CHAPTER

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Semantic Memory

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Abstract

Semantic memory refers to general knowledge about the world, including concepts, facts, and beliefs (e.g., that a lemon is normally yellow and sour or that Paris is in France). How is this kind of knowledge acquired or lost? How is it stored and retrieved? This chapter reviews evidence that conceptual knowledge about concrete objects is acquired through experience with them, thereby grounding knowledge in distributed representations across brain regions that are involved in perceiving or acting on them. Damage to these brain regions compromises semantic knowledge. The authors suggest that such distributed representations result in flexible concepts that can vary depending on the task and context, as well as on individual experience. Further, they discuss the role of brain regions important for selective attention in supporting such conceptual flexibility. Finally, the authors consider the neural bases of other aspects of conceptual knowledge, such as the ability to generalize (e.g., to map lemons and grapes onto the category of fruit), and the ability to represent knowledge that does not have direct sensorimotor correlates (e.g., abstract concepts, such as peace).

Key Words: semantic memory, concepts, categories, representation, knowledge, sensorimotor

Introduction

What Is Semantic Memory?

How do we know what we know about the world? For instance, how do we know that a cup must be concave, or that a lemon is normally yellow and sour? Psychologists and cognitive neuroscientists use the term *semantic memory* to refer to this kind of world knowledge. In his seminal article, "Episodic and Semantic Memory," Endel Tulving borrowed the term *semantic* from linguists to refer to a memory system for "words and other verbal symbols, their meaning and referents, about relations among them, and about rules, formulas, and algorithms for manipulating them"[1] (Tulving, 1972, p. 386).

Today, most psychologists use the term *semantic memory* more broadly—to refer to all kinds of general world knowledge, whether it is about words or concepts, facts or beliefs. What these types of world knowledge have in common is that they are made up of knowledge that is independent of specific experiences; instead, it is general information or knowledge that can be retrieved without reference to the circumstances in which it was originally acquired. For example, the knowledge that lemons are shaped like mini-footballs would be considered part of semantic memory, whereas knowledge about where you were the last time you tasted a lemon would be considered part of *episodic memory*. This division is reflected in a prominent taxonomy of long-term memory (Squire, 1987), in which semantic and episodic memory are characterized as distinct components of the explicit (or *declarative)* memory system for facts (semantic knowledge) and events (episodic knowledge).

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What Is the Relationship Between Semantic Memory and Episodic Memory?

Although semantic memory and episodic memory are typically considered distinct, the degree to which semantic memory is dependent on episodic memory is a matter of ongoing debate. This is because in order to possess a piece of semantic information, there must have been some episode during which that information was learned. Whether this means that all information in semantic memory begins as information in episodic memory (i.e., memory linked to a specific time and place) is an open question. According to Tulving, the answer is no: "If a person possesses some semantic memory information, he obviously must have learned it, either directly or indirectly, at an earlier time, but he need not possess any mnemonic information about the episode of such learning …" (p. 389). In other words, it may be possible for information to be incorporated into our semantic memory in the absence of ever having conscious awareness of the instances in which we were exposed to it. Alternatively, episodic memory may be the "gateway" to semantic memory (see Squire & Zola, 1998, for review)—that is, it may be the route through which semantic memory must be acquired (although eventually this information may exist independently). Most of the evidence brought to bear on this debate has come from studies of patients with selective episodic or semantic memory deficits. We turn to these patients in the following two subsections.

How Is Semantic Memory Acquired?

Children who develop amnesia in early childhood (consequent to bilateral hippocampal damage) are relevant to the question of whether the acquisition of semantic information depends on episodic memory. If semantic knowledge is acquired through episodic memory, then because these children had limited time to acquire semantic knowledge before developing amnesia, they should have limited semantic knowledge. Interestingly, despite their episodic memory impairments, amnesic children's semantic knowledge appears relatively intact (Bindschaedler et al., 2011; Gardiner et al., 2008; Vargha-Khadem et al., 1997). Furthermore, studies on the famous amnesic patient H.M. have revealed that he acquired some semantic knowledge after the surgery that led to his amnesia (for words that came into common use [Gabrieli et al., 1988] and for people who became famous [O'Kane et al., 2004] after his surgery). Thus, the evidence suggests that semantic knowledge can be acquired independently of the episodic memory system. However, semantic knowledge in these amnesic patients is not normal (e.g., it is acquired very slowly and laboriously). It is therefore possible that the acquisition of semantic memory normally depends on the episodic system,[2] but other points of entry can be used (albeit less efficiently) when the episodic system is damaged. Alternatively, these patients may have enough remaining episodic memory to allow the acquisition of semantic knowledge (Squire & Zola, 1998).

Can Semantic Memories Be "Forgotten"?

Everyone occasionally experiences difficulty retrieving episodic memories (what *did* I eat for dinner last night?), but can people lose their knowledge of what things are? Imagine walking through an orchard with a friend: Your friend has no trouble navigating among the trees; then—to your surprise—as you stroll under a lemon tree, she picks up a lemon, holds it up and asks, "What is this thing?"

In an early report, Elizabeth Warrington (1975) described three patients who appeared to have lost this kind of knowledge. The syndrome has subsequently been termed *semantic dementia* (also known as the temporal variant of fronto-temporal dementia), a neurodegenerative disease that causes gradual and selective atrophy of the anterior temporal cortex (predominantly on the left; see Garrard & Hodges, 1999 ; Mesulam et al., 2003; Mummery et al., 1999). Although semantic dementia patients typically speak fluently and without grammatical errors, as the disease progresses, they exhibit severe word-finding difficulties and marked deficits in identifying objects, concepts, and people (Snowden et al., 1989) irrespective of stimulus modality (e.g., pictures or written or spoken words; Bozeat et al., 2000; Hodges et al., 1992; Patterson et al., 2006, 2007; Rogers & Patterson, 2007; Snowden et al., 1994, 2001).

Semantic dementia patients' performance on tests of visuo-spatial reasoning and executive function is less impaired (e.g., Hodges et al., 1999; Rogers et al., 2006). Importantly, they also have relatively preserved episodic memories (e.g., Bozeat et al., 2002a, 2002b, 2004; Funnell, 1995a, 1995b, 2001; Graham et al., 1997, 1999; Snowden et al., 1994, 1996, 1999). Research on semantic dementia thus provides further evidence that the neural structures underlying episodic memory are at least partially independent of those underlying retrieval from semantic memory.

How one conceives of the relationship between semantic and episodic memory is complicated by the fact that (as we discuss in the following section) there are different kinds of semantic knowledge. It may be that for sensorimotor aspects of semantic knowledge (e.g., knowledge about the shape, size, or smell of things), "new information enters semantic memory through our perceptual systems, not through episodic memory" (Tulving, 1991. p. 20), whereas semantic knowledge of information that does not enter directly through our senses (e.g., "encyclopedic knowledge," such as the fact that trees photosynthesize) depends more heavily on contextual information. Moreover, sensorimotor and nonsensorimotor components of semantic knowledge may be stored in different areas of the cortex. Of note, even encyclopedic knowledge is often acquired indirectly; for example, knowing that apple trees photosynthesize allows you to infer that lemon trees also photosynthesize. Semantic knowledge may support the ability to make these kinds of generalizations. In the next section, we introduce some influential hypotheses about what the different components of semantic knowledge might be.

What Are the Different Aspects of Semantic Memory?

Psychologists began to ask questions about how our knowledge about the world is organized following observations of different kinds of impairments in patients with brain injuries. More than 25 years ago, Warrington and McCarthy (1983) described a patient who had more difficulty identifying nonliving than living things. Shortly after, Warrington and Shallice (1984) described four patients exhibiting a different pattern of impairments: more difficulty identifying living than nonliving things. These and other observations of category-specific impairments led to the proposal that semantic memory might be organized in domains of knowledge such as living things (e.g., animals, vegetables, fruits) and nonliving things (e.g., tools, artifacts), which can be selectively impaired after brain injury (Warrington & McCarthy, 1994). Thus, one possible organizational framework for semantic knowledge is *categorical* (also referred to as *domain specific*; e.g., Caramazza & Shelton, 1998).

Early functional neuroimaging studies, however, suggested that semantic memory may be organized along *featural* (also known as *modality*- or *attribute-specific*) lines—either instead of or in addition to domain-specific lines. These studies showed neuroanatomical dissociations between visual and nonvisual object attributes, even within a category (e.g., Thompson-Schill et al., 1999). For example, Martin and colleagues (1995) reported that retrieving the color of an object was associated with activation in ventral temporal cortex bilaterally, whereas retrieving action-related information was associated with activation in middle temporal and frontal cortex.

Further observations from neuropsychological patients have suggested even finer subdivisions within semantic memory (e.g., Buxbaum & Saffran, 2002; Saffran & Schwartz, 1994). In particular, in categorical frameworks, living things can be further divided into distinct subcategories (e.g., fruits and vegetables). Similarly, in featural frameworks, nonvisual features can be subdivided into knowledge about an object's function (e.g., a spoon is used to eat) versus knowledge about how it is manipulated (e.g., a spoon is held with the thumb, index, and middle fingers, at an angle; Buxbaum, Veramonti, & Schwartz, 2000; Kellenbach, Brett, & Patterson, 2003; Sirigu et al., 1991); likewise, visual features can be subdivided into different attributes (e.g., color, size, form, or motion; see Thompson-Schill, 2003, for review).

In the remainder of this chapter, we present a number of different theories cognitive neuroscientists have proposed for the organization of semantic knowledge, and we discuss experimental evidence on how this organization might be reflected in the brain. Although some findings would appear, at first, to be consistent with an organization of semantic memory by categories of information, we will conclude that the bulk of the evidence supports an organization by features or attributes that are distributed across multiple brain regions.

How Is Semantic Memory Organized?

How is knowledge in semantic memory organized? Is it organized like files appear on a computer, with separate folders for different kinds of information (Applications, Documents, Music, Movies, etc.), and subfolders within those folders providing further organization? That is, is semantic knowledge organized hierarchically? Or is it organized more like how information is actually stored in computer (e.g., RAID) memory, wherein data are stored in multiple (frequently redundant) drives or levels to increase access speed and reliability? That is, is semantic knowledge organized in a distributed fashion? In this section we briefly describe four different classes of models that have been put forth to describe the organization of semantic memory.

Traditional Cognitive Perspectives

Classical cognitive psychological theories have described the organization of knowledge in semantic memory in terms of a hierarchy (e.g., a tree is a plant and a plant is a living thing; Collins & Quillian, 1969) that is structured according to abstract relations between concepts (i.e., the propositions, rules, or procedures that determine where a concept fits in the hierarchy) and that may be inaccessible to conscious experience (e.g., Pylyshyn, 1973). Cognitive theorists have also considered whether semantic knowledge may be acquired and stored in multiple formats akin to verbal and visual codes (e.g., Paivio, 1969, 1971, 1978). Historically, these theories have not described brain mechanisms that might support conceptual knowledge, but these sorts of descriptions foreshadow the theories about the organization of semantic memory (category vs. attribute based) that characterize cognitive neuroscience today.

Domain-Specific Category-Based Models

As described above, a number of observations from patients with brain injuries suggest that different object categories (i.e., living and nonliving things) might be differentially influenced by brain damage. One way to instantiate the evident neural dissociation between living and nonliving things is to posit that there are distinct neural regions dedicated to processing different categories of objects. The "domain-specific" category-based model (Caramazza & Shelton, 1998) does just that. According to this model, evolutionary pressure led to the development of adaptations to facilitate recognition of categories that are particularly relevant for survival or reproduction, such as animals, plant life (i.e., fruits and vegetables), conspecifics, and possibly tools; and these adaptations led to objects from these different categories having distinct, non-overlapping neural representations. Such a system would have adaptive value to the extent that having dedicated neural mechanisms for recognizing these objects could make for faster and more accurate classification—and subsequent appropriate response.

Although a fundamental principle of this model is that representations of concepts from these different categories are processed in distinct regions and thus do not overlap, it does not speak to how conceptual knowledge is represented *within* these categories. In fact, an elaboration of this model (Mahon & Caramazza, 2003) is partially distributed and partially *sensorimotor based* in that it suggests that representations may be distributed over different sensory modalities. However, within each modality, the representations of different categories remain distinct.

Sensory-Functional and Sensorimotor-Based Theories

A complication for category-based models is that despite the "category-specific" label, patients' recognition problems do not always adhere to category boundaries—deficits can span category boundaries or affect only part of a category. This suggests a need for an account of semantic memory that does not assume a purely category-specific organization. Sensory-functional theory provides an alternative account. According to this model, conceptual knowledge is divided into anatomically distinct sensory and functional stores, and so-called category-specific deficits emerge because the representations of different kinds tend to rely on sensory and functional information to different extents (Farah & McClelland, 1991; Warrington & McCarthy, 1987). For example, representations of living things depend more on visual information than do artifacts, which depend more on functional information. Consequently, deficits that partially adhere to category boundaries can emerge even without semantic memory being categorically organized per se.

Sensory-functional theory is not without its own problems, however. There exist numerous patients whose deficits cannot be captured by a binary sensory-functional divide (see Caramazza & Shelton, 1998, for a review), which demonstrates that a simple two-way partitioning of semantic attributes is overly simplistic. A related but more fully specified proposal by Alan Allport addresses this concern by pointing out that sensory information should not be considered a unitary entity but rather should be divided into multiple attributes (e.g., color, sound, form, touch). Specifically, Allport (1985) suggests that the sensorimotor systems used to experience the world are also used to represent meaning: "The essential idea is that the *same* neural elements that are involved in coding the sensory attributes of a (possibly unknown) object presented to eye or hand or ear also make up the elements of the auto-associated activity-patterns that represent familiar object-concepts in 'semantic memory'" (1985, p. 53).[3] Hence, according to Allport's model, representations are *sensorimotor based*, and consequently, the divisions of labor that exist in sensorimotor processing should be reflected in conceptual representations. More recently, other sensorimotor-based models have made similar claims (e.g., Barsalou, 1999; Damasio, 1989; Lakoff & Johnson, 1999; in a later section, we discuss empirical studies that address these predictions).

One question that often arises with respect to these sensorimotor-based theories is whether, in addition to sensorimotor representations and the connections between them, it is useful to posit one or more specific brain regions, often called a *hub* or *convergence zone*, where *higher order* similarity—that is, similarity *across* sensory modalities—can be computed (e.g., Damasio, 1989; Simmons & Barsalou, 2003). Such an architecture may facilitate capturing similarity among concepts, thereby promoting generalization and the formation of categories (see Patterson et al., 2007, for a review). We return to these issues in later sections, where we discuss generalization and the representation of knowledge that is abstract in that it has no single direct sensorimotor correlate (e.g., the purpose for which an object is used, such as "to tell time" for a clock).

Correlated Feature-Based Accounts

The final class of models that we discuss is commonly referred to as *correlated feature-based accounts* (Gonnerman et al., 1997; McRae, de Sa, & Seidenberg, 1997; Tyler & Moss 2001). According to these models, the "features" from which concepts are built comprise not only sensorimotor-based features (such as shape, color, action, and taste) but also other (experience-based) attributes that participants produce when asked to list features of objects. For instance, for a tiger, these features might include things such as "has eyes," "breathes," "has legs," and "has stripes," whereas for a fork, they might include "made of metal," "used for spearing," and "has tines."

Importantly, different classes of objects are characterized by different degrees of co-occurrence of particular types of features. For example, for a given living thing, participants tend to list features that are shared with other living things (e.g., "has eyes," "breathes," "has legs"), whereas for artifacts, they tend to list features that are not shared with other artifacts (e.g., "used for spearing," "has tines"). When features tend to co-occur, they can be said to be *correlated*. For example, if something has legs, it is also likely to breathe and to have eyes. Because correlated feature-based models consider that living and nonliving things can be described through component features, they are at least partially compatible with both sensorimotor and domain-specific theories.[4]

According to one influential correlated feature-based model (Tyler & Moss, 2001), highly correlated shared features tend to support knowledge of a category as a whole, whereas distinctive features tend to support accurate identification of individual members. Further, the correlations between features enable them to support each other, making these features robust. Hence, because living things have many shared features, general category knowledge is robust for them. On the other hand, because individual living things tend to have few and uncorrelated distinctive features (e.g., "has stripes" or "has spots"), distinctive information about living things is particularly susceptible to impairment. In contrast, features that distinguish individual artifacts from others tend to be correlated (e.g., "has tines" is correlated with "used for spearing"), making this information robust. While differing in some details, Cree and McRae's (2003) feature-based account similarly posits that objects (living and nonliving) differ with respect to number of shared versus distinctive features and that these factors vary with object category. Hence, correlated feature-based accounts hypothesize that the reason for category-specific deficits is not domain of knowledge per se, but instead is differences in the distribution of features across domains (see also Rogers & Patterson, 2007).

Summary of Models

The main division between domain-specific category-based models, on the one hand, and sensorimotor-based and correlated feature-based accounts, on the other, concerns how category knowledge is represented. For domain-specific models, object category is a primary organizing principle of semantic memory, whereas for the other accounts, category differences emerge from other organizational properties. In many ways, correlated feature-based accounts echo sensorimotor-based theories. In particular, these two classes of models are parallel in that categories *emerge* through co-occurrence of features, with the relevance of different features depending on the particular object, and with different parts of a representation supporting one another. The major distinguishing aspect is that sensorimotor-based theories focus on sensorimotor features—specifying that the same brain regions that encode a feature represent it. In contrast, because none of the fundamental principles of correlated feature-based accounts require that features be sensorimotor based (in fact, a concern for these models is how features should be defined), these accounts do not require that features be situated in brain regions that are tied to sensory or motor processing.

Incorporating a convergence zone type of architecture into a sensorimotor-based model may help integrate all three classes of models. Convergence zone theories posit dedicated regions for integrating across sensorimotor-based features, extracting statistical regularities across concepts, and ultimately producing a level of representation with a category-like topography in the brain (Simmons & Barsalou, 2003).

What Are the Neural Systems that Support Semantic Memory, and How Do We Retrieve Semantic Information from These Systems?

Are Different Categories Supported by Different Brain Regions?

Functional neuroimaging techniques like positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have allowed cognitive neuroscientists to explore different hypotheses regarding the neural organization of semantic memory in undamaged brains. By means of these methodologies, researchers observe regional brain activity while participants perform cognitive tasks such as naming objects, deciding whether two stimuli belong in the same object category, or matching pictures of stimuli to their written or spoken names.

Early work attempted to examine whether specific brain regions are selectively active for knowledge of different object categories (e.g., animals or tools). These studies found that thinking about animals tends to produce increased neural activity in inferior posterior areas, including inferior temporal (Okada et al., 2000; Perani et al., 1995) and occipital regions (Grossman et al., 2002; Martin et al., 1996; Okada et al., 2000; Perani et al., 1995), whereas thinking about tools tends to activate more dorsal and frontal areas, including left dorsal (Perani et al., 1995) or inferior (Grossman et al., 2002; Okada et al., 2000) prefrontal regions, as well as left premotor (Martin et al., 1996), inferior parietal (Okada et al., 2000), and posterior middle temporal areas (Grossman et al., 2002; Martin et al., 1996; Okada et al., 2000). Further, *within* the inferior temporal lobe, the lateral fusiform gyrus generally shows increased neural activity in response to animals, while the medial fusiform tends to respond more to tools (see Martin, 2007, for a review).

Although these findings might seem at first glance to provide unambiguous support for a domain-specific, category-based organization of semantic memory, the data have not always been interpreted as such. Sensory-functional theories can also account for putatively category-specific activations because they posit that different regions of neural activity for animals and tools reflect a tendency for differential weighting of visual and functional features for objects within a given category, rather than an explicit category-based organization (e.g., Warrington & McCarthy, 1987).

The hypothesis that a feature's weight can vary across objects raises the possibility that even for a given object, a feature's weight may vary depending on its relevance to a given context. In other words, the extent to which a particular feature becomes active for a given object may be contextually dependent not only on long-term, object-related factors (i.e., is this feature relevant in general for the identification of this object?) but also on short-term, task-related factors (i.e., is this feature relevant for the current task?). The following sections describe evidence suggesting that both the format of the stimulus with which semantic memory is probed (i.e., words vs. pictures) and the demands of the task influence which aspects of a given concept's semantic representation are activated.

Does the Format of the Stimulus Influence Semantic Memory Retrieval?

Studies of neuropsychological patients have suggested dissociations in performance between semantic knowledge tasks that use pictorial or verbal stimuli. For example, patients with optic aphasia are unable to identify objects presented visually, whereas their performance with lexical/verbal stimuli remains unimpaired (e.g., Hillis & Caramazza, 1995; Riddoch & Humphreys, 1987). On the other hand, Saffran and colleagues (2003a) described a patient whose object recognition performance was enhanced when prompted with pictures but not with words. This neuropsychological evidence suggests that pictures and words may have differential access to different components of semantic knowledge (Chainay & Humphreys, 2002; Rumiati & Humphreys, 1998; Saffran et al., 2003b). That is, damage to a component accessed by one stimulus type (e.g., words) can spare components accessed by a different stimulus type (e.g., pictures).

Consistent with the neuropsychological observations, studies of healthy participants have found that although the patterns of brain activation produced when accessing the same concept from pictures and words can overlap significantly, there are also differences (e.g., Gates & Yoon, 2005; Vandenberghe et al., 1996; see also Sevostianov et al., 2002). Bright, Moss, and Tyler (2004; see also Wright et al., 2008) performed a meta-analysis of four PET studies involving semantic categorization and lexical decision tasks with verbal and pictorial stimuli. They found evidence for a common semantic system for pictures and words in the left inferior frontal gyrus and left temporal lobe (anterior and medial fusiform, parahippocampal, and perirhinal cortices) and evidence for modality-specific activations for words in both temporal poles and for pictures in both occipito-temporal cortices. Overall, evidence from studies examining access to semantic knowledge from pictures versus words suggests that concepts are distributed patterns of brain activation that can be differentially tapped by stimuli in different formats.

Does the Type of Task Influence Semantic Memory Retrieval?

Retrieval from semantic memory can be influenced not only by the format of the stimuli used to elicit that information (as described above) but also by specifics of the task, such as the information that the participant is asked to produce and the amount of time provided to respond. For example, in an elegant PET experiment, Mummery and colleagues (1998) showed participants the names of living things or artifacts and asked them to make judgments about either a perceptual attribute (color) or a nonperceptual attribute (typical location). Different attribute judgments elicited distinct patterns of activation (increased activation in the left temporal-parietal-occipital junction for location and increased activation in the left anterior middle temporal cortex for color). Moreover, differences between attributes were larger than differences between category (i.e., living things vs. artifacts), suggesting that the most prominent divisions in semantic memory may be associated with attributes rather than categories—a structure consistent with distributed, feature-based models of semantic memory (see also Moore & Price, 1999).

The amount of time provided to respond also appears to affect which aspects of a concept become active. In an early semantic priming study, Schreuder and colleagues (1984) observed that priming for perceptual information (e.g., between the concepts *apple* and *ball*, which are similar in shape) emerges when task demands encourage a rapid response, whereas priming for more abstract information (e.g., between *apple* and *banana*, which are from the same category) emerges only when responses are slower (see Yee et al., 2011, for converging evidence). More recently, Rogers and Patterson (2007) provided additional evidence that speed of response influences which semantic features are available: When participants were under time pressure, responses were more accurate for categorization judgments that did not require specific information, such as between categories (e.g., distinguishing birds from vehicles), and less accurate for categorization that did require access to specific information, such as within a category (e.g., distinguishing between particular kinds of birds). When participants were allowed more time to respond, the pattern reversed. Thus, the results of these studies suggest that the specifics of the task influence which aspects of a representation become measurably active.

In sum, retrieval from semantic memory can be influenced not only by the format of the stimuli used to elicit the information (e.g., words vs. pictures) but also by the timing of the task and the information that the participant is asked to provide.

Is Retrieval Influenced by Interactions Between Category and Task?

The format- and task-related effects reviewed earlier suggest that the most prominent division in semantic memory might be in terms of attribute domains and not, necessarily, category domains, thus offering support for distributed, feature-based models of semantic memory. Clearly, though, differences in format or task cannot account for the fact that differences between categories can be observed even with the same format and task. However, the presence of both format and task effects in semantic knowledge retrieval raises the possibility that *interactions* between stimulus modality and task type can elicit category effects that these factors do not produce independently. In this section we explore how the organization of semantic memory might accommodate stimulus, task, and category effects.

For instance, the particular combinations of sensorimotor attributes retrieved from semantic memory might be determined by an interaction between task-type and sensorimotor experience (Thompson-Schill et al., 1999). For example, for living things, retrieval of both visual and nonvisual information should require activation of visual attributes because semantic memory about living things depends largely on knowledge about their visual features. To illustrate, people's experience with zebras is largely visual; hence, retrieval of even nonvisual information about them (e.g., *Do zebras live in Africa*?) will engage visual attributes because one's knowledge about zebras is built around their visual features (assuming that retrieving more weakly represented attributes depends on the activation of more strongly represented attributes; see Farah & McClelland, 1991). In contrast, for nonliving things, only retrieval of visual information should require activation of visual attributes. For instance, because people's experience with microwave ovens is distributed across a wide range of properties (e.g., visual, auditory, tactile), retrieval of nonvisual information about them (e.g., *Do microwave ovens require more electricity than refrigerators?*) will not necessarily engage visual attributes.

Thompson-Schill and colleagues (1999) found evidence for just such a dissociation: The left fusiform gyrus (a region linked to visual knowledge) was activated by living things regardless of whether participants made judgments about their visual or nonvisual properties. In contrast, for nonliving things, the same visual region was active only when participants were asked to make judgments about visual properties. The complementary pattern has also been observed: A region linked to action information (the left posterior middle temporal cortex) was activated by tools for both action and nonaction tasks, but was activated by fruit only during an action task (Phillips et al., 2002). These and related findings (Hoenig et al., 2008) suggest that category-specific activations may reflect differences in which attributes are important for our knowledge of different object categories (but see Caramazza, 2000, for an alternative perspective).

Related work has demonstrated that ostensibly category-specific patterns can be eliminated by changing the task. Both patients with herpes simplex virus encephalitis and unimpaired participants exhibit apparently category-specific patterns when classifying objects at the "basic" level (i.e., at the level of *dog* or *car*) as revealed by errors or by functional activity in ventral temporal cortex, respectively. However, these differences can be made to disappear when objects are classified more specifically (e.g., *Labrador* or *BMW*, instead of *dog* or *car*; Lambon Ralph et al., 2007; Rogers et al., 2005). Why might level of classification matter? One possibility relates to correlated feature-based models (discussed earlier): Differences in the structure of the stimuli that are correlated with category may interact with the task (e.g., Humphreys et al., 1988; Price et al., 2003; Tarr & Gautier, 2000; see also Cree & McRae, 2003). For instance, at the basic level, animals typically share more features (e.g., consider *dog* vs. *goat*), than do vehicles (e.g., *car* vs. *boat*). This greater similarity for animals may produce a kind of "crowding" that makes them particularly difficult to differentiate at the basic level (e.g., Rogers et al., 2005; Noppeney et al., 2007; Tyler & Moss, 2001; but cf. Wiggett et al., 2009, who find that interactions between category and task do not always modulate category effects).

Hence, the studies described in this section provide further evidence that apparently category-specific patterns may be due to interactions between stimuli and task. More broadly, numerous studies have explored whether semantic memory is organized in the brain by object category, by perceptual or functional features, or by a multimodal distributed network of attributes. Thus far, the findings are compatible with correlated feature and sensorimotor-based accounts and appear to suggest a highly interactive distributed semantic system that is engaged differently depending on object category and task demands (for a review, see Thompson-Schill, 2003).

Do the Same Neural Regions Underlie Perceptual and Conceptual Processing of Objects?

The preceding evidence largely supports one main tenet of sensorimotor, feature-based accounts—that semantic memory is distributed across different brain regions. However, an additional claim of sensorimotor theory is that the brain regions that are involved when perceiving and interacting with an object also encode its meaning. To address this claim, research has attempted to explore the extent to which the different sensorimotor properties of an object (e.g., its color, action, or sound) activate the same neural systems as actually perceiving these properties.

With respect to color, for example, Martin and colleagues (1995) measured changes in regional cerebral blood flow using PET when participants generated the color or the action associated with pictures of objects or their written names. Generating color words led to activation in the ventral temporal lobe in an area anterior to that implicated in color perception, whereas generating action words was associated with activation in the middle temporal gyrus just anterior to a region identified in the perception of motion. Martin and colleagues interpreted these results as indicative of a distributed semantic memory network organized according to one's sensorimotor experience of different object attributes (see also Ishai et al., 2000; Wise et al., 1991). More recent studies have reported some direct overlap[5] between regions involved in color perception and those involved in retrieval of color knowledge about objects (Hsu et al., 2011; Simmons et al., 2007).

With respect to action, analogous findings have been reported regarding overlap between perceptual-motor and conceptual processing. Chao and Martin (2000; see also Chao, Haxby, & Martin, 1999; Gerlach et al., 2000) showed that the left ventral premotor and left posterior parietal cortices (two areas involved in planning and performing actions) are selectively active when participants passively view or name pictures of manipulable tools. The involvement of these regions despite the absence of a task requiring the retrieval of action information (i.e., even during passive viewing) can be explained if the representations of manipulable objects include areas involved in planning and performing actions. In a recent study (Yee, Drucker, & Thompson-Schill, 2010) we obtained additional evidence supporting this hypothesis: In left premotor cortex and inferior parietal sulcus, the neural similarity of a pair of objects (as measured by fMRI-adaptation; see later) is correlated with the degree of similarity in the actions used to interact with them. For example, a piano and a typewriter, which we interact with using similar hand motions, have similar representations in action regions, just as they should if representations are sensorimotor based. Moreover, reading action words (e.g., *lick, pick, kick*) produces differential activity in or near motor regions activated by actual movement of the tongue, fingers, and feet, respectively (Hauk et al., 2004). Interestingly, it appears that this motor region activation can be modulated by task: Reading an action verb related to leg movement (e.g., *kick*) activates motor regions in literal (*kick the ball*) but not figurative (*kick the bucket*) sentences (Raposo et al., 2009).

Although visual and motor features have been studied most often, other modalities also supply evidence for overlap between conceptual and perceptual processing. Regions involved in auditory perception and processing (posterior and superior middle temporal gyri) are active when reading the names of objects that are strongly associated with sounds (e.g., *telephone*; Kiefer et al., 2008; see also Goldberg et al., 2006; Kellenbach et al., 2001; Noppeney & Price, 2002). Similarly, an orbitofrontal region associated with taste and smell is activated when making decisions about objects' flavor (Goldberg et al., 2006), and simply reading words with strongly associated smells (e.g., *cinnamon*) activates primary olfactory areas (Gonzalez et al., 2006).

Patients with brain damage affecting areas involved in sensorimotor processing are also relevant to the question of whether regions underlying perception and action also underlie conceptual knowledge. A sensorimotor-based account would predict that damage to an auditory, visual, or motor area (for example), should affect the ability to retrieve auditory, visual, or motor information about an object, whereas access to features corresponding to undamaged brain regions would be less affected. There is evidence that this is indeed the case. For instance, patients with damage to left auditory association cortex have problems accessing concepts for which sound is highly relevant (e.g., *thunder* or *telephone*; Bonner & Grossman, 2012; Trumpp et al., 2013). Likewise, a patient with damage to areas involved in visual processing (right inferior occipito-temporal junction) had more difficulty naming pictures of objects whose representations presumably rely on visual information (e.g., living things that are not ordinarily manipulated) than objects whose representations are presumably less reliant on visual information (e.g., living or nonliving things that are generally manipulated); the patient's encyclopedic and auditory knowledge about both types of objects, in contrast, was relatively preserved (Wolk et al., 2005).

Similarly, apraxic patients, who have difficulty performing object-related actions—and who typically have damage to the premotor or parietal areas subserving these actions—show abnormally delayed access to manipulation information about objects (Myung et al., 2010). Studies with normal participants using transcranial magnetic stimulation (TMS), which produces a temporary and reversible "lesion" likewise suggest that motor areas are involved in processing motor-related concepts (e.g., Pobric et al., 2010; see Hauk et al., 2008, for review), as do studies requiring normal participants to perform an explicit motor task designed to interfere with activating object-appropriate motor programs (e.g., Witt et al., 2010; Yee et al., 2013). Finally, Gainotti (2000) conducted a comprehensive review of category-specific deficits, focusing on relationships between location of brain damage and patterns of impairment. These relationships, Gainotti observed, suggest that the categorical nature of the deficits is produced by correlations between (damaged) brain regions and sensorimotor information that is central to various categories.

Overall, findings from neuroimaging, neuropsychological, and TMS studies converge to suggest that semantic knowledge about objects is built around their sensorimotor attributes and that these attributes are stored in sensorimotor brain regions.

Which Neural Regions Underlie the Generalization of Semantic Knowledge?

A critical function of semantic memory is the ability to generalize (or abstract) over our experiences with a given object. Such generalization permits us to derive a representation that will allow us to recognize new exemplars of it and make predictions about aspects of these exemplars that we have not directly perceived. For example, during analogical thinking, generalization is critical to uncover relationships between a familiar situation and a new situation that may not be well understood (e.g., that an electron is to the nucleus like a planet is to the sun). Thus, analogical thinking involves not only retrieving information about the two situations but also a *mapping* between their surface elements based on shared abstract relationships (see Chrysikou & Thompson-Schill, 2010). Similarly, knowing that dogs and cats are both animals (i.e., mapping them from their *basic* to their *superordinate* level categories) may facilitate generalization from one to the other. A full treatment of the process of generalization would be beyond the scope of this chapter. However, we briefly touch on some of the things that cognitive neuroscience has revealed about the generalization process.

Several findings are consistent with the idea that different brain regions support different levels of representation. For instance, an anterior temporal region (the perirhinal cortex, particularly in the left) was activated when naming pictures at the basic level (e.g., *dog* or *hammer*), but not at the superordinate level (e.g., *living* or *manmade*), whereas a posterior temporal region (fusiform gyrus bilaterally) was activated for both levels (Tyler et al., 2004, but cf. Rogers et al., 2006). In addition, greater anterior temporal lobe activity has been observed during word–picture matching at a specific level (e.g., *robin? kingfisher*?) than at a more general level (e.g., *animal? vehicle?*; Rogers et al., 2006). Further, processing may differ for different levels of representation: Recordings of neural activity (via magnetoencephalography) suggest that during basic level naming, there are more recurrent interactions between left anterior and left fusiform regions than during superordinate level naming (Clark et al., 2011).

One interpretation of these findings is that there exists a hierarchically structured system along a posterior-anterior axis in the temporal cortex—with posterior regions more involved in coarse processing (such as the presemantic, perceptual processing required for superordinate category discrimination) and anterior regions more involved in the integration of information across modalities that facilitates basic-level discrimination (e.g., *cat* vs. *dog*; see Martin & Chao, 2001). More broadly, these and related findings (e.g., Chan et al., 2011; Grabowski et al., 2001; Kable et al., 2005) are consistent with the idea that semantic knowledge is represented at different levels of abstraction in different regions (see also Hart & Kraut, 2007, for a mechanism by which different types of knowledge could be integrated).

If true, this may be relevant to a puzzle that has emerged in neuroimaging tests of Allport's (1985) sensorimotor model of semantic memory. There is a consistent trend for retrieval of a given physical attribute to be associated with activation of cortical areas 2 to 3 cm anterior to regions associated with perception of that attribute (Thompson-Schill, 2003). This pattern, which has been interpreted as coactivation of the "same areas" involved in sensorimotor processing, as Allport hypothesized, could alternately be used as grounds to reject the Allport model. What does this anterior shift reflect?

We believe the answer may lie in ideas developed by Rogers and colleagues (2004). They have articulated a model of semantic memory that includes units that integrate information across all of the attribute domains (including verbal descriptions and object names; McClelland & Rogers, 2003). As a consequence, "abstract semantic representations emerge as a product of statistical learning mechanisms in a region of cortex suited to performing cross-modal mappings by virtue of its many interconnections with different perceptual-motor areas" (Rogers et al., 2004, p. 206). The process of abstracting away from modality-specific representations may occur gradually across a number of cortical regions (perhaps converging on the temporal pole). As a result, a gradient of abstraction may emerge in the representations throughout a given region of cortex (e.g., the ventral extrastriate visual pathway), and the anterior shift may reflect activation of a more abstract representation (Kosslyn & Thompson, 2000). In other words, the conceptual similarity space in more anterior regions may depart a bit from the similarity space in the environment, moving in the direction of abstract relations.

A gradient like this could also help solve another puzzle: If concepts are sensorimotor based, one might worry that thinking of a concept would cause one to hallucinate it or execute it (e.g., thinking of *lemon* would cause one to hallucinate a lemon, and thinking of *kicking* would produce a kick). But if concepts are represented (at least in part) at a more abstract level than that which underlies direct sensory perception and action, then the regions that underlie, for example, action execution, need not become sufficiently active to produce action. More work is needed to uncover the nature of the representations—and how the similarity space may gradually change across different cortical regions.

Summary of the Neural Systems Supporting Semantic Memory

In this section we have briefly summarized a large body of data on the neural systems supporting semantic memory (see Noppeney, 2009, for a more complete review of functional neuroimaging evidence for sensorimotor-based models). We suggested that in light of the highly consistent finding that sensorimotor regions are active during concept retrieval, the data largely support sensorimotor-based models of semantic memory. However, there is a question that is frequently raised about activation in sensorimotor regions during semantic knowledge retrieval: Could it be that the activation of sensorimotor regions that has been observed in so many studies is "epiphenomenal"[6] rather than indicating that aspects of semantic knowledge are encoded in these regions? (See Mahon & Caramazza, 2008, for discussion.) For example, perhaps activation in visual areas during semantic processing is a consequence of generating visual images, and not of semantic knowledge per se. The patient, TMS, and behavioral interference work described above help to address this question: It is not clear how an epiphenomenal account would explain the fact that lesioning or interfering with a sensorimotor brain region affects the ability to retrieve the corresponding attribute of a concept. These data therefore suggest that semantic knowledge is at least partially encoded in sensorimotor regions.

However, the task effects described above raise another potential concern. Traditionally, in the study of semantic representations (and, in fact, in cognitive psychology more broadly) it is assumed that only effects that can be demonstrated across a variety of contexts should be considered informative with regard to the structure and organization of semantic memory. If one holds this tenet, then these task effects are problematic. Yet, as highlighted by the work described in this section, task differences can be accommodated if one considers an important consequence of postulating that the representations of concepts are distributed (recall that all but traditional approaches allow for a distributed architecture): Distributed models allow attention to be independently focused on specific (e.g., contextually relevant) properties of a representation through partial activation of the representation (see Humphreys & Forde, 2001, for a description of one such model). This means that if a task requiring retrieval of action information, for example, produces activation in premotor and parietal regions, but a task requiring retrieval of color does not, the discrepancy may reflect differential focus of attention within an object concept rather than that either attribute is not part of the object concept.

Thus, the differences between effects that emerge in different contexts lead to important questions, such as how we are able to flexibly focus attention on relevant attributes. We turn to this in the next section.

Biasing Semantic Representations

If our semantic knowledge is organized in a multimodal, highly interactive, distributed system, how is it that we are able to weight certain attributes more heavily than others depending on the circumstance—so that we can, for example, retrieve just the right combinations of features to identify or answer questions about concepts like a horse, a screwdriver, or an airplane? In other words, how does our brain choose, for a given object and given the demands of the task at hand, the appropriate pattern of activation? A number of studies have suggested that the prefrontal cortex, particularly the left ventrolateral regions, produces a modulatory signal that biases the neural response toward certain patterns of features (e.g., Frith, 2000; Mechelli et al., 2004; Miller & Cohen, 2001; Noppeney et al., 2006). For example, when, during semantic knowledge retrieval, competition among different properties is high, a region in the left inferior frontal gyrus is activated (Thompson-Schill et al., 1997; see also Kan & Thompson-Schill, 2004; Thompson-Schill et al., 1998; Thompson-Schill, D'Esposito, et al., 1999).

Several mechanisms have been proposed regarding this region's role in selective activation of conceptual information, among them that prefrontal cortical activity during semantic tasks reflects the maintenance of different attributes in semantic memory (e.g., Gabrieli et al., 1998) or that this region performs a "controlled retrieval" of semantic information (e.g., Badre & Wagner, 2007). We and others have suggested that this region, although critical in semantic memory retrieval, performs a domain-general function as a dynamic filtering mechanism that biases neural responses toward task-relevant information while gating task-irrelevant information (Shimamura, 2000; Thompson-Schill, 2003; Thompson-Schill et al., 2005). In other words, when a context or task requires us to focus on specific aspects of our semantic memory, the left ventrolateral prefrontal cortex biases which aspects of our distributed knowledge system will be most active.

Individual Differences in Access to and in the Organization of Semantic Memory

Earlier, we discussed two types of evidence that support sensorimotor models of semantic memory: (1) sensorimotor regions are active during concept retrieval, and (2) damage to a sensorimotor region affects the ability to retrieve the corresponding attribute of an object. However, we have not yet addressed an additional claim of sensorimotor-based theories: If it is true that the sensorimotor regions that are active when an object is perceived are the same regions that represent its meaning, then an individual's experience with that object should shape the way it is represented. In other words, the studies that we have described so far have explored the way that concepts are represented in the "average" brain, and the extent to which the findings have been consistent presumably reflects the commonalities in human experience. Yet studying the average brain does not allow us to explore whether, as predicted by sensorimotor-based theories, differences in individuals' experiences result in differences in their representation of concepts. In this section we describe some ways in which individual differences influence the organization of semantic memory.

Are There Individual Differences in Semantic Representations?

Semantic representations appear to vary as a consequence of lifelong individual differences in sensorimotor experience: For instance, recruitment of left parietal cortex (a region involved in object-related action) during the retrieval of object shapes was modulated by the amount of lifetime tactile experience associated with the objects (Oliver et al., 2009). Similarly, right- and left-handed people, who use their hands differently to perform various actions with manipulable objects, employ homologous but contralateral brain regions to represent those objects: When participants named tools, handedness influenced the lateralization of premotor activity (Kan et al., 2006). Critically, handedness was not a predictor of premotor lateralization for objects that are not acted on manually (animals). In related work, while reading action verbs (e.g., *write, throw*) right-handed participants activated primarily left premotor cortex regions, whereas left-handed participants activated primarily right premotor cortex regions (Willems et al., 2010). No such difference was observed for nonmanual action verbs (e.g., *kneel, giggle*). Analogous findings have been observed for long-term experience with sports: When reading sentences describing ice hockey (but not when reading about everyday experiences), professional ice hockey players activated premotor regions more than nonplayers did (Beilock et al., 2008). Further, such differences are not limited to motor experience: When professional musicians identified pictures of musical instruments (but not control objects), they activated auditory association cortex and adjacent areas more than nonmusicians did (Hoenig et al., 2011).

Even with much less than a lifetime of experience, the neural representation of an object can reflect specific experience with it. Oliver and colleagues (2008) asked one set of participants to learn (by demonstration) actions for a set of novel objects, perform those actions, and also view the objects, whereas a second set of participants viewed the same objects without learning actions but had the same total amount of exposure to them. In a subsequent fMRI session in which participants made judgments about visual properties of the objects, activity in parietal cortex was found to be modulated by the amount of tactile and action experience a participant had with a given object. These and related findings (Kiefer et al., 2007; Weisberg et al., 2007) demonstrate a causal link between experience with an object and its neural representation, and also show that even relatively short-term differences in sensorimotor experience can influence an object's representation.

Intriguingly, changes in individual experience may also lead to changes in the representation of *abstract* concepts. Right-handers' tendency to associate "good" with "right" and "bad" with "left" (Casasanto, 2009) can be reversed when right hand dominance is compromised because of stroke or a temporary laboratory-induced handicap (Casasanto & Chrysikou, 2011).

What Happens When a Sensory Modality Is Missing?

As would be expected given the differences observed for handedness and relatively short-term experience, more dramatic differences in individual experience have also been shown to affect the organization of semantic knowledge. For instance, color influences implicit similarity judgments for sighted but not for blind participants (even when blind participants have good explicit color knowledge of the items tested; Connolly et al., 2007). Interestingly, this difference held only for fruits and vegetables, and not for household items, consistent with a large literature demonstrating that the importance of color for an object concept varies according to how useful it is for recognizing the object (see Tanaka & Presnell, 1999, for review).

However, differences in sensory experience do not always produce obvious differences in the organization of semantic knowledge. For instance, when making judgments about hand action, blind, like sighted, participants selectively activate left posterior middle temporal areas that in sighted people have been associated with processing visual motion (Noppeney et al., 2003). Furthermore, blind participants demonstrate category-specific (nonliving vs. animal, in this case) activation in the same visual areas as sighted participants (ventral temporal and ventral occipital regions; Mahon et al., 2009). Because sensorimotor-based theories posit that visual experience accounts for the activation in visual areas, the findings in these two studies may appear to be inconsistent with sensorimotor-based theories and instead suggest an innate specification of action representation or of living/nonliving category differences. However, given the substantial evidence that cortical reorganization occurs if visual input is absent (for a review, see Amedi, Merabet, Bermpohl, & Pascual-Leone, 2005), another possibility is that in blind participants these "visual" regions are sensitive to nonvisual factors (e.g., shape information that is acquired tactilely) that correlate with hand action and with the living/nonliving distinction.

Summary of Individual Differences in Semantic Memory

At first glance, the individual differences that we have described in this section may seem surprising. If our concept of a lemon, for example, is determined by experience, then no two individuals' concepts of a lemon will be exactly the same. Further, your own concept of a lemon is likely to change subtly over time, probably without conscious awareness. Yet the data described above suggest that this is, in fact, what happens. Because sensorimotor-based models assume that our representations of concepts are based on our experiences with them, these models can easily account for, and in fact predict, these differences and changes. It is a challenge for future research to explore whether there are factors that influence the extent to which we attend to different types of information, and that constrain the degree to which representations change over time.

Abstract Knowledge

Our discussion of the organization of semantic memory has thus far focused primarily on the physical properties of concrete objects. Clearly, though, a complete theory of semantic memory must also provide an account for how we represent abstract concepts (e.g., *peace*) as well as abstract features of concrete objects (e.g., "used to tell time" is a property of a clock). According to the "concreteness effect," concrete words are processed more easily than abstract words (e.g., Paivio, 1991) because their representations include sensory information that abstract words lack. However, there have been reports of semantic dementia patients who have more difficulty with concrete than abstract words (Bonner et al., 2009; Breedin et al., 1994; but cf. Hoffman & Lambon-Ralph, 2011, and Jefferies et al., 2009, for evidence that the opposite pattern is more common in semantic dementia), suggesting that there must be more to the difference between these word types than quantity of information. Additional evidence for a qualitative difference between the representations of concrete and abstract words comes from work by Crutch and Warrington (2005). They reported a patient AZ, with left temporal, parietal, and posterior frontal damage, who, for concrete words, exhibits more interference from words closely related in meaning (e.g., synonyms) than for "associated" words (i.e., words that share minimal meaning but often occur in similar contexts), whereas for abstract words, she displays the opposite pattern.

Neuroimaging studies that have compared abstract and concrete words have identified an inconsistent array of regions associated with abstract concepts: the left superior temporal gyrus (Wise et al., 2000), right anterior temporal pole, or left posterior middle temporal gyrus (Grossman et al., 2002). These inconsistencies may be due to the differing demands of the tasks employed in these studies or to differences in how "abstract" is operationalized. The operational definition of abstract may be particularly important because it varies widely across studies—ranging from words without sensorimotor associations to words that have low imageability (i.e., words that are difficult to visualize) to emotion words (e.g., *love*). We surmise that these differences likely have a particularly significant influence on where brain activation is observed.

Using abstract stimuli intended to have minimal sensorimotor associations, Noppeney and Price (2004) compared fMRI activation while subjects made judgments about words (comprising nouns, verbs, and adjectives) referring to visual, auditory, manual action, and abstract concepts. Relative to the other conditions, abstract words activated the left inferior frontal gyrus, middle temporal gyrus, superior temporal sulcus, and anterior temporal pole. Because these are classical "language" areas, the authors suggest that the activations are a consequence of the representations of abstract words being more reliant on contextual information provided by language. Recently, Rodriguez and colleagues (2011) observed activation in these same regions for abstract verbs. They also observed that a greater number of regions were active for abstract relative to concrete verbs—leading them to hypothesize that because abstract words appear in more diverse contexts (Hoffman et al., 2011), the networks supporting them are more broadly distributed.

Like abstract words, abstract features (e.g., "used to tell time") have no direct sensorimotor correlates. Our ability to conceive of abstract concepts and features—i.e., knowledge that cannot be directly perceived from any individual sensory modality—demonstrates that there must be more to semantic knowledge than simple sensorimotor echoes. How might abstract concepts or features be represented in the kind of distributed architecture that we have described? Rogers and colleagues' model of semantic memory (introduced above in the context of generalization) may be of service here as well. They argue that the interaction between content-bearing perceptual representations and verbal labels produces a similarity space that is not captured in any single attribute domain, but rather reflects abstract similarity (cf. Caramazza, Hillis, Rapp, & Romani, 1990; Chatterjee, 2010; Damasio, 1989; Plaut, 2002; Tyler, Moss, Durrant-Peatfield, & Levy, 2000).

Based on the abundant interconnections between the temporal pole and different sensorimotor areas, and on the fact that temporal pole degeneration is associated with semantic dementia (introduced in earlier), Rogers and colleagues suggest that this region may support abstract knowledge and generalization. Semantic dementia, in particular, has had a large influence on ideas about the anterior temporal lobes' role in semantic memory. In this disorder, relatively focal degeneration in the anterior temporal lobes accompanies semantic memory deficits (e.g., problems naming, recognizing, and classifying objects, regardless of category), whereas other cognitive functions are relatively spared (see Hodges & Patterson, 2007, for a review). The concomitance of the anatomical and cognitive impairments in semantic dementia therefore lends credence to the idea that the anterior temporal lobes are important for supporting semantic memory (see Patterson et al., 2007, for a review). Additional research is needed to explore whether brain regions beyond the anterior temporal lobe serve similar "converging" functions.

Methodological Advances

The studies reviewed in this chapter employed behavioral, neuropsychological, and neuroimaging techniques to explore the organization and function of semantic memory. A number of methodologies that have recently been introduced in cognitive neuroscience hold much promise for the study of semantic memory.

First, new approaches in experimental design and data analysis for neuroimaging-based studies allow cognitive neuroscientists to address more fine-grained questions about the neural representation of concepts. For example, questions relating to representational similarity can be explored with fMRI adaptation (e.g., Grill-Spector & Malach, 2001). This technique relies on the assumption that when stimuli that are representationally similar are presented sequentially, the repeated activation of the same set of neurons will produce a reduced fMRI response. If the stimuli are representationally distinct, no such adapted response should be observed. This method can be applied to address a number of questions pertaining, for instance, to relationships between regions implicated in the processing of different object attributes (e.g., color, shape, and size; see Yee et al., 2010, for function and manipulation), or to the degree to which the *same neurons* are involved in perception and in conceptual representation. Similarly, multivoxel pattern analysis (e.g., Mitchell et al., 2008; Norman et al., 2006; Weber et al., 2009) and functional connectivity approaches allow for analyses that exploit the distributed nature of brain activation, rather than focusing on focal activation peaks (see Rissman & Wagner, 2012).

Second, noninvasive brain stimulation techniques, specifically TMS and transcranial direct current stimulation (tDCS), allow researchers to temporarily "lesion" a given brain region and observe the effects on behavior (e.g., Antal et al., 2001, 2008; Walsh & Pascual-Leone, 2003). In contrast to studying patients in the months and years after brain injuries that produce permanent lesions, using these "virtual lesions" allows cognitive neuroscientists to examine the role of a given brain region without the possibility that reorganization of neural function has occurred.

Third, cognitive neuroscience has benefited from advances in eye-tracking research, in which eye movements to objects are monitored as participants listen to spoken language (Cooper 1974; Tanenhaus et al., 1995). Hearing a word (e.g., *piano*) produces eye movements toward pictures of semantically related objects (e.g., a trumpet; Yee & Sedivy, 2006), and the probability of looking at the related object is predicted by how far away it is in "semantic space" (calculated in terms of the degree of featural overlap; Huettig & Altmann, 2005). This semantic eye-tracking paradigm has been used to explore specific dimensions of featural overlap (e.g., shape, color, manipulation) and is well suited to investigating semantic representations in patients with brain damage (Mirman & Graziano, 2012; Myung et al., 2010). Such behavioral paradigms inform cognitive neuroscience of the behavioral consequences of the manner in which semantic memory is organized.

Implications and Future Directions

Is There Something Special about Action?

Much of the work in cognitive neuroscience that has been the focus of this chapter indicates that semantic representations are at least partially sensorimotor based. One sensorimotor modality in particular, action, has received a great deal of attention, perhaps because of the discovery of "mirror neurons"—cells that respond both when an action is perceived and when it is performed (Rizzolatti & Craighero, 2004). This focus on action has led to a common criticism of sensorimotor-based theory: Being impaired in performing actions does not entail being unable to conceive of objects with strongly associated actions—suggesting that action may not, in fact, be part of these conceptual representations.[7]

There are at least three important points to keep in mind with respect to this criticism. First, concepts are more than associated actions (and in fact many concepts—e.g., *bookshelf* or *tree*—may have weakly if any associated actions). As a result, sensorimotor-based representations can include many different components (e.g., visual, auditory, and olfactory as well as action oriented) that are distributed across cortex. For this reason, under a sensorimotor-based account it would be surprising if all of these components were damaged simultaneously. This means that losing part of a representation does not entail losing the entire concept—just as losing one finger from a hand does not entail loss of the entire hand. Moreover, as highlighted in our discussion of abstract features, all of the various sensorimotor components still make up only part of conceptual knowledge—because semantic knowledge is only *partially* sensorimotor. Second, even concepts that at first glance seem predominantly action based generally comprise more than action alone. For example, our knowledge of kicking may include not only the action but also the contexts in which kicking is likely to occur (see Taylor & Zwaan, 2009, for a discussion of the many possible components of action knowledge and the resulting implications for "fault-tolerant comprehension").

Third, recent research (reviewed earlier) suggests that depending on the demands of the task, we are able to dynamically focus our attention on different aspects of a concept. This means that sensorimotor-based distributed models are not inconsistent with finding that an action is not routinely activated when the concept is activated, or that patients with disorders of action can respond successfully to concepts that are action based if the task does not require access to action information. In fact, such findings fall naturally out of the architecture of these models. Such models allow for semantic memory to exhibit some degree of *graceful degradation* (or *fault tolerance*) in that representations can continue to be accessed despite the loss of some of their components.

Is Semantic Memory Really "Shared Knowledge"?

Semantic memory is often referred to as "shared knowledge," to distinguish it from the individual experiences that make up episodic memory. Yet in this chapter we have emphasized that individual experience, task, and context all influence the extent to which different aspects of an object's representation become active over time. Thus, when conceiving of an object, there may be no fixed representational "outcome" that is stable across different episodes of conceiving of it (or even across time within an episode), let alone across individuals. This raises a significant challenge for how to define and understand semantic memory: Because semantic memory is "shared knowledge" only to the extent that our experiences (both long and short term) are shared, understanding the representation and retrieval of semantic knowledge may depend on our ability to describe aspects of these representations that are *not* shared. Future work must therefore do more than discover the extent to which various attributes *are* routinely activated for certain concepts. It should also attempt to characterize variations in the neural bases of semantic memory, as well as the neural mechanisms by which context or task demands modulate which aspects of a concept are activated (and at what rate), allowing for continuously changing outcomes (for further discussion, see Spivey, 2007).

From Categories to Semantic Spaces

Many of the studies described in this chapter explored the organization of semantic memory by comparing the neural responses to traditionally defined categories (e.g., animals vs. tools). However, a more fruitful method of understanding conceptual representations may be to compare individual concepts to one another, and extract dimensions that describe the emergent similarity space. The newer methods of analyzing neuroimaging data discussed above (such as fMRI adaptation and multivoxel pattern analysis, or MVPA) are well suited to the task of describing these types of neural similarity spaces. Further, by making inferences from these spaces, it is possible to discover what type of information is represented in a given cortical region (e.g., Mitchell et al., 2008; Weber et al., 2009; Yee et al., 2010). Overall, our understanding of semantic memory can benefit more from studying individual items (e.g., Bedny et al., 2007) and their relations to each other, than from simply examining categories as unified wholes.

Where Does Semantic Memory Fit in the Traditional Taxonomy of Memory?

Traditionally, semantic memory is considered to be part of the declarative (explicit) memory system (Squire, 1987). Yet the sensorimotor-based frameworks we have discussed in this chapter suggest that semantic memory is also partially composed of information contained in sensorimotor systems and can be probed through (implicit) perceptual priming. The amnesic patients we discussed in the first section of this chapter also support the idea that semantic memory is at least partially implicit, in that they are able to acquire some semantic knowledge despite severely impaired episodic memories. Hence, the current conception of semantic memory does not seem to fit cleanly into existing descriptions of either declarative (explicit) or nondeclarative (implicit) memory. Rather, our knowledge about the world and the objects in it appears to rely on both declarative and nondeclarative memory.

Summary

In this chapter we have briefly summarized a wide variety of data pertaining to the cognitive neuroscience of semantic memory. We reviewed different schemes for characterizing the organization of semantic memory and argued that the bulk of the evidence converges to support sensorimotor-based models (which extend sensory-functional theory). Because these models allow for, and in fact are predicated on, a role for degree and type of experience (which will necessarily vary by individual and by concept), they are able to accommodate a wide variety of observations. Importantly, they can also make specific, testable predictions regarding experience. Finally, it is important to emphasize that although often pitted against one another in service of testing specific hypotheses, sensorimotor and correlated feature-based models are not at odds with a categorical-like organization. In fact, both were developed to provide a framework in which a categorical organization can emerge from commonalities in the way we interact with and experience similar objects.

Notes

1. Linguists use the term *semantic* in a related, but slightly narrower way— to refer to the meanings of words or phrases.
2. There is mounting evidence that the reverse may also be true: semantic memory has been found to support episodic memory acquisition (Kan et al., 2009) and retrieval (Graham et al., 2000; Greve et al., 2007).
3. These ideas about the relationship between knowledge and experience echo those of much earlier thinkers. For example, in "*An Essay Concerning Human Understanding*," John Locke considers the origin of "ideas," or what we now refer to as "concepts," such as "whiteness, hardness, sweetness, thinking, motion, elephant …", arguing: "Whence comes [the mind] by that vast store, which the busy and boundless fancy of man has painted on it with an almost endless variety? … To this I answer, in one word, From experience." Furthermore, in their respective works on aphasia, Wernicke (1874) and Freud (1891) both put forth similar ideas (Gage & Hickok, 2005).
4. Recall that the domain-specific hypothesis allows for distributed representations within different categories.
5. Moreover (returning to the task effects discussed in 4.3), it has been suggested that the presence or absence of direct overlap may reflect the existence of multiple types of color representations that vary in *resolution* (or abstraction) with differences in task-context influencing whether information is retrieved at a fine (high-resolution) level of detail or a more abstract level. Retrieving high- (but not necessarily low-) resolution color knowledge results in overlap with color perception regions (Hsu et al., 2011).

6. We use the word "epiphenomenal" here to remain consistent with the objections that are sometimes raised in this literature; however, we note that the literal translation of the meaning of this term (i.e., an event with no effectual consequence) may not be suited to descriptions of neural activity, which can always be described as having an effect on its efferent targets.
7. Note that an analogous critique—and importantly, a response analogous to the one that follows—could be made for any sensorimotor modality.

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