a specific region is associated with the subject's performance on certain kinds of tasks.

Although human studies suggest a role of the APF in facilitating performance especially on tasks that require cognitive operations, no single-unit study has been performed on the APF because of the technical difficulty in recording unit activity from this region in monkeys. There is also an issue of whether the monkey APF is equivalent to the human APF (Ramnani & Owen 2004). Which subset of rule-specific neurons found in extensive prefrontal regions in monkeys contributes to the facilitation of task performance remains to be determined. The neurons close to the output of the rule-configuring network may play roles in task performance. Consistent with this idea, when monkeys performed pro- and antisaccade tasks, task-selective activity of the DLPFC neurons, which had been identified as directly projecting to the superior colliculus, was inversely

correlated with saccade RT (Johnston & Everling 2006).

Task Set Activity Determines Task Execution Activity

Task set activity likely determines the activity in areas involved in task execution. Phonological and semantic processes are known to be subserved, at least in part, by the ventral PM and anterior VLPFC, respectively. Larger pretask activity in the lateral APF was associated with a decrease in PM activity during performance on a phonological task. By contrast, larger pretask activity in the lateral APF was associated with a decrease in anterior VLPFC activity during performance on a semantic task (Sakai & Passingham 2006) (**Figure 6a**). During the pretask period, the PM and anterior VLPFC may have been primed by the top-down task-specific signals from the APF, and a part of the task-related process was established in these areas. As shown in this study, implementation of a task rule is mediated by interactions between areas involved in representation of a task rule such as APF and areas involved in actual task performance such as PM and anterior VLPFC.

Patient studies suggest dissociation between maintenance and implementation of a task rule. Patients with lesions in the APF were impaired in following task instructions but could report the task instructions correctly when they were asked to do so (Burgess et al. 2000). Similarly, patients with prefrontal lesions show perseveration errors on a Wisconsin card sorting task but could report the relevant rule correctly (Milner 1963).

Then, is the APF necessary to induce task set activation in the task-specific posterior areas? An imaging study on patients with left APF lesions shows that this may not be the case (Rowe et al. 2007). In these patients, the task-selective posterior frontal areas show sustained pretask activity at a level comparable to that in normal subjects. Rather, the APF may play a role in setting up interregional interaction between task-relevant areas. In these patients, the correlation of activity in the posterior regions was signifi-

cantly lower than that of the normal subjects. Efficient implementation of a task set seems to be mediated by the interaction between posterior regions under the APF's control, especially when subjects are required to switch between multiple tasks.

Top-Down and Bottom-Up Signals

In addition to the top-down, task-specific signals, task item information, when it is presented, is conveyed as bottom-up signals from the lower-order sensory areas to areas involved in task execution. In Sakai & Passingham (2006), activity in the ventral PM and anterior VLPFC during performance of phonological and semantic tasks was positively correlated with activity in the fusiform gyrus, which is involved in processing of a visually presented word (**Figure 6a**). This correlation was observed for both the ventral PM and anterior VLPFC regardless of the kinds of tasks. Thus the neural activity associated with task execution can be regarded as a product of task-specific and region-specific top-down signals from anterior prefrontal regions and nonspecific bottom-up signals from lower-order sensory regions.

A recent study, however, suggests that the bottom-up process can also be modulated by a task set (Nakamura et al. 2006). A brief interruption of neural processing in the lateral temporal and inferior parietal cortex abolished the effects of a masked prime on a lexical and a pronunciation task, respectively. The results suggest that the information about the task item is conveyed through different routes depending on the task that the subjects intend to perform, even when the task item is not consciously perceived.

Whereas imaging studies suggest that focal brain areas are the sites at which the top-down and bottom-up signals interact, single-unit studies show that the interaction occurs at every region examined. When monkeys performed a location-match or shape-match task, neurons in the prefrontal cortex demonstrated activity specific to the sample stimuli, task rules,

Bottom-up signals: signals triggered by external environment thought to flow from lower-order to higher-order areas

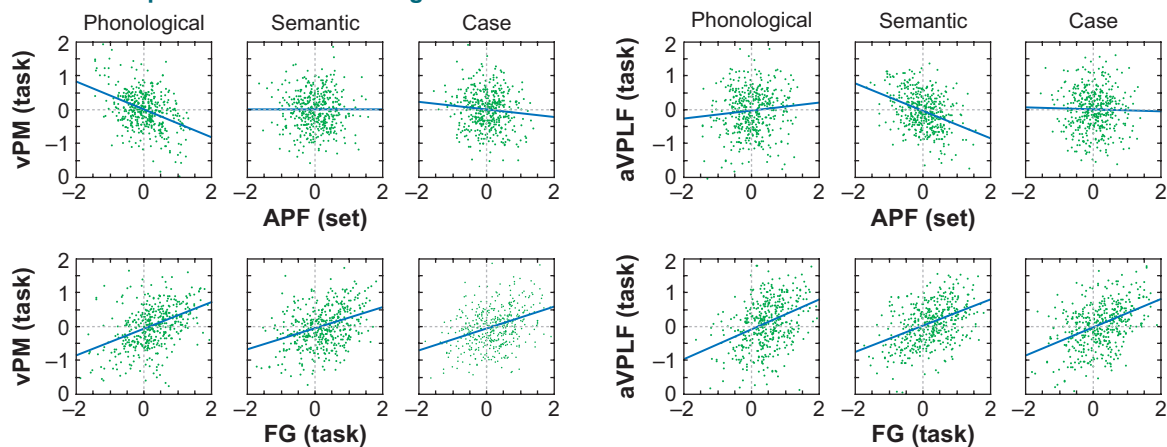
Top-down signal: control signals thought to flow from higher-order to lower-order areas

and responses within the same prefrontal regions (Hoshi et al. 2000). Activity in these different sets of neurons is temporally structured in a way that is strategically appropriate for the rule-based selection of response (Figure 6b).

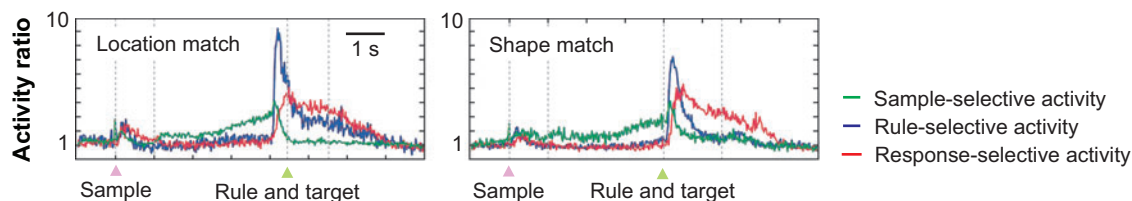
The information represented by each neuron also shows variable degrees of interaction between the rule and the response (Asaad et al. 2000, Genovesio et al. 2005, Hoshi et al.

1998, Wallis & Miller 2003). Furthermore the information represented by each single neuron can change during a single trial of task performance. Wallis & Miller (2003) found that one third of the prefrontal and premotor neurons that initially coded match or nonmatch rules demonstrated selectivity to a particular type of the matching outcome, i.e., whether the sample and test stimuli matched or did not match (Figure 7). Another subset of rule-selective

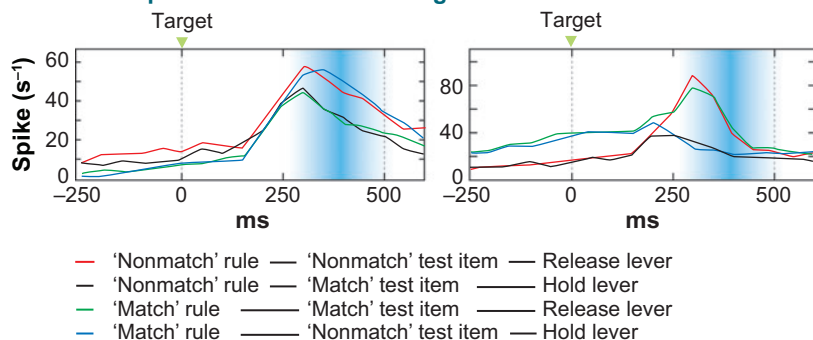
a Task set implementation across regions



b Task set implementation across neurons



c Task set implementation within a single neuron



neurons demonstrated selectivity to a particular motor response, i.e., whether the monkeys released or held a response lever.

In sum, facilitation of task performance is mediated by interactions between representations of a task rule and a target item that occur across brain areas, across neurons within the same area, and within a single neuron. Future studies should be directed to understand how these neural processes at different levels are related to each other.

INTENTION AND TASK SET

Voluntary Selection of Task Set

One of the most controversial topics in studies on task sets is whether there exists a truly endogenous mechanism to prepare for a task (Logan et al. 2007, Monsell & Mizon 2006). One extreme idea is that the task cue automatically sets up the task and that there is no endogenous mechanism to prepare for the task. Neural data also provide mechanistic, self-regulatory accounts of task set mechanisms without the need to assume a “homunculus.” However, we can freely select a task without an explicit task cue, suggesting the presence of some sort of

“endogenous” mechanism (Arrington & Logan 2005).

When brain activation during voluntary task selection was compared with that during externally cued task selection, ACC activation increased (Forstmann et al. 2006). Other imaging studies have shown that the more anterior part of the medial prefrontal cortex is involved in voluntary selection. In a branching task, the lateral APF was active when the onset of the secondary task was unpredictable, whereas the medial APF was active when the onset of the secondary task was predictable (Koechlin et al. 2000). The medial APF was also active in a task-switching paradigm when the order of the two tasks and the timing of the task switch were predictable (Dreher et al. 2002). Performance of a predictable task sequence is regulated endogenously, thus the results suggest a role of the medial APF in voluntary task set selection.

Does this result also suggest that activation in the medial prefrontal cortex is the neural correlate of a cognitive homunculus? Haynes et al. (2007) have shown that, in a voluntary selection of arithmetic operations, medial APF activity reflects the specific task that the subjects intend to perform. Thus a task is not

Homunculus: a small, clever, imaginary person who lives in the brain and controls human thought and behavior

Figure 6

Neuronal activity associated with implementation of task sets. (*a*) *Left three panels:* The activity in the ventral premotor cortex (vPM) during task performance is plotted against anterior prefrontal cortex (APF) activity during the task preparation period (*top*) and the word-selective fugiform gyrus (FG) activity (*bottom*). The activity in the vPM and APF was negatively correlated only on the phonological task, whereas the activity in the vPM and FG was positively correlated in all task conditions. *Right three panels:* Activity in the anterior ventrolateral prefrontal cortex (aVLPFC) was inversely correlated with activity in the APF only in the semantic task, whereas it is positively correlated with FG activity in all task conditions. The values on the abscissa and ordinate are normalized values of the increase in magnetic resonance signals relative to the resting period. The blue oblique line on each panel indicates the estimate of linear regression. Adapted with permission from Sakai & Passingham (2006). (*b*) Time course of population activity of neurons showing selectivity to a particular sample stimulus, task rule, and response. Activity in location-match and shape-match tasks is shown separately. Sample-selective neurons showed gradually incrementing activity until the task instruction was presented (*green*). Rule-selective neurons then showed a sharp increase of activity peaking at 200 ms after the task instruction (*blue*), followed by an increase in activity of response-selective neurons, which peaked at 400 ms after the task instruction (*red*). The ordinates indicate activity ratio, which is calculated by dividing the neurons' discharge rate during the task by that during the intertrial interval. Adapted with permission from Hoshi et al. (2000). (*c*) Time course of activity of a single neuron when a monkey performs a match task and a nonmatch task. *Left:* A single neuron in the prefrontal cortex that initially shows higher activity in the nonmatch task than in the match task comes to show an increase of activity when the outcome of the actual comparison between the sample and test stimuli is the nonmatch. *Right:* A single neuron in the premotor cortex that initially shows more activity in the match task than in the nonmatch task showed an increase in activity when the monkey released a lever for a response. The ordinates indicate the discharge rate of the neuron (per second). Gradient shading in blue on each panel corresponds to the time window of the monkey's response. Adapted with permission from Wallis & Miller (2003).

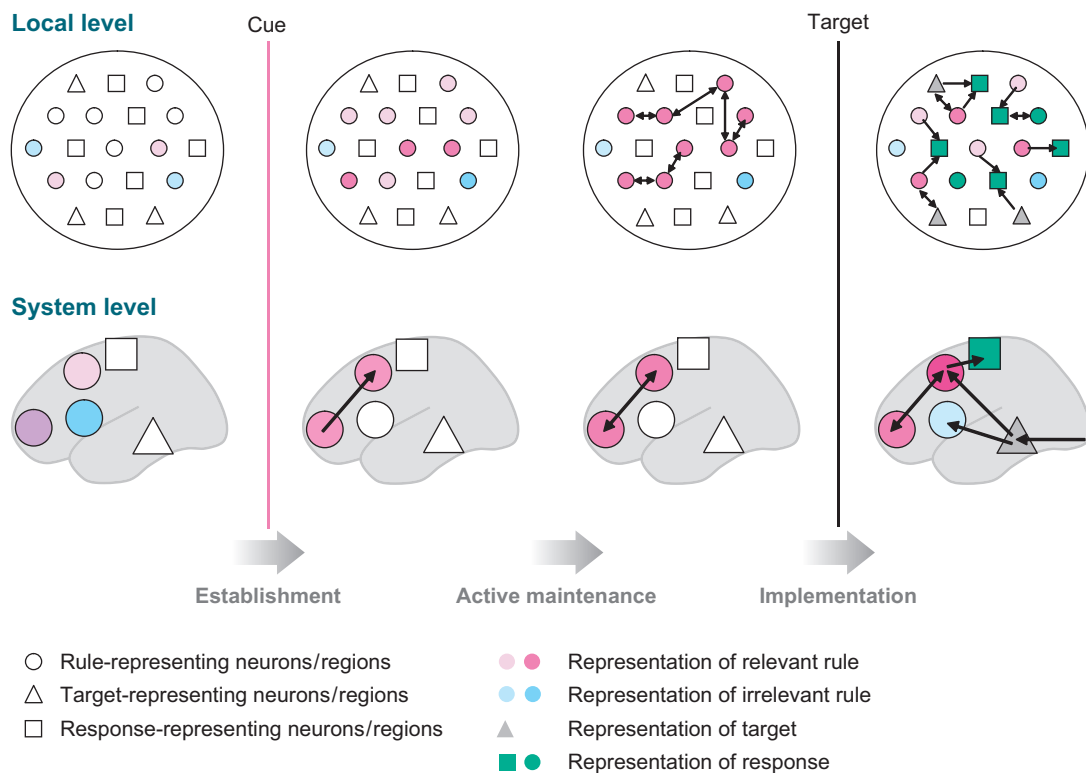


Figure 7

Scheme of neural mechanisms associated with task sets. *Top*: At a local level, establishment, maintenance, and implementation of a task set were mediated by a change in activity of a single neuron representing a task rule, target, and response (indicated by a circle, triangle, and square, respectively). After presentation of a task cue, activity and the number of neurons representing the rule of the relevant task increase (pink). Neuron activity representing the irrelevant task still remains, which causes a residual cost and a mixing cost. When target is presented, the rule-representing neurons interact with neurons representing the target item (gray triangle) and then interact with neurons representing a particular response, causing an increase in the activity of these neurons (green square). Some of the rule-representing neurons also show selectivity to the response (green circle). Interneuronal interactions likely play roles in these processes, but the mechanisms remain open (arrows). *Bottom*: At a system level, processes associated with task sets are mediated by interactions between different brain regions. Posterior frontal regions selectively represent a particular task (pink and blue), and anterior prefrontal regions represent both tasks (purple). When a task cue is presented, the anterior prefrontal region interacts with the posterior frontal region selectively involved in the cued task (pink). Subsequently, when a target is presented, the lower-order sensory region involved in target processing becomes active (gray triangle), and this region interacts nonspecifically with posterior frontal regions. The task-relevant posterior frontal region then sends signals to the region associated with response (green square). The regional segregation according to task rules, as indicated in pink and blue in the posterior frontal regions, is less clear when operations rules, rather than domain rules, differ.

selected by a homunculus in the medial prefrontal cortex; rather, the representation of an intended task emerges in this region. An interesting possibility is that specific information about the to-be-performed task is represented in different areas depending on whether the task is selected on the basis of free will or external cues.

Awareness of Intention to Select Task Set

It is not “us” but the self-regulatory mechanism of the brain that selects the task set. The question is how these neural events are associated with awareness of intention to perform a particular task. As the first step to answer the

question, studies have been conducted to establish the boundaries between processes that can run subconsciously and those that require awareness (Mayr 2004).

Lau & Passingham (2007) asked subjects to perform a phonological or semantic task based on a cue. Before each cue, a masked prime that was similar in shape to the cue was also presented. When the prime and cue indicated different tasks, the subjects were slower to perform the task, and activation in the task-relevant brain areas was reduced. These results suggest that an invisible prime may have influenced the task set activation established by a visible task cue. This effect was observed only when the primes were invisible. The congruency between a prime and task cue affected the activation in different brain areas depending on whether the prime was visible. The ACC was more active on incongruent trials than on congruent trials when the prime was visible, whereas the DLPFC was more active on incongruent trials when the prime was invisible.

ACC activation was also associated with awareness of a conflict at a response-selection stage (Dehaene et al. 2003). In this study, schizophrenic patients, who show reduced ACC activation, were impaired in monitoring conscious conflicts. Also patients with lesions in the medial frontal lobe, including the ACC, sometimes showed an alien hand syndrome, during which one of the patient's hands moves automatically and performs a complex task such as picking up a cup and pouring extremely hot coffee into the patient's mouth. The patients try to stop this alien hand using the other hand. This suggests dissociation between the patients' intentions and the task set automatically established by environmental stimuli. This may also suggest that the activation in the medial frontal regions is necessary for awareness of intention to select a task set.

The most significant question pertains to identifying the causal mechanisms by which these medial frontal regions create awareness. Awareness of intention to act and attend is proposed to be mediated by efference copy signals (Driver & Frith 2000). Given similarities in the

mechanisms between attentional sets and task sets, one approach would be to test the possibility that efference copy signals are sent from task execution areas to the medial frontal regions during conscious establishment of a task set.

CONCLUSION

This review has attempted to provide neural accounts of task sets. Single-unit studies have shown that representing, updating, and implementing task sets are subserved by interactions among different sets of neurons in the same region of the prefrontal cortex. By contrast, imaging studies have shown that each of these processes is subserved by distinct regions in the prefrontal cortex and other areas. These results may suggest a parallel processing at different levels of brain organization: Competitions and interactions between representations of task rules, task items, and responses occur at the single-neuron level, within a single region, and across multiple regions during preparation and execution of a task (Figure 7).

Single-unit and imaging studies also provide different viewpoints for the neural mechanisms associated with task sets. Single-unit studies provide a representational view, by which brain functioning is considered on the basis of a set of specific information represented by single neurons (Wood & Grafman 2003). By contrast, imaging studies provide a processing-oriented view, by which the inferences are based on the correlation of regional brain activation with behavior changes. For example, the ACC activity during task switching is, from a processing-oriented view, thought to reflect conflict monitoring. From a representational point of view, the ACC activity reflects a change in the strength of task representations. Thus the two approaches, when considered together, provide comprehensive accounts of how the cognitive processes regulate our behavior and how these processes are configured by specific representations.

The key feature of a task set is its prospective and predictive nature. In this sense, the task set is a crucial concept in elucidating the causal

mechanisms of the brain in creating complex behaviors and abstract thoughts. As discussed above, studies have shown significant progress in this attempt. This review also suggests the

importance of identifying specific task information represented in each brain region and clarifying the relationship between representations and task-related behavioral changes.

SUMMARY POINTS LIST

1. A task set is maintained by sustained rule-specific activity of single neurons in the prefrontal cortex. Imaging studies have also identified the neural correlate of a task set as a rule-specific pattern of signals across multiple voxels within a region or a rule-specific pattern of interactions between multiple regions in the prefrontal cortex.
2. Establishing a task set takes several hundred milliseconds, which reflects the build-up of rule-specific activity of a single neuron or pattern of interactions between brain regions. This process is associated with preparation effects.
3. Task switching is associated with an increase of activity in areas selectively involved in the previous task, which results in residual costs. The right VLPFC in human and pre-SMA in monkeys are likely involved in inhibition of a previous task set.
4. Imaging studies have identified the VLPFC, ACC, and pre-SMA as involved specifically in monitoring and resolution of conflicts during task switch. Single-unit studies have shown that task switching is associated with changes in the strength and onset of task representation in ACC neurons.
5. Imaging studies have identified the ACC and anterior insula/operculum as commonly involved in active maintenance of task sets across different tasks. Imaging studies have also identified the IFJ as commonly involved in updating task sets across different tasks.
6. Imaging studies show that the APF is involved in preparation of cognitive operations. The APF is also involved in active maintenance of multiple task sets, and this demand is associated with mixing costs.
7. Activity in areas involved in task execution can be predicted on the basis of the rule-specific activity in higher-order prefrontal areas and the activity in areas involved in processing of task items, which in turn determines task performance. Active maintenance of a task rule can be thought of as a process to implement the rule for subsequent task performance.
8. The ACC and medial APF are active in voluntary task selection. The ACC is also associated with awareness of conflicts among task rules and responses.

FUTURE ISSUES

1. Many questions about the rule specificity of neural activity remain unanswered. First we need to test whether the rule-specific activity could be observed outside the context of a given experimental setting. We also need to investigate how the representations of rules at different levels of abstraction are associated with anatomically defined functional fingerprints of prefrontal regions. Experiments should be designed such that specific cognitive components are manipulated among the tasks that are compared.

2. The mechanisms of conflict monitoring and resolution need to be understood in terms of the competitions among representations of task-relevant information. More specifically, whether a winner-take-all mechanism can explain the neural processes associated with selection among task sets should be formally tested.
3. It is time to move beyond the analysis of correlation between brain activation and behavior. Future studies should be aimed at clarifying the causal relationship between them. For example, to demonstrate the causality of task set over subsequent task performance, it is necessary to manipulate the task set activity and examine its influence over behavior.
4. To obtain comprehensive accounts of the neural mechanisms associated with task sets, we need to clarify the dynamics in the relationships between the neural processes and representations at different levels of brain organization, from a single neuron to a network of multiple regions.
5. The core task set system including the ACC and anterior insula/operculum contains human-specific giant spindle neurons. Also, the human APF, which is involved in setting up cognitive operations and managing multiple task sets, has an expanded layer of synaptic connections. The IFJ, which is involved in updating tasks in human, may interact with neighboring language areas. An interesting possibility is that these evolutionary changes are associated with humans' capacity to manage a wide repertoire of task sets and represent highly abstract concepts.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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