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Semantic memory retrieval circuit: Role of pre-SMA, caudate, and thalamus

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ABSTRACT

We propose that pre-supplementary motor area (pre-SMA)–thalamic interactions govern processes fundamental to semantic retrieval of an integrated object memory. At the onset of semantic retrieval, pre-SMA initiates electrical interactions between multiple cortical regions associated with semantic memory subsystems encodings as indexed by an increase in theta-band EEG power. This starts between 100–150 ms after stimulus presentation and is sustained throughout the task. We posit that this activity represents initiation of the object memory search, which continues in searching for an object memory. When the correct memory is retrieved, there is a high beta-band EEG power increase, which reflects communication between pre-SMA and thalamus, designates the end of the search process and resultant in object retrieval from multiple semantic memory subsystems. This high beta signal is also detected in cortical regions. This circuit is modulated by the caudate nuclei to facilitate correct and suppress incorrect target memories.

1. Introduction

Many conceptual and mechanistic models for semantic memory storage and retrieval have been proposed over the years, mostly informed by lesion/deficit observations and functional imaging studies, and less frequently by electrophysiology studies (Caramazza, Hillis, & Rapp, 1990; Caramazza & Shelton, 1998; Gainotti, 2000; Hillis, Rapp, Romani, & Caramazza, 1990; Humphreys & Forde, 2001; Mahon & Caramazza, 2003; Moss, Tyler, & Devlin, 2002; Tyler & Moss, 2001; Warrington & McCarthy, 1987; Warrington & Shallice, 1984). Each of these models has focused on different and important aspects of semantic memory storage and retrieval. Semantic object memory in particular has been a focus of these models given that objects are tractable stimuli for experimental manipulation. Although these models have been refined over the years to better explain the anatomical and neurophysiological basis of semantic object storage and retrieval, they remain incomplete.

Hart, Kraut and colleagues (for a more detailed description see Hart et al., 2007 or Hart & Kraut, 2007; Kraut, Calhoun, Pitcock, Cusick, & Hart, 2003; Kraut, Pitcock, & Hart, 2004) proposed a model of semantic object memory called the Neural Hybrid Model of Semantic Object Memory (ver. 1.1), which posits multiple semantic memory subsystems that encode object representations in sensorimotor and higher-order cognitive systems (e.g., lexical–semantic, visual, auditory, tactile, etc.). The neural representations in these cortical regions contain both *feature-based* (see Hart & Gordon, 1992; Haxby et al., 2001; Miceli et al., 2001 for further description of featural organization) and *category-based* (Kraut et al., 2006) neural representations for several of these sensorimotor/cognitive domains. The model supports the idea of functional–anatomic organizations for featural representations within modality-specific sensorimotor/cognitive domains that encode for features of either items or groups of items in a category (e.g., visual–perceptual features for animals; Hart & Gordon, 1992; Haxby et al., 2001; Miceli et al., 2001; Sartori & Job, 1988; Sartori, Job, Miozzo, Zago, & Marchiori, 1993) or across groups of items/categories (e.g., manipulability as a feature, detected in the premotor regions for both tools and fruit and vegetables, Kraut, Moo, Segal, & Hart, 2002; threat as a feature in the auditory- and visual semantic subsystems, Calley et al., in press; Kraut et al., 2006). The model also proposes a categorical organization, consistent with multiple accounts, including the domain-specific account.

In our model, these categorical and featural stores can link with each other in a variety of ways (for example, additive, distributed), partly depending on modality of the stores (see Hart & Kraut, 2007 for details). Here, "additive" means when two separate anatomic

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nodes, each encoding for distinct and separate qualities (e.g., in nonverbal sound memory, one region for threatenening sounds and another for animal sounds), are both activated when both qualities are associated with an object representation probed by the stimulus; "distributed" as used here means that a given quality is encoded across multiple nodes, with the possibility that each node may be responsive to more than one quality. Semantic 'links' that could be mediated by neural activity in these stores include intra-modal as well as multimodal (across multiple sensorimotor or cognitive domains) relationships between semantic entities from different subsystems that subserve semantic memory. An example of an intra-modal interaction is the lexical–semantic association for the meaning of the words "wing" and "bird", while an example of a multimodal semantic relationship is the association between the visual memory representation of a dog's tail and the word "dog" (Beauchamp, Lee, Argall, & Martin, 2004; Hart & Gordon, 1992).

The hybrid nature of the model extends from both the functional and anatomic domains consisting of combinations of differing neural architectures (e.g., nodes representing a population of neurons for the implementation of cognitive operations, spatially distributed neural patterns that encode for specific entities, etc.) to account for the dynamic mechanisms of storage, operations upon, and retrieval of semantic object knowledge. Neuronal nodal populations in this model have been imputed to perform a variety of operations including the following ones: (1) processing semantic information or performing semantic operations, (2) integration of input from multiple representational levels (Beauchamp et al., 2004; Hart & Gordon, 1990), (3) access to individual memory encodings that are represented by spatially or spatiotemporally distributed patterns, to name several. Examples of specific operations utilizing semantic representations include category, property, synonym judgments, multimodal integration (Hart et al., 1998; Hillis et al., 2001); selection of semantic knowledge amongst alternative choices (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997); categorization of animals and artefacts (Perani et al., 1995); and selection of color attribute or location (Mummery, Patterson, Hodges, & Price, 1998). Other semantic processes and regions that form a network of regions engaged in semantic operations continue to be identified (Binder, Desai, Graves, & Conant, 2009).

An important cognitive process in semantic memory is object retrieval. In this review, we delineate interactions between the rostral aspect of dorsomedial Brodmann Area 6 (referred to hereafter as for pre-supplementary motor area), thalamus, and caudate for semantic object retrieval, further specifying the neural underpinnings of this aspect of the Neural Hybrid Model. We have previously posited that retrieval of an integrated object concept in semantic memory involves the co-activation of representations of features and categories that characterize an object, which are then integrated by means of synchronized neural activity modulated by the thalamus (Kraut, Kremen, et al., 2002; Slotnick, Moo, Kraut, Lesser, & Hart, 2002). We will further elaborate on the cognitive constructs mediated by pre-SMA, caudate, and thalamus in this retrieval circuit. We have begun to impute roles to these structures using a variety of investigative techniques in both normal control participants and in patient populations (e.g., schizophrenia, Gulf War Illness, stroke, and dementia) and using several semantic memory tasks (semantic object retrieval tasks, semantic inhibition tasks).

Several findings motivated the proposition of the neural hybrid nature of the model. First, the reports of evidence of both category and feature representations in multiple semantic object memory subsystems implies a mechanism to integrate these dissociable representational units (Hart, Berndt, & Caramazza, 1985; Hart & Gordon, 1992; Sartori & Job, 1988; Warrington & McCarthy, 1987). Lesion deficit studies have also demonstrated that damage to discrete anatomic regions disrupts specific semantic processes, across categories and features, leaving other processes intact (Demb et al., 1995; Fiez, 1997; Hart & Gordon, 1990; Posner, Petersen, Fox, & Raichle, 1988). This led to the proposal that specific anatomic regions are involved in the mechanism of combining object components into an integrated object memory. As the object components are represented across multiple modalities, the idea emerged that some anatomic regions process semantic properties within a domain (domain-specific) while others are likely engaged in more general cognitive processing (domain-general).

Several semantic-specific and domain-general regions were proposed to be involved in the semantic retrieval process. We hypothesize that the primary regions critical to this process are the pre-SMA, caudate and thalamus with other regions subserving more specific retrieval roles. As the pre-SMA is involved in semantically driven word generation (Crosson et al., 2001), particularly in searching for item members of a particularly category (Crosson et al., 2003), we hypothesized that the pre-SMA is essential in initiating an item search. The caudate has been found in both motor (Picard & Strick, 1996) and cognitive functions (Crosson, Benjamin, & Levy, 2007) to be engaged in enhancing neural activity related to correct choices and suppressing activity related to incorrect ones, including in selecting meanings for words (Copland, Chenery, & Murdoch, 2000, 2001). Importantly, the caudate engagement appears to be dependent upon task/stimulus difficulty, suggesting that it will be variably engaged depending on the complexity of the retrieval task and likely utilized in semantically difficult or complex retrievals (Copland, 2003). The thalamus has been proposed to gate information flow between spatially separated cortical regions (Nadeau & Crosson, 1997) or to modulate activation of mental representations (von Zerssen, Mecklinger, Opitz, & von Cramon, 2001), either of which would be essential in integrating multiple semantic memory subsystems into a cohesive memory. Other plausible regions that may be engaged in semantic retrieval include those associated with multimodal semantic processing – inferior parietal–posterior temporal (Beauchamp et al., 2004; Grossman et al., 2003; Hart & Gordon, 1990), temporal poles (Damasio, 1990), temporo-parietal-occipital (TPO) junction (Mummery et al., 1998), and left lingual–fusiform gyri region (Hart et al., 1998; Perani et al., 1995) – and any or all of these areas may play roles in the elicitation of an integrated memory. In our work we clarified the individual roles played by the pre-SMA, caudate and thalamus in semantic retrieval as well as evidence of how these regions are engaged.

2. Semantic Object Retrieval Task (SORT) and its fMRI, time-dependent beta-band EEG power change, and ERP correlates

The functional–anatomic organization within modality-specific sensorimotor/cognitive domains include perceptual (e.g., visual–perceptual features; Hart & Gordon, 1992; Haxby et al., 2001; Miceli et al., 2001; Sartori & Job, 1988; Sartori et al., 1993), sensorimotor (e.g., manipulability, as encoded in hand-related in premotor regions for both tools and fruit and vegetables; Kraut, Moo, et al., 2002), or emotional features (threat as detected in the nonverbal sound system, Kraut et al., 2006, visual semantic system, Calley et al., in press) as well as category level knowledge and other potential subcomponents related to objects. We posited that a unified object representation is retrieved in semantic memory by integrating these anatomically separated, modality-specific representations. This proposal is in contrast to assertions that information flows from each different modality to an amodal semantic system, with these amodal, semantic-specific regions encompassing where an integrated object memory is encoded and retrieved (e.g., temporal pole, Damasio, 1990). To test the validity of our hypothesis, we constructed a task that probes object retrieval from the integration of