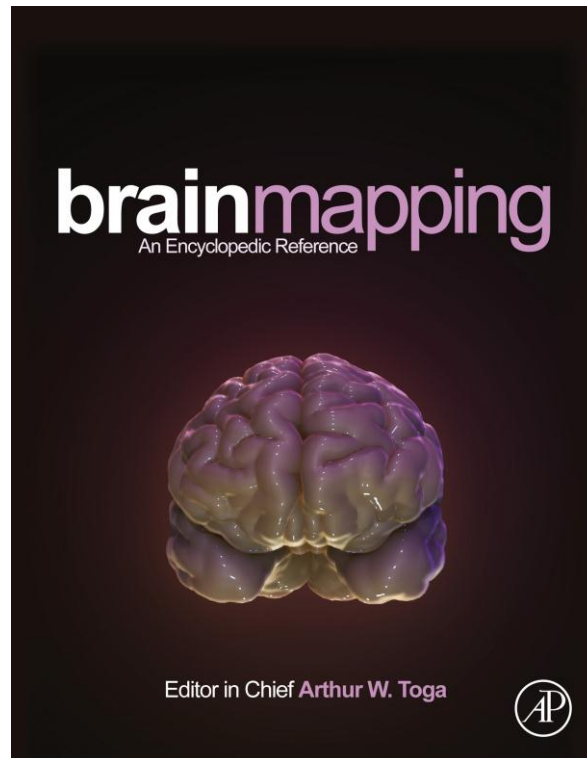


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## Rule Representation

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Rule representation refers to the processes that construct and maintain associations between stimuli and responses in the service of guiding task-relevant actions in context. This collection of central cognitive processes falls under the umbrella of executive functioning. Rule representation comes in different flavors from simple stimulus–response associations, to conditional associations that specify different responses for particular stimuli, to general task-setting rules that generalize beyond stimulus and response details. For instance, some contexts might require very specific rule representations: When the red light goes off in the nuclear reactor, push the red button to shut the reactor down. In other contexts, people have to extract more general rule representations: It is acceptable for children to move about the classroom and talk during free time, but they are expected to sit in a circle during reading time and only talk when called upon by the teacher.

The large variety of rule representations has made this a challenging topic to study. This extends to the neural level where different neural regions become involved in rule representation processes depending on rule complexity. Rule representations are also challenging to understand because they change dramatically over time. This includes over learning within a task, as well as over development. For instance, very young children (e.g., 1- to 3-year-olds) can form rule representations but often perseverate on a first rule when the rule is changed (Buss & Spencer, 2014; Zelazo, Muller, Frye, & Marcovitch, 2003). By contrast, human adults can construct quite elaborate rules (Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Crone, Wendelken, Donohue, & Bunge, 2006) and often show rule-based behaviors after only a single instruction.

In the sections in the succeeding text, we focus on rule representation processes in the brain and how these processes differ relative to the nature of the task (e.g., which modalities are used), the demands of the task (e.g., whether people must switch from one set of rules to another), and the type of task coordination (e.g., when people are asked to multitask). We then extend this discussion to examine how rule representations change over learning and development. Finally, we highlight recent theories of rule representation that are shedding new light on how rule representations are implemented in the brain.

### Neural Representation of Tasks and Rules

At the neural level, rule representation, as with other aspects of executive function, not only relies upon processes that are localized to the frontal lobe but also involves processing in the parietal lobe, temporal lobe, and basal ganglia. At the most basic level, associations between actions and reward are supported by processing in the orbitofrontal cortex. This form of learning is preserved if other regions of the frontal lobe, such as

the dorsolateral prefrontal cortex (dlPFC) and ventrolateral prefrontal cortex (vlPFC), are damaged (Izquierdo & Murray, 2004; Izquierdo, Suda, & Murray, 2004). dlPFC neurons, however, do encode the identity or magnitude of a predicted reward (Watanabe, 1996).

More complex rules such as categorical rules where a range of feature values are associated with each response not only are most commonly localized to the lateral prefrontal cortex (IPFC) but also involve a distributed network of temporal, parietal, and subcortical regions. PFC receives extensive inputs from subcortical, sensory, and motor regions (Fuster, 2000; Miller & Cohen, 2001), making this region well positioned to link perceptual or semantic information with response contingencies. Processing within PFC is also mediated by the activation of basal ganglia that regulates the updating of rules or task goals (Miller & Cohen, 2001; O'Reilly, 2006).

The IPFC is also sensitive to manipulations of the task type. For instance, the IPFC is more active when the task contains conditional rules as opposed to a response that is directly cued. Conditional rules can specify, for example, a right-hand button press in response to a green stimulus and a left-hand button press in response to a blue stimulus. This type of rule could also be more abstract and based on the relationship among stimuli. For example, participants could be instructed to press a right-hand button if two successively presented images are the same but to press a left-hand button if two successively presented images are different.

Importantly, rule-representation processes extend beyond the frontal cortex with complex interactions between frontal and more posterior cortical regions. The IPFC, along with posterior middle temporal cortex, shows robust activation in response to cues indicating which task to perform on an ensuing trial, suggesting these regions are involved in the retrieval of task rules (Bunge et al., 2003). Posterior middle temporal cortex is thought to represent semantic information (Buckner, Raichle, & Petersen, 1995; Fiez, 1997; Poldrack et al., 1999). This region, then, associates semantic information with response information.

vlPFC, presupplementary motor area (preSMA), and inferior/superior parietal areas are involved in the maintenance of task rules. Evidence for this comes from tasks that require sustained activation of the task rule across a delay period between the cue and the start of a trial. vlPFC, preSMA, and parietal areas all show robust activation in such tasks, and sustained activation is greater when the demands on rule representation are greater such as in conditional-rule tasks compared with simple response cuing tasks (Bunge et al., 2003). Further, activation in the left anterior insula and preSMA increases as more stimulus–response pairings must be maintained in a given task (Stelzel, Kraft, Brandt, & Schubert, 2008). The vlPFC also appears to support the retrieval of rules in a way that is sensitive to rule complexity.

In addition to maintaining task rules, the parietal cortex shows stronger activation when multiple responses are cued by additional irrelevant stimuli, such as in the flanker task (Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002). This indicates that the parietal cortex plays a role in maintaining response contingencies. Functionally, IPFC activation precedes that of the parietal cortex (Brass, Ullsperger, Knoesche, von Cramon, & Phillips, 2005), suggesting that the IPFC provides a task-relevant top-down biasing signal to help select appropriate response contingencies in the parietal cortex. Results from pattern analysis of fMRI data also show that the IPFC, anterior insula, and intraparietal sulcus (IPS) encode general task representations when there are multiple tasks that could be cued.

Rule representations have also been reported in premotor and visual areas. For instance, neurons in the IPFC and premotor cortex selectively respond based on particular stimulus–response associations (Asaad, Rainer, & Miller, 2000; Muhammad, Wallis, & Miller, 2006; Wallis, Anderson, & Miller, 2001; Wallis & Miller, 2003). In addition, neurons in the visual cortex are sensitive to task mappings and response coding along with the encoding of color stimuli (Mirabella et al., 2007; Woolgar, Hampshire, Thompson, & Duncan, 2011).

### Rule Representation Across Modalities

A key aspect of rule representation is that any stimulus can potentially be associated with any response. Standard research paradigms have focussed on either visual or auditory stimuli that are associated with spatial or vocal responses. Interestingly, it is typically easier to associate visual stimuli with manual responses and auditory stimuli with vocal responses. This is presumably due to the overlap between visual–manual dimensions and auditory–vocal dimensions.

Examination of this aspect of rule representation at the neural level has revealed distinct networks that are associated with different task modalities. Spatial response selection is associated with activation in the right middle frontal gyrus (MFG), bilateral dorsal premotor cortex, left superior parietal lobule, and precuneus. Nonspatial response selection, by contrast, is associated with activation in the left MFG, left inferior parietal lobule, left posterior parietal cortex, left middle temporal cortex, and right middle occipital areas (Jiang & Kanwisher, 2003; Schumacher, Elston, & D'Esposito, 2003).

There are also areas that are commonly activated across tasks regardless of the modality, including bilateral IPS, right precuneus, bilateral frontal eye field, right cerebellum, and bilateral middle frontal cortex (Jiang & Kanwisher, 2003). Finally, research has identified a frontoparietal network composed of the anterior IPFC, dlPFC, posterior IPFC, and posterior parietal cortex that shows highly variable connectivity patterns. This network could provide a means of rapidly establishing functional networks, linking different perceptual/conceptual dimensions to different motor networks (Cole et al., 2013). Such flexible processing 'hubs' might underlie humans' impressive ability to associate virtually any stimulus with any response.

### Rule Switching

Rule representation processes have also been studied using task-switching paradigms that require participants to alternate between sets of rules or tasks. These tasks can involve univalent (single-valued) rules in which different stimuli are used for each task or bivalent (two valued) rules in which different responses must be made for the same stimuli. For example, participants can be instructed to respond with their index finger to a house stimulus and middle finger for a flower stimulus in one task but respond with the opposite fingers for a different task (Hazeltine, Ruthruff, & Remington, 2006; Schumacher et al., 2003; Stelzel, Schumacher, Schubert, & D'Esposito, 2006).

The vlPFC and left superior parietal cortices show stronger activation for bivalent rules compared with univalent rules and stronger activation for rule switches compared with rule repetitions. Further, the caudate nucleus, a region of the basal ganglia, and SMA/preSMA are selectively activated on bivalent rule-switching trials (Crone, Wendelken, Donohue, & Bunge, 2006).

Bivalent rules can also involve processes of selective or dimensional attention. For example, one task can specify responding based on the color of a stimulus and the other task can involve responding based on the shape of a stimulus. Dimension switching activates a particular network of regions including the left inferior frontal gyrus, IPS, superior parietal cortex, and supramarginal gyrus (Morton, Bosma, & Ansari, 2009; Nagahama et al., 2001; Philipp, Weidner, Koch, & Fink, 2013). Interestingly, switching response modalities, rather than stimulus dimensions, only activates the left IPS and the supramarginal gyrus (Philipp et al., 2013). Inferior frontal junction (IFJ) shows a more complex pattern in related tasks: different types of switches – switching rules versus switching response hands – yield different patterns of functional connectivity. In particular, switching rules reveals connectivity with the anterior PFC, superior frontal cortex, and hippocampus, but switching response hands reveals connectivity with motor regions around the central sulcus (Stelzel, Basten, & Fiebach, 2011).

### Rules and Task Coordination

In multitasking situations, participants are asked to perform two tasks simultaneously (dual-task paradigms) or in rapid succession (as in the psychological refractory period paradigm). The inferior frontal cortex, a region of the vlPFC, shows robust activation in multitasking situations. This is the case across any different pairing of stimulus (visual or auditory) or response (manual or vocal) modality (Dux et al., 2009; Stelzel et al., 2006, 2008, 2011), suggesting that the inferior frontal cortex is uniquely associated with task order control (Stelzel et al., 2008).

Although the inferior frontal cortex is robustly activated by any pairing of stimulus and response modality, the specific details of the pairing modulate the neural response. Tasks can be characterized as using a standard pairing if they pair visual–manual or auditory–vocal dimensions or as

using a nonstandard pairing if they pair visual–vocal or auditory–manual dimensions. With nonstandard pairings, there are larger behavioral interference and larger dual-task related activation in the IFJ (Stelzel et al., 2006). Thus, IFJ is sensitive to the amount of overlap or the amount of translation that needs to be accomplished when mapping a stimulus dimension onto a response dimension in multitasking situations.

### Rule Representation over Learning and Development

Studies have also examined changes in performance and neural activation as rule representations change over the timescales of learning and development. One line of work has examined how rule use changes as a task is practiced. Early in learning, the vLPFC shows the strongest rule-related activation. With practice, however, SMA/preSMA shows the strongest rule-related activity (Boettiger & D'Esposito, 2005; Muhammad et al., 2006). IFJ shows a similar pattern: over learning, neural activation in IFJ is reduced as performance on dual-task trials becomes equivalent to performance in single-task conditions (Dux et al., 2009).

Other tasks, such as the Wisconsin Card Sorting Test, require participants to learn rules based on trial and error feedback. In this task, participants sort cards containing multiple dimensions, such as color, shape, and number. Participants must learn the correct rule on the fly based on spontaneous sorting and feedback from the experimenter (i.e., 'correct' or 'incorrect'). Critically, as the task progresses, the experimenter changes the rule and participants must flexibly switch or update the rules they are using.

As might be expected from the complex nature of this task, rule learning and updating are mediated by a large network of regions including the left fusiform cortex, angular gyrus, MFG, medial frontal gyrus, bilateral inferior frontal gyrus, retrosplenium, middle temporal gyrus, striatum, and superior parietal lobule. Further, regions including the rostral/caudal anterior cingulate cortex (ACC), bilateral temporal parietal junction, right posterior supplementary frontal sulcus, right superior frontal gyrus, right MFG, right anterior supplementary frontal sulcus, and left anterior inferior frontal sulcus are more strongly activated when rules must be deduced from feedback compared with when the relevant dimension is directly cued (Lie, Specht, Marshall, & Fink, 2006). Finally, bilateral inferior frontal sulcus is sensitive to the number of dimensions involved in the task (Konishi et al., 1998).

Another type of paradigm in which rules must be deduced from feedback is categorical rule learning. In this paradigm, participants are shown a sequence of stimuli that vary along a single or multiple dimensions. As participants categorize the stimuli, they must determine where a response category boundary lays along the stimulus dimension(s). Category boundaries can be verbalizable (e.g., the boundary requires attention to a single dimension) or implicitly learned by integrating across multiple dimensions. Verbalizable rules are associated with activation of anterior medial temporal lobe, along with clusters of regions in the superior and medial PFC. Implicit category learning, on the other hand, is associated with activation in the caudate body and lentiform nucleus (Nomura et al., 2007).

Thus, implicit category learning does not seem to recruit rule-representation processes in the frontal cortex.

In addition, neural activation changes in categorical rule learning tasks as stimulus features become familiar through practice with different networks activated in response to novel or familiar rules. The MFG (right dlPFC), precentral gyrus, preSMA, bilateral insula, inferior frontal sulcus, frontal operculum, and caudate show stronger activation for novel category members compared with familiar category members that were previously presented. Superior frontal gyrus, frontopolar gyrus, rostral ACC, and insula, however, show stronger activation for familiar category members compared with novel category members (Boettiger & D'Esposito, 2005).

Developmentally, research has examined changes in neural activation as rule representation develops. A region of the bilateral LPFC shows increases in activation as task switching emerges in early childhood between 3 and 5 years (Moriguchi & Hiraki, 2009). Neural activation continues to change into later childhood as rule-representation processes are refined. Specifically, 8- to 12-year-olds display a less-differentiated pattern of neural activation relative to adults. These children engage the preSMA for rule representation, not simply for rule switching as with adults. Further, while adults show heightened vLPFC activation for bivalent rules on both rule-repeat and rule-switching trials, children show greater activation in this area for both univalent rules and switch trials (Crone, Donohue, Honomichl, Wendelken, & Bunge, 2006). Finally, data suggest refinement of rule-switching processes in adolescence in that adults show larger activation than adolescents in rule-switching tasks in the superior frontal cortex, thalamus, superior parietal cortex, and fusiform cortex (Morton et al., 2009).

### Theories of Rule Representation

Rule representation processes are clearly complex – there are different types of rules, complex patterns of neural activity depending on the type of rule and the type of task, and changes in rule representations over learning and development. How can we make sense of this level of complexity? One approach is to use theoretical models that implement critical aspects of rule representation and executive processes.

For instance, Anderson and colleagues had implemented a production model using the ACT-R framework to explain human performance across a variety of rule-guided situations (Anderson, Taatgen, & Byrne, 2005; Anderson et al., 2004; Jilk, Lebiere, O'Reilly, & Anderson, 2008). This model has accounted for human performance across a diverse array of cognitive processes and has shed light on how people organize knowledge and produce goal-directed behavior. Other computational approaches mimic key aspects of neural function in an effort to understand both brain and behavior. For instance, O'Reilly and colleagues (Huang, Hazy, Herd, & O'Reilly, 2013; O'Reilly, 2006; Rougier, Noelle, Braver, Cohen, & O'Reilly, 2005) had implemented a parallel distributed processing model, focussing on the role of the basal ganglia in the mediation of representations in the frontal cortex. This work has demonstrated how simplified biological neurons can establish

links between neural and behavioral processes in human response selection. Moreover, recent work by Huang et al. (2013) demonstrates how this system can construct task mappings on the fly.

A different theoretical perspective – dynamic field theory – has also made important strides integrating the behavioral and neural processes that underlie rule representation. Dynamic field models capture key aspects of neural population dynamics within cortical fields (Bastian, Riehle, Erhagen, & Schöner, 1998; Bastian, Schöner, & Riehle, 2003; Erhagen, Bastian, Jancke, Riehle, & Schöner, 1999; Jancke et al., 1999; Markounikau, Igel, Grinvald, & Jancke, 2010) in a way that integrates cognitive and sensorimotor processes (Spencer, Perone, & Johnson, 2009; Spencer & Schöner, 2003). For instance, Buss and colleagues (Buss & Spencer, 2014; Buss, Wifall, Hazeltine, & Spencer, 2014; Spencer & Buss, 2013) had implemented a distributed rule representation system using multiple coupled dynamic fields. In these models, the IPFC is involved in representing different dimensions or modalities that are relevant for a given task. Neural activation within IPFC biases processing in object representation areas that directly associate stimuli with responses via two-dimensional neural fields that are tuned to different sensory and motor dimensions. This framework has quantitatively simulated the behavioral and neural dynamics associated with the emergence of flexible rule use in early childhood (Buss & Spencer, 2014; Spencer & Buss, 2013) and has also been used to understand changes in IFJ activation over learning in a dual-task paradigm (Buss et al., 2014; see also Dux et al., 2009).

## Summary

Rule representation relies on an extensive network of frontal, temporal, parietal, and subcortical regions. Systematic manipulation of different aspects of rule representation has revealed specific functions across areas. The IPFC is involved in associating stimuli with responses, the inferior frontal cortex is involved with attention to dimensions and modalities, SMA and preSMA are engaged in rule representation for well-learned tasks, the parietal cortex is involved with maintaining and selecting response contingencies for a particular task, and different regions of the temporal cortex are involved with modality-specific representations of stimuli and their associated responses. Neurocomputational models show promise for integrating behavioral and neural dynamics over the multiple timescales across which rule representation unfolds. Although the current literature has mapped out key aspects of rule representation and rule use, future research will need to account for the processes that allow tasks to be constructed ‘in the moment,’ how different input and output modalities can be flexibly associated to form a task representation, and how neural representations of rules are used to guide action and attention.

**See also:** INTRODUCTION TO ANATOMY AND PHYSIOLOGY: Basal Ganglia; Cytoarchitectonics, Receptorarchitectonics, and Network Topology of Language; Functional Connectivity; Lateral and

Dorsomedial Prefrontal Cortex and the Control of Cognition; Motor Cortex; Posterior Parietal Cortex: Structural and Functional Diversity; Topographic Layout of Monkey Extrastriate Visual Cortex; INTRODUCTION TO COGNITIVE NEUROSCIENCE: Category Learning; Memory Attribution and Cognitive Control; Motor Decision-Making; Neural Correlates of Motor Skill Acquisition and Consolidation; Neuropsychopharmacology of Cognitive Flexibility; Perceptual Decision Making; Performance Monitoring; Reward Processing; Task Switching Processes; Working Memory; INTRODUCTION TO METHODS AND MODELING: Resting-State Functional Connectivity; The Emergence of Spontaneous and Evoked Functional Connectivity in a Large-Scale Model of the Brain; INTRODUCTION TO SYSTEMS: Brain Mapping of Control Processes; Hubs and Pathways; Network Components; Neural Correlates of Motor Deficits in Young Patients with Traumatic Brain Injury; Reward; Working Memory.

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