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## Is prefrontal cortex necessary for the storage and acquisition of relational concepts?

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### Abstract

The ability to make analogies requires building higher order relations and so keeping track of multiple independently varying dimensions of the concepts being compared. Frontal cortex may be well suited to support this type of function, as Speed's review makes clear. However, Speed goes further in arguing that PFC neurons necessarily support the storage and acquisition of relational concepts. This claim is evaluated in the context of broader perspectives on storage and acquisition of semantic knowledge.

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It remains an open question how to characterize the functional organization of frontal cortex. For example, though there is growing evidence that progressively rostral frontal neurons support increasingly abstract control processing (Badre & D'Esposito, 2007; Christoff, Keramiatan, Gordon, Smith, & Madler, 2009; Koechlin, Ody, & Kouneiher, 2003), what makes those processes or neural representations more abstract remains controversial (Badre, 2008; Botvinick, 2008). Some have focused on timescale, noting that rostral portions of frontal cortex maintain information that provides the context for action over longer time intervals (Kouneiher, Charron, & Koechlin, 2009). My colleagues and I have emphasized policy abstraction or the degree to which a goal or rule that guides action generalizes over more specific goals or rules (Badre, Hoffman, Cooney, & D'Esposito, 2009). Speed articulates a third account, namely that prefrontal (PFC) neurons are tuned for different degrees of relational complexity (also see Christoff et al., 2001; Kroger et al., 2002).

These perspectives on rostral-caudal organization are not mutually exclusive. For example, abstract policy and complex relations both require keeping track of multiple independently varying dimensions. So, the ability to reason about higher order relations could rely on the same architecture that permits control over multi-leveled policy.

Importantly, however, Speed also appears to go beyond assigning a role in relational reasoning to PFC, but makes the further claim that PFC is the site of storage of relational concepts and that striato-frontal mechanisms are necessary for their acquisition. For example, she suggests that rostral PFC may respond preferentially to highly relational concepts, like that of a *life cycle*. Similarly, learning about Rutherford's model of an atom requires fronto-striatal learning circuits in order to tune frontal neurons for the relational representations that support this concept. In this claim, Speed appears to move somewhat beyond other perspectives on frontal organization. In particular, frontal neurons do not simply modulate processing of semantic representations stored elsewhere with respect to goal-relevant relations. Rather, processing relational semantics requires a necessary route through PFC because this is where this knowledge is stored.

A distinction is often drawn in cognitive neuroscience between stored semantic knowledge, like that of a life cycle, and control functions – including reasoning processes like analogy – that act on those stored representations to produce responses or to generatively discover new knowledge via inference. This distinction arises partly from the neuropsychological literature (Martin & Chao, 2001). Damage to posterior neocortical structures, particularly those in lateral temporal regions, is often associated with a loss of semantic knowledge (Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Martin & Chao, 2001). Conversely, PFC patients can have an intact semantic store but problems in strategically using this knowledge. For example, Sylvester & Shimamura (2002) studied a group of PFC patients who demonstrated deficits in tests of strategic episodic and semantic retrieval. The patients also performed triadic comparison and ordered similarity tasks that are highly dependent on stored relational semantics. Using multidimensional scaling, the “semantic space” of these patients was constructed from their responses on these tasks. In contrast to their deficits in strategic retrieval, their semantic space did not differ from the controls. Hence, stored relational semantics may not depend exclusively on PFC.

Similarly, not all relational semantics need be acquired via reinforcement-based striatal learning mechanisms. Consider that I could learn about the analogy between the solar system and Rutherford’s model of the atom not just through a process of analogy but alternatively by reading Speed’s review, which tells me the analogy between these concepts. In this latter case, my episodic memory system can immediately encode this novel relationship. Over time, this knowledge can be consolidated into semantic memory. This process requires the medial temporal lobe (MTL) memory system, rather than the striatum. Hence, amnesia arising from damage to MTL prevents acquisition of new semantic knowledge (Cohen, Eichenbaum, & Poldrack, 1997; Squire, 1994). Thus, fronto-striatal mechanisms may not be required for acquisition of relational semantics.

Recent perspectives on the functional organization of frontal cortex highlight its ability to keep track of multiple independent dimensions in order to internally guide thought and action. Such an architecture is important for analogy making. And, PFC may form abstract representations of the types of relations that will be useful for generating future analogies. However, these abstract PFC representations may be distinct from abstract representations stored elsewhere that form our store of semantic knowledge.

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