

# Semantic Memory: Cognitive and Neuroanatomical Perspectives

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## Glossary

**Abstract concept** A concept with weak or non-specific sensorimotor feature associations, such as the concepts *hope*, *mercy*, and *desire*.

**Concrete concept** A concept with strong sensorimotor feature associations, such as the concepts *dog* and *apple*.

**Episodic memory** Autobiographical memories for specific personal experiences, which depend critically on the context of the personal event.

**Heteromodal brain region** A brain region with a high-level of connectivity to many sensory and motor modality-specific association cortices as well as other heteromodal

cortices. Heteromodal brain regions are specialized for high-level multimodal processing.

**Semantic memory** Basic world knowledge of words, objects, people, and places.

**Sensorimotor brain region** Brain regions that are specialized for processing specific modalities of perceptual inputs or motor outputs.

**Sensorimotor features** Sensory and motor associations of concepts (e.g., stored knowledge about the shape of a *hammer* and the sound that it makes).

**Superordinate concept** Relatively higher-rank and more generalized classification for a concept (e.g., 'child' is the superordinate concept for 'girl' or 'boy').

Nothing, at first view, may seem more unbounded than the thought of man, which not only escapes all human power and authority, but is not even restrained within the limits of nature and reality. To form monsters, and join incongruous shapes and appearances, costs the imagination no more trouble than to conceive the most natural and familiar objects. But though our thought seems to possess this unbounded liberty, we shall find, upon a nearer examination, that it is really confined within very narrow limits, and that all this creative power of the mind amounts to no more than the faculty of compounding, transposing, augmenting, or diminishing the materials afforded us by the senses and experience.

David Hume, 1777

## Introduction

Memory allows us to capture information from our life experiences and take advantage of this information in the future. One of the advantages of memory, as Hume observed, is that we can use it to construct a seemingly unbounded variety of thoughts in imagination. This stored knowledge about the world makes up what is known as our semantic memory. This type of memory differs from the autobiographical memory of past experiences, known as episodic memory. This observation is consistent with advances in psychology over the last half century that have taught us that not all memories are created equal. There is now a great deal of evidence that there are different kinds of memory. In this article, we will focus on a particular type of memory – semantic memory. We will begin by placing semantic memory within a broader context and discussing the major division between episodic memory and semantic memory. We will then review what is known about the cognitive and neuroanatomical architecture of the semantic memory system.

## Declarative Memory: Episodic and Semantic

At the beginning of the twentieth century, memory was typically characterized as a single entity without clear-cut

subdivisions. One useful distinction within the memory literature emerged in 1972 when Endel Tulving articulated a theoretical framework that discriminated between two different types of memory: episodic and semantic. Both of these types of memory are considered part of our declarative memory (also known as explicit memory), which is our memory for knowledge and events that can be consciously recalled. According to Tulving, episodic memory refers to our autobiographical memories for specific personal experiences, which depend critically on the context of the personal event. Semantic memory refers to our general knowledge about the world, including knowledge about people, places, and facts. Semantic memories are not tied to specific personal events, but instead reflect an abstraction across these specific events that captures the critical features that these events have in common. For example, remembering the experience of your last canoe trip relies on episodic memory, whereas understanding the meaning of *canoe* (we use italics to indicate a concept) relies on a distillation of the commonalities associated with all of our experiences with canoes (i.e., something like 'a light, narrow, pointed boat that is paddled').

Early neuropsychological evidence from patients with focal brain lesions supported the distinction between these two types of memory. For example, patients with lesions affecting the medial temporal lobe showed a particularly severe impairment of episodic memory but relatively intact semantic memory (Scoville & Milner, 1957; Squire & Zola, 1998; Warrington, 1975). In other words, these patients had little trouble understanding the meaning of words and objects, but they had almost no ability to remember events they had experienced. There also appear to be dissociations between how semantic and episodic memories are acquired. It has been shown, for example, that children who develop amnesia after incurring hippocampal damage early in life can still acquire seemingly normal semantic knowledge throughout development even though they have difficulty acquiring new episodic memories (Gardiner, Brandt, Baddeley, Vargha-Khadem, & Mishkin, 2008; Vargha-Khadem et al., 1997). Furthermore, it appears

that patients with profound episodic memory difficulty due to Alzheimer's disease can still acquire and retain the meaning of new words and objects (Grossman et al., 2007; Murray, Koenig, Antani, Mccawley, & Grossman, 2007).

Other works described patients with the opposite dissociation – prominent semantic memory difficulty with relatively spared episodic memory (Warrington, 1975). Subsequent studies associated this pattern of impaired semantic memory with atrophy in inferolateral and anterior portions of the temporal lobe in patients with a syndrome known as semantic dementia (now referred to as semantic variant of primary progressive aphasia) (Mummery et al., 2000). These patients show a severe deficit in semantic memory, evident in their difficulty understanding the meaning of words and objects, but have relatively intact episodic memory (Grossman, 2010; Hodges & Patterson, 2007; Hornberger & Piguet, 2012; Warrington, 1975).

The dissociation between episodic memory and semantic memory provided a useful framework on which to build cognitive and neurobiological theories of human declarative memory. Early work from patients with focal brain damage led to the general conclusion that the medial temporal lobe regions primarily support episodic memory, whereas the lateral temporal regions primarily support semantic memory. And indeed, behavioral and neuroimaging studies in healthy subjects further indicated that these two types of memory relied on distinct brain networks (Cabeza et al., 1997; Jacoby & Dallas, 1981; Posner & Keele, 1968; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996). Nonetheless, there is still much ongoing debate over the degree to which these memory systems are independent and rely on distinct neural substrates. For example, some models of hippocampal functioning posit a role for medial temporal structures in the formation of semantic memories (Davis, Love, & Preston, 2012; Love, Medin, & Gureckis, 2004), and there is evidence implicating neocortical structures in episodic memory (Hayama, Vilberg, & Rugg, 2012; Rugg & Yonelinas, 2003). With the continued development of brain imaging techniques, it has become increasingly evident that the episodic and semantic memory systems rely on partially overlapping large-scale brain networks that include not only the medial and lateral temporal lobes but also portions of the frontal and parietal lobes. Thus, although the theoretical distinction between episodic memory and semantic memory has proven useful in many ways and there is much evidence for gross anatomical distinctions between the two systems, at a more fine-grained anatomical level, the distinctions are not as clear-cut.

In the remainder of this article, we will consider in greater detail how the semantic memory system is organized in the brain. Although semantic memory encompasses a broad range of knowledge, we will focus mostly on the semantic representation of single objects and words. Indeed, many investigations of semantic memory have focused on these basic semantic representations, which lend themselves to controlled experimental investigation. We will first consider the neural and psychological perspectives for the organization of concrete semantic knowledge (i.e., knowledge about concepts that have a physical existence in the world such as knowledge about objects, people, and places) and then consider the perspectives for how abstract semantic knowledge is organized in

the brain (i.e., knowledge about concepts that do not have an easily identifiable physical existence, such as the concepts *hope*, *mercy*, and *desire*). Next, we will consider perspectives on how semantic knowledge is integrated and abstracted across concepts in the brain.

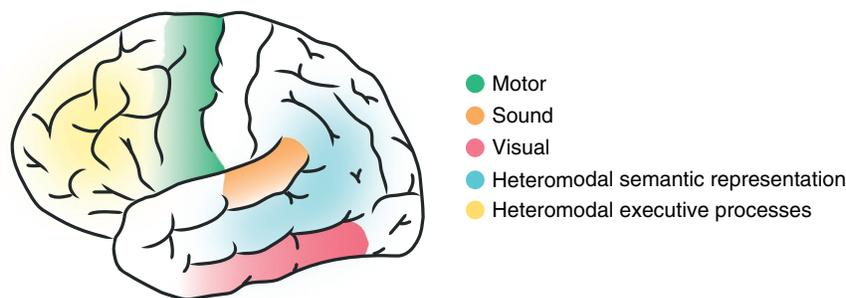
## Organizing Principles of Semantic Memory

### Grounded Knowledge

When Tulving proposed partitioning declarative memory into episodic memory and semantic memory, he characterized the semantic memory component as a single, amodal system in which all semantic knowledge is stored (Tulving, 1972). Alternative theories about the organization of semantic memory were subsequently proposed that contradicted this amodal framework. These proposals, originating in the neuropsychology literature, described patients with selective deficits for a single category of knowledge within semantic memory, rather than damage to the entire semantic memory network. In 1983, for example, Warrington and McCarthy described a patient with a semantic memory deficit that was worse for nonliving objects (e.g., tools and furniture) than for natural kinds (e.g., animals, food, and plants). The next year, Warrington and Shallice (1984) reported a group of patients with the opposite pattern of semantic impairment – worse performance on living than on nonliving objects. Such semantic deficits were referred to as ‘category-specific.’ These observations suggested that the semantic memory system is subdivided into different components based on the content of concepts. Interestingly, many other forms of category-specific semantic deficits have been reported in the literature (Gainotti, Silveri, Daniele, & Giustolisi, 1995; Goodglass, Klein, Carey, & Jones, 1966; Shapiro, Shelton, & Caramazza, 2000), such as selective impairments for color (Damasio, Mckee, & Damasio, 1979) and for body parts (Dennis, 1976).

There has been much debate over how these category-specific impairments emerge. One theory proposed that semantic knowledge is organized into specific domains, such as animate (e.g., animals) and inanimate (e.g., tools and furniture), as a result of evolutionary constraints. According to this account, known as the domain-specific account, specialized neural circuitry evolved to facilitate a recognition advantage for certain categories necessary for survival (Caramazza & Shelton, 1998). These evolutionary constraints would then give rise to separate knowledge stores for specific categories. An example is the innate ability for 3-month-olds to distinguish between biological motion and nonbiological motion (Bertenthal, Proffitt, & Cutting, 1984).

Other accounts proposed that different semantic categories rely on different sensorimotor features (Allport, 1985; Gage & Hickok, 2005; Warrington & Mccarthy, 1987; Wernicke, 1900), which we refer to here as the sensorimotor account. The central idea behind sensorimotor accounts of semantic memory is that the sensory and motor feature associations of object concepts constitute the primary organizing principle in semantic memory. In this view, object concepts are composed, in part, of sensory and motor feature associations that are critical to their meaning, and these features are stored in or near the corresponding sensory and motor regions of the brain. According to



**Figure 1** Sensorimotor brain regions that are thought to support sound (orange), action (green), and visual (pink) conceptual features are illustrated in or near the primary auditory, motor, and ventral visual cortical regions, respectively. Heteromodal brain regions for representing integrated conceptual information (light blue) and heteromodal brain regions for performing executive processes (yellow) are highly interconnected to sensorimotor brain regions. Furthermore, the heteromodal regions in the frontal, temporal, and parietal cortices are also highly interconnected with each other. For illustrative purposes, we only depict the broad categories of sensorimotor features.

this theory, semantic representations rely on distributed networks of features, and these networks parallel the anatomical distribution of the brain's sensory and motor systems (Figure 1). For example, the concept *hammer* has visual perceptual features associated with it that identify its appearance, and it is hypothesized that these features are represented in ventral portions of visual association cortex. *Hammer* also has motor features associated with how to grasp and make use of it, and it is proposed that they are represented in or near motor and premotor brain regions. Other features of *hammer* may include characteristic motion features in or near motion perception regions of the visual association cortex and auditory features, such as the pounding sound of a hammer, represented in or near the auditory association cortex. This account attributes category-specific deficits to the fact that these categories have differentially weighted sensorimotor feature associations. For example, because tool concepts like *hammer* have more motor features than animal concepts like *cat*, they tend to rely more heavily on representations in the motor and premotor association cortices.

Several lines of investigation lend support to this account. For example, patients with a neurodegenerative motor disorder known as amyotrophic lateral sclerosis have greater difficulty naming and understanding concepts like *hammer* that are associated with motor actions (Grossman et al., 2008). Disease in the auditory association cortex appears to compromise the representation of concepts such as *thunder* that depend on auditory feature knowledge more than concepts that do not have auditory feature associations (Bonner & Grossman, 2012). Natural kind concepts such as *cat* appear to rely heavily on the representation of their visual appearance and thus may be relatively vulnerable to disease in visual association cortices. In line with this, patients with Alzheimer's disease, who have a substantial neurodegenerative burden in ventral portions of visual association cortex, often have difficulty with animal concepts (Garrard & Carroll, 2006; Garrard, Lambon Ralph, Patterson, Pratt, & Hodges, 2005; Libon et al., in press). Findings such as these suggest that category-specific semantic deficits arise, in part, because damage to a sensorimotor association region differentially degrades the modality-specific feature knowledge associated with different semantic categories.

While both the domain-specific account and the sensorimotor account predict category-specific deficits for

fundamentally different reasons, the evidence to date has provided stronger support for a sensorimotor account of semantic memory. Much of this evidence comes from functional neuroimaging studies in healthy young adults. An early functional neuroimaging study of semantic memory (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995) demonstrated that the same object could evoke activation in markedly different brain regions depending on the type of feature that was being retrieved. Specifically, these researchers found that retrieving the color of an object evoked activation in the ventral visual association cortices, while retrieving an action feature of the same object evoked activation in the middle temporal and frontal cortices. This finding suggested that the neural processing associated with conceptual knowledge of objects was not static and localized to a specific brain region but was distributed throughout numerous cortical regions, including the sensory and motor cortices. Along similar lines, Mummery, Patterson, Hodges, and Price (1998) showed participants the names of living things or artifacts and asked them to perform judgments of color or location. The pattern of brain activation differed depending on the attribute judgment (e.g., left anteromedial temporal cortex activation for color and left temporoparietal junction activation for location). However, there was little difference in activation across category domains (living versus manufactured artifacts), suggesting that sensorimotor attributes accounted for a greater degree of the variance in functional activation elicited during semantic processing.

Thus far, we have discussed differences between broad categories of semantic features, such as visual or motor features. However, there are many subdivisions within these sensorimotor feature domains that have been reported in the literature. For example, there is functional neuroimaging evidence that visual feature knowledge of shape (Ganis, Thompson, & Kosslyn, 2004; Oliver & Thompson-Schill, 2003), color (Chao & Martin, 1999; Grossman et al., 2013; Hsu, Kraemer, Oliver, Schlichting, & Thompson-Schill, 2011), motion (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Martin, Ungerleider, Haxby, & Gazzaniga, 2000), and size (Kellenbach, Brett, & Patterson, 2001) is represented in or near the distinct anatomical regions within the visual association cortex involved in the perception of those specific visual features. It has also been reported that knowledge of action (Martin et al., 1995), sound (Bonner & Grossman, 2012;

Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008), and smell (González et al., 2006) features depends, in part, on representations in or near the corresponding sensorimotor regions. There is even evidence that motor knowledge associated with action concepts follows the somatotopic organization of the motor cortex: knowledge of face, arm, and leg actions activates areas adjacent to and overlapping with the corresponding regions for tongue, finger, and foot movements (Hauk, Johnsrude, & Pulvermüller, 2004).

There are many aspects of the semantic memory system that have not been fully resolved by sensorimotor theories of semantic memory. For example, it is important to keep in mind that the neural substrates of the semantic memory system are not necessarily the same as those underlying perception and action. Though the semantic system seems to parallel the distribution of the sensory and motor systems, these systems may still be distinct at a fine-grained neural level (Chatterjee, 2010). One specific hypothesis that addresses this issue suggests that there is an anterior shift in the location where the abstract sensorimotor knowledge is stored relative to where the perception of that sensory or motor feature is processed (Chao & Martin, 1999; Kable et al., 2005; Martin et al., 1995). Additionally, the degree to which sensorimotor information is accessed may be highly influenced by the particular demands of the task. For example, concepts in semantic memory can be considered superficially or in detail, and the degree to which activations for semantic and sensorimotor processes overlap may depend on the depth of processing required for a particular semantic task (Hsu et al., 2011). Furthermore, the semantic attributes of object concepts do not consist solely of sensorimotor knowledge. There is also ‘world knowledge’ that is more difficult to represent in a manner that is mediated by the sensorimotor system. For example, an aspect of our world knowledge for oranges is that ‘oranges grow in Florida,’ but this information may be difficult to represent with only a set of sensorimotor features. Even within the domain of object concepts, superordinate concepts like *fruit* seem to be more abstract and rely less on sensorimotor features than basic-level concepts like *apple*. Answers to some of these issues may come from a better understanding of how abstract and cross modal information is represented in the brain, topics that are discussed in the next two sections.

### Abstract Knowledge

Many of the studies discussed up to this point illustrate how the sensory and motor features of concrete concepts are represented in the brain. How does the brain represent conceptual features without direct physical referents in the world? For example, how would abstract concepts like *hope* or *truth* be stored in the brain? Much less is known about the neural basis of abstract concepts, though imaging evidence suggests that abstract and concrete concepts have partially distinct neural substrates.

An early cognitive theory, known as the dual-coding theory, suggested that abstract concepts rely primarily on a system of verbal associations, while concrete concepts rely on both verbal and sensory feature associations (Paivio, 1971). This cognitive hypothesis would predict distinct neural correlates for

these two processes, and indeed, it seems to be the case that they elicit activation in partially distinct regions.

Two recent meta-analyses examined the most common loci of activation in fMRI and PET studies comparing abstract and concrete conceptual representations and found that abstract concepts tend to elicit greater activity in the left inferior frontal gyrus, left anterior middle temporal gyrus, and left anterior superior temporal gyrus (Binder, Desai, Graves, & Conant, 2009; Wang, Conder, Blitzer, & Shinkareva, 2010). It is possible that the greater activity in the lateral temporal and inferior frontal portions of the left hemisphere, regions traditionally associated with language processes, is due to the strong reliance of abstract concepts on verbal associations, consistent with the dual-coding theory. There is additional evidence that abstract concepts rely less on sensorimotor regions, such as the visual association cortex, than concrete concepts. For example, these fMRI meta-analyses show that concrete concepts result in more activation in visual association regions of the ventral temporal lobe than abstract concepts (Binder et al., 2009; Wang et al., 2010). Additionally, a phenomenon known as ‘reversal of the concreteness effect’ has been reported in some patients with semantic dementia. Patients with reversal of the concreteness effect exhibit a relatively worse deficit for knowledge of concrete concepts compared with that of abstract concepts, and it is thought that this deficit is due in part to atrophy of the ventral temporal visual association regions that results in the degradation of visual feature knowledge crucial for concrete concepts (Bonner et al., 2009; Breedin, Saffran, & Coslett, 1994; Hoffman, Jones, & Ralph, 2013).

Others have suggested that abstract concepts may be grounded in sensorimotor systems, similar to the way that concrete concepts are grounded (Barsalou, 1999; Lakoff, 1987). These theorists suggest that abstract concepts rely on sensorimotor simulations of experiences that intuitively capture their meaning. However, to date, there are only a small number of studies in the neuroimaging literature that support this account (Barsalou, 1999; Desai, Binder, Conant, Mano, & Seidenberg, 2011).

It has become clear that we need a better understanding of the dimensions along which abstract concepts are organized (Crutch, Troche, Reilly, & Ridgway, 2013). Typically, words are categorized into abstract and concrete categories using imageability ratings. However, it may be valuable for future studies to identify the features associations that compose abstract concepts at a more fine-grained level. For example, recent work has indicated that emotional valence is an important feature dimension to consider when studying abstract concepts (Kousta, Vigliocco, Vinson, Andrews, & Del Campo, 2011), and it has been demonstrated that the emotional information associated with abstract concepts may be embodied near regions of the brain that underlie the perception of emotion (Vigliocco et al., 2013).

### Heteromodal Brain Regions and High-Level Semantic Functions

Carl Wernicke, a well-known neurologist of the nineteenth century, theorized that concepts were composed of ‘memory traces in sensory and motor regions of cortex,’ which is strikingly similar to how sensorimotor accounts would describe

semantic memory a century later. But he also went on to speculate that other neural mechanisms were needed to integrate the distributed features of the memory system. As he put it, there must be some “additional mechanisms, which would explain the process of association” (Gage & Hickok, 2005; Wernicke, 1900). We now turn to this issue of higher-order association in semantic memory and address the key questions: How is distributed semantic knowledge integrated into the representation of a unified concept and how do concepts interact or associate with each other?

Contemporary neuroscience has begun to address this issue mostly through the consideration of heteromodal brain regions. Heteromodal brain regions are located at the convergence of multiple sensory and motor modalities and have reciprocal white matter projections to multiple, modality-specific association regions and other heteromodal cortices (Pandya & Seltzer, 1982; Seltzer & Pandya, 1978; Yeterian & Pandya, 1985). Anatomically, these regions display characteristics that reflect a specialization for high-level multimodal processing: they tend to have larger and more complex dendritic fields (Elston, Benavides-Piccione, & Defelipe, 2001; Jacobs et al., 2001), lower neuron density (Collins, Airey, Young, Leitch, & Kaas, 2010), and lower myelin content (Glasser & Van Essen, 2011) when compared with primary sensory or motor cortices. Heteromodal brain regions are thus well situated to perform an integrative function in higher-level conceptual processing. From a theoretical perspective, it has been proposed that heteromodal regions act as convergence zones where distributed features are integrated into more abstract combinations of knowledge – for example, where information about shape and motion converges in the conceptual representation of a particular type of animal or where information about shape and action converges in the conceptual representation of a particular type of tool (Damasio, 1989).

Indeed, these regions are among the most commonly activated neuroanatomical regions in functional neuroimaging investigations of semantic memory (Binder et al., 2009). These regions include lateral temporal, inferior parietal, and prefrontal cortices (Seltzer & Pandya, 1978; Yeterian & Pandya, 1985), and they are thought to support higher-level conceptual representations, including the binding of conceptual features and the selection of semantic information (Binder & Desai, 2011; Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997). However, there is still much debate over which of these heteromodal regions are critical for representations in semantic memory and exactly what kind of information is represented in each region.

One well-known heteromodal account is the hub-and-spoke model. This account hypothesizes that the anterior temporal lobe is the critical locus for heteromodal semantic representations, functioning as a hub that binds together distributed semantic feature knowledge (the spokes) (Patterson, Nestor, & Rogers, 2007). The key motivation for this account has come from the investigation of patients with semantic dementia, which results from neurodegenerative disease affecting regions of the anterior and inferior temporal lobes. Patients with semantic dementia have a pronounced impairment of semantic memory with a relative sparing of most other cognitive domains (Bonner, Ash, & Grossman, 2010; Grossman, 2010;

Hodges & Patterson, 2007; Mummery et al., 2000). The deficit in semantic dementia is often characterized as amodal in nature because it is claimed that all categories of semantic information are equally affected (Patterson et al., 2007). This is consistent with the hypothesis that the anterior temporal lobe is an amodal semantic hub that contributes to all categories of semantic knowledge. However, some patients with semantic dementia seem to have a deficit that disproportionately affects concrete concepts, discussed before as ‘reversal of the concreteness effect’ (Bonner et al., 2009; Hoffman et al., 2013; Maccoir, 2009). Furthermore, it is unclear whether the semantic representations in the anterior temporal lobe reflect modality-specific or heteromodal processes (Libon et al., in press; Visser, Embleton, Jefferies, Parker, & Ralph, 2010) and exactly which particular portions of the anterior lobe are critical for this heteromodal function (Bonner & Price, 2013).

Others have suggested that semantic representations rely on numerous heteromodal association regions, emphasizing the importance of the lateral temporal and inferior parietal lobes in semantic representation (Binder & Desai, 2011; Bonner, Peelle, Cook, & Grossman, 2013). The angular gyrus, a region of the inferior parietal lobe, is argued to play an important role in semantic representation by integrating the sensory and motor features of concepts into higher-level representations during thought and language, similar to how the anterior temporal lobe is viewed in the hub-and-spoke model. This cortical region has undergone rapid evolutionary expansion in humans relative to monkeys (Hill et al., 2010; Orban, Van Essen, & Vanduffel, 2004; Sherwood, Subiaul, & Zawadzki, 2008). It is also one of the most commonly activated regions in studies of semantic memory (Binder et al., 2009). However, there is no specific patient group with focal lesions affecting the angular gyrus bilaterally, and thus, findings from the patient literature have yet to provide clear converging evidence for this function. Nonetheless, it does appear to be the case that lesions affecting the inferior parietal lobe, where the angular gyrus is located, often result in some degree of lexical-semantic impairment in patients (Ardila, Concha, & Rosselli, 2000; Benson, 1979; Cipolotti, Butterworth, & Denes, 1991; Damasio, 1981; Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004; Grossman et al., 1997, 2003; Kertesz, Sheppard, & Mackenzie, 1982; Rapcsak & Rubens, 1994). Future work will need to address the specific role of heteromodal regions, such as the angular gyrus, as hubs in integrating and representing semantic knowledge.

The prefrontal cortex is another important heteromodal brain region implicated in semantic processing and consistently activated in semantic memory tasks (Binder et al., 2009). The functions of prefrontal cortex are thought to be distinct from the mechanisms that support representations in semantic memory and are often characterized as being domain-general ‘processes’ that act on semantic concepts and other mnemonic and perceptual representations (Jefferies, Baker, Doran, & Ralph, 2007; Thompson-Schill et al., 1997). For example, prefrontal cortex is thought to support a number of high-level executive processes in semantic memory, such as retrieving specific information from semantic memory (Wagner, Pare-Blagoev, Clark, & Poldrack, 2001) and selecting the appropriate representation from a number of semantic alternatives (Thompson-Schill et al., 1997). Others suggest that prefrontal cortex plays an active role in organizing

information represented in semantic memory (Grossman et al., 2013). These investigators argue that in contrast to posterior heteromodal regions where the features of object concepts are integrated into a representation, prefrontal regions mediate executive functions, such as logical and rule-based processes, in semantic memory. For example, there are instances in which a concept is determined by a set of abstract criteria, such as the concept *uncle*, which refers to individuals who fulfill the criterion ‘the brother of a parent.’ It is argued that prefrontal executive mechanisms support such rule-based processes in both the acquisition and representation of concepts (Grossman et al., 2002, 2007; Koenig et al., 2005; Peelle, Troiani, & Grossman, 2009). Although more work is needed to further specify the many functions of prefrontal cortex in semantic memory, this region appears to be critical to the organization, retrieval, and use of semantic representations.

## Summary

Intriguing patient data and advances in functional neuroimaging methods have allowed the field of semantic memory to build upon what philosophers of the eighteenth and nineteenth centuries could only surmise. Over the last 30 years, researchers have provided much evidence that the biological principles of perception and motor control have important implications for theories of semantic memory. Future work will benefit from understanding the degree to which semantic memory relies on an abstraction from sensory and motor experiences and the mechanisms for how this process takes place. Heteromodal regions may be critical to abstraction and flexibility in the semantic system, but there is still much work to be done to fully understand how these regions contribute to higher-level semantic memory functions.

**See also:** INTRODUCTION TO CLINICAL BRAIN MAPPING: Alzheimer’s Disease; Frontotemporal Dementias; Language; Organic Amnesia; Primary Progressive Aphasia; INTRODUCTION TO COGNITIVE NEUROSCIENCE: Category Learning; Familiarity; Imaging Studies of Reading and Reading Disability; Memory Attribution and Cognitive Control; Semantic Processing; The Medial Temporal Lobe and Episodic Memory; INTRODUCTION TO SOCIAL COGNITIVE NEUROSCIENCE: Action Perception and the Decoding of Complex Behavior; Biological Motion; INTRODUCTION TO SYSTEMS: Action Understanding; Cortical Action Representations; Hubs and Pathways; Memory; Naming.

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