HANDBOOK OF FUNCTIONAL NEUROIMAGING OF COGNITION

Second Edition

edited by Roberto Cabeza and Alan Kingstone

A Bradford Book
The MIT Press
Cambridge, Massachusetts
London, England

6

Functional Neuroimaging of Semantic Memory

Sharon L. Thompson-Schill, Irene P. Kan, and Robyn T. Oliver

Five senses; an incurably abstract intellect; a haphazardly selective memory; a set of preconceptions and assumptions so numerous that I can never examine more than a minority of them—never become even conscious of them all. How much of total reality can such an apparatus let through?
—C. S. Lewis

Nothing, at first view, may seem more unbounded than the thought of man.
—David Hume

Centuries of philosophers, psychologists, and, most recently, neuroscientists have become fascinated with questions of what we know and how we know it, and their attempts to find answers have taken many forms. This chapter approaches these questions using the new tools, and hopefully new insights, of the first generations of cognitive neuroscientists, who have searched for knowledge about knowledge in images of the brain.

Introduction

Linguists use the term "semantics" to refer to the meaning of a word or phrase. Thus, Endel Tulving borrowed the word "semantic" 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 (Tulving, 1972, 386). Today, most psychologists conceive of a broader meaning than "meaning" when they use the term "semantic memory." In the previous edition of this *Handbook*, Alex Martin defined semantic memory as "a broad domain of cognition composed of knowledge acquired about the world, including facts, concepts, and beliefs" (2001, 153). Following in this tradition, we use the term "semantic memory" to refer to *world* knowledge, not just *word* knowledge.

The study of world knowledge has its origins in philosophy, although the terminology has changed across the years: Where Locke wrote of "ideas," psychologists today would substitute the word "concepts" to refer to "those expressed by the words 'whiteness, hardness, sweetness, thinking, motion, man, elephant, army, drunkenness,' and others." And while the British empiricists asked about "human understanding," cognitive neuroscientists today speak of "semantic memory" to refer to our shared knowledge of the world. Despite the new vocabulary, many of the central themes remain. Consider the question of the relation between knowledge and experience: Locke argued "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." Three centuries later, the British psychologist Alan Allport, continuing in the tradition of his empiricist compatriots, argued 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, 53). Allport's theory, which is reminiscent of a description of concepts offered by Freud in his 1891 monograph on aphasia, was derived from a consideration of patterns of impairments to semantic memory following brain damage. In this chapter, we examine evidence from neuroimaging studies for an isomorphism between the architecture of semantic memory and the architecture of our sensorimotor systems. These neuroimaging studies provide new insights about the relation between knowledge and experience, using methods that Locke may never have imagined possible.

We have organized the review into three main divisions that reflect parallel (but interacting) lines of inquiry into the neural bases of semantic memory.

Semantic Memory—Episodic Memory Distinction

Is semantic memory a distinct memory system from episodic memory? If so, what neural systems are involved in learning and retrieval of semantic memory? The putative division between knowledge of the world and memories of personal events emerged in philosophical writings of Broad and Furlong in the first half of the twentieth century, although it was not introduced into the language of cognitive psychology until 1972 (Tulving, 1972). Today, the extent to which the distinction between semantic memory and episodic memory is realized in neural systems is the subject of ongoing debate. Much of the evidence brought to bear on this question has come from studies of selective impairments of either semantic memory or episodic memory. In this section, we highlight some of the complementary neuroimaging findings that have addressed this distinction.

Organization of Semantic Memory

What psychological distinctions are realized in the neural systems that support semantic memory? Does the neural architecture of semantic memory obey categorical subdivisions among concepts? Is conceptual knowledge distributed among distinct sensorimotor systems? How is abstract knowledge represented? Distributed theories of semantic memory, such as those of Freud and Allport described above, emphasize the relation between concepts and their sensorimotor features. In contrast, many psychological investigations of concepts have focused on the hierarchical relations among them (see Margolis & Laurence, 1999). Discussion of the neural instantiation of these relations has been fueled by reports of selective degradation of branches of this putative hierarchy (e.g., animals). We begin by reviewing historical and recent evidence that bears on the question of how taxonomic category relations may be represented. Then, following a more in-depth discussion of sensorimotor theories, we reconsider the interpretation of some of these startlingly specific impairments, drawing on new insights from neuroimaging studies of the sensorimotor organization of semantic memory. We end with a brief discussion of the representation of abstract semantic knowledge—brief, because investigations of the representations of physical attributes and categorical relationships have, by and large, excluded consideration of abstract concepts and features. In particular, we discuss the proposal that distributed sources of information are united in a neural "convergence zone" that represents abstract relations.

Semantic Memory Retrieval

During retrieval of semantic memory, do different input modalities have preferential access to certain representations? How do executive control mechanisms guide the retrieval process? Our review of sensorimotor theories of object knowledge naturally relates to debates about the representation of visual knowledge—Is it propositional, is it imagistic, or are there multiple representations? We present evidence that the input modality affects the way in which knowledge is retrieved (rather than the format in which it is stored). Finally, once semantic memory has been taken apart, we are left with the problem of how to put Humpty together again. One consequence of distributed concept representations is the likely occurrence of representational conflict when partial, incompatible representations are activated. At the end of this section, we argue for the important role that prefrontal cortex (PFC) plays in guiding the selection of representations when there are conflicting sources of information.

Throughout this tour of neuroimaging studies of semantic memory, we occasionally make reference to contributions from other methodologies; however, in keeping with the goals of this volume, our focus will remain on the recent advances that have been made in our understanding of semantic memory by examining regional hemodynamic changes in normal volunteers who are busy thinking about the world.

Functional Neuroimaging of Semantic Memory

Semantic Memory—Episodic Memory Distinction

Tulving's proposal for a distinction between episodic and semantic memory went beyond the mere difference in the *content* of the memories (i.e., about a personal episode vs. about the world). He argued for two functionally distinct memory systems on the basis of a dozen sources of evidence, ranging from "armchair speculation" to stochastic independence (1984). Since Tulving's treatise on the organization of memory, the cognitive psychology and cognitive neuroscience communities have continued to debate the relation between semantic and episodic memory and the extent to which this distinction should be viewed as anything more than a useful heuristic (e.g., Graham et al., 2000).

Studies of patients with medial temporal lobe amnesia, which were so instrumental in separating episodic and procedural memory, generally have reported impairments in both episodic and semantic memory (Gabrieli et al., 1988; Stefanacci et al., 2000). However, the study of children with early hippocampal damage (i.e., "developmental amnesia") has revealed grossly impaired episodic memory but seemingly normal semantic memory (Vargha-Khadem et al., 2001). These data argue against hypotheses that semantic memory is an abstraction of accumulated episodic memories. On the flip side, numerous patients have been described who show a progressive and profound deterioration in the knowledge of facts, object concepts, and vocabulary, despite otherwise normal language, memory, and perception (Hodges et al., 1994). Patients with *semantic dementia*, as this syndrome is commonly called, typically have a temporal variant of frontotemporal dementia, with extensive but asymmetric (left more than right) polar and inferolateral temporal atrophy (Galton et al., 2001).

The description of these neuropsychological impairments, now coupled with increasingly sophisticated methods for quantitatively describing the location and extent of lesions, has increased attention to the relation between semantic and episodic memory systems (e.g., Graham et al., 2000). Neuroimaging studies provide a complementary source of evidence for the divide between medial and lateral temporal cortical contributions to these systems. Direct comparisons of semantic and episodic memory have revealed activation specific to semantic memory in lateral temporal and parietal cortex, lateral and medial PFC, and the dorsomedial nucleus of the thalamus (e.g., Maguire & Frith, 2004). The content of the memory (whether episodic or semantic) can affect the patterns of activation, as studies of concrete words (Dalla Barba et al., 1998), musical tunes (Platel et al., 2003), and spatial information (Mayes et al., 2004) have illustrated. Some of the previously reported differences between episodic and semantic retrieval may reflect confounded differences in content (e.g., semantic retrieval of spatial information activates the hippocampus; Mayes et al., 2004).

One of the more controversial hypotheses about the neural substrates of episodic and semantic memory to emerge from the neuroimaging literature is referred to by the acronym HERA (Hemispheric Encoding-Retrieval Asymmetry). The HERA model describes the relative specialization of left and right PFC for episodic encoding and retrieval, respectively (Tulving et al., 1994). Although formulated as an explanation of differences during encoding and retrieval of *episodic* memory, many of the studies cited as investigations of episodic encoding could just as easily be characterized as studies of semantic retrieval (but see Lee, Robbins et al., 2002 for an example of an attempt to dissociate episodic encoding and semantic retrieval). Thus, the bulk of the data speak to a Hemispheric Episodic Semantic Asymmetry (though we hesitate to introduce the acronym HESA in any way other than jest!) that is relevant for the current discussion. While the HERA model focuses on differences in PFC activation patterns, commonalities across semantic and episodic retrieval tasks have been reported in a number of studies (Buckner et al., 1995; Dalla Barba et al., 1998; Nyberg et al., 2003; Wiggs et al., 1999). In particular, both semantic and episodic retrieval activate regions in the anterior cingulate and left PFC; we discuss a possible domain-general role for PFC that may be relevant to these observations near the end of the chapter.

One problem with the attempt to form generalizations about the neural bases of semantic memory based on a list of studies such as those briefly reviewed here is that the devil lies in the details. Each new way of manipulating or measuring semantic retrieval is likely to affect the component processes, of which there are almost certainly many, that are involved in each task. The operations involved in monitoring a list of words for animals (Dalla Barba et al., 1998) will not be identical to those involved in completing a word stem (Buckner et al., 1995). Differences in the results across studies may be noise, or they may reflect the systematic (but perhaps as yet unidentified) manipulation of processes beyond semantic retrieval per se. For example, at the end of the chapter we present one such hypothesis for the role of left PFC in (some) semantic retrieval tasks. As we argue, the extent to which PFC is engaged by a semantic memory task depends on factors that are not, strictly speaking, semantic.

That said, neuroimaging studies comparing episodic and semantic memory can be roughly summarized thusly: semantic memory and episodic memory systems rely in part on common neural circuitry, activation of which might be understood in terms of variables orthogonal to the episodic/semantic distinction, such as content (e.g., spatial, verbal) or cognitive control processes. Nonetheless, semantic memory retrieval does have a distinct neural signature, which includes regions of temporal and frontal cortex. In the remaining sections of this chapter, we will begin to tease apart the unique contributions that these regions make to semantic memory processes.

Organization of Semantic Memory

Categories of Semantic Memory

Throughout the twentieth century, clinical neurologists began to notice strikingly selective language impairments: anecdotal case studies described patients who were unable to understand or produce the names of colors (A. R. Damasio et al., 1979), body parts (Dennis, 1976), people (McKenna & Warrington, 1980), actions (Goodglass et al., 1966), concrete entities (Warrington, 1975), inanimate objects (Nielsen, 1936), small, manipulable objects (Konorski, 1967), and indoor objects (Yamadori & Albert, 1973). However, it was not until the systematic, experimental investigations of Elizabeth Warrington and her colleagues that these so-called category-specific deficits began to change the way cognitive psychologists thought about the organization of semantic memory.

In 1983, Warrington and McCarthy described a patient with a specific impairment of understanding object names. The next year, Warrington and Shallice (1984) described four patients who showed the reverse dissociation, a selective impairment in visual identification and verbal comprehension of living things and foods. Thus began, in the words of two of its leaders, "the modern era of the study of the representation of object concepts in the human brain" (Martin & Caramazza, 2003, 195). It is a question for historians of science why these two papers captivated the field in a way that those which came before had not. But the outcome is clear: not only did these studies alter the course of investigations of semantic memory, but they also provided a foundational example of the critical role that neuropsychology could play in cognitive science (Shallice, 1988).

There are several excellent reviews of the growing literature reporting category-specific deficits (e.g., Capitani et al., 2003; Saffran & Schwartz, 1994). Here, we highlight just a few of the important points to emerge from these investigations, emphasizing those which have relevance in subsequent sections of this chapter.

First, in most cases, category-specific impairments are observed across multiple testing modalities (e.g., pictorial and verbal stimuli). However, deficits have been described that are restricted to a single modality (e.g., Hart et al., 1985), and within-modality item consistency can exceed between-modality consistency (Warrington

& Shallice, 1984). These observations have been interpreted by some as evidence for multiple formats of semantic memory.

Second, selective impairments in knowledge of both living things (something described as "animate" or "biological kinds") and nonliving things (sometimes described as "inanimate" or "artifacts") have been reported, but the frequency of these two deficits is not equal. In a 2003 review, Martin and Caramazza identified reports of over 100 patients with a living things deficit in contrast to about 25 patients with a nonliving things deficit. Although artifactual accounts of living things deficits (e.g., complexity, familiarity) have been ruled out in some cases (Basso et al., 1988; Farah et al., 1991), it is possible that confounding variables have created part of the discrepancy in the incidence of these two types of category-specific deficits. However, the disparity could also reflect important differences in the way living and nonliving things are represented that affect the susceptibility of semantic knowledge.

Third, the neuroanatomical correlates of category-specific disorders are hardly precise, given the extent of damage present in many cases, but a few generalities have been proposed: patients with a living things deficit most commonly have lesions that include anterior, inferior, and medial temporal cortex, bilaterally (but left more than right). In contrast, patients with a nonliving things deficit typically have large, left frontoparietal lesions. However, exceptions to these patterns have been noted in both cases (Caramazza & Shelton, 1998; Tippett et al., 1996).

Fourth, finer-grained examinations of category-specific deficits have been both informative and controversial. In some cases these analyses revealed impairments that are broader than "living things": patients with impaired knowledge of animals, fruits, and vegetables have been reported to have concurrent deficits identifying gemstones (Warrington & Shallice, 1984), liquids and materials (Borgo & Shallice, 2001), and musical instruments (Silveri & Gainotti, 1988). In other cases, these analyses have revealed strikingly narrow category-specific impairments of knowledge of only fruits and vegetables (Crutch & Warrington, 2003) or only animals (Caramazza & Shelton, 1998). These exceptions to the broad living/nonliving distinction continue to inform theories of the organization of semantic memory.

The dozens of neuropsychological studies reporting category-specific impairments are now complemented by dozens of investigations of category-specificity in neurologically intact subjects using functional neuroimaging. One rich source of data about category-specificity comes from studies of visual responses to highly specific object categories, such as faces (Kanwisher et al., 1997), places (Epstein & Kanwisher, 1998), and body parts (Downing et al., 2001). These studies, and the controversy that surrounds them (Haxby et al., 2001; Tarr & Gauthier, 2000), are discussed in detail in Kanwisher (2003). The neuroimaging studies of category-specificity reviewed in this chapter are confined to those in which the subject was required to retrieve some unpictured information about an object (e.g., its name, color, size, etc.). We have excluded studies in which subjects had to passively view or briefly remember an object; the difficulty in determining where to draw this line highlights the continuity between these two areas of inquiry.

Initial reports of category-specific activation during semantic processing came from studies of word retrieval. For example, a comparison of PET activation during verbal fluency (generation of examplars of living and nonliving things) revealed differences in left anteromedial temporal cortex (increased for living things) and left posterior temporal cortex (increased for nonliving things; Mummery et al., 1996). Martin and colleagues (1996) found increased PET activation in left medial occipital cortex during animal-naming and in left premotor and middle temporal cortex during tool-naming. Both animal-naming and tool-naming activated common regions of ventral temporal cortex bilaterally and left PFC; however, in a subsequent fMRI study (with better spatial resolution), this group observed multiple, small category-specific sites (for animals, tools, faces, and houses) in ventral temporal cortex (Chao et al., 1999). Spitzer and colleagues (Spitzer et al., 1998; Spitzer et al., 1995) also reported small regions of category-specific activity in frontal and temporoparietal cortex during covert naming of living and nonliving things. Although there were no consistent areas of category-specific activation across subjects, consistent activation was observed in one subject on two scanning dates. These findings were taken as evidence for category-specific semantic representations that are highly variable across subjects as a result of different life histories. Damasio and colleagues (H. Damasio et al., 1996; Grabowski et al., 1998) reported category-specific PET activation in the left hemisphere during naming of people (temporal pole), animals (middle portion of inferior temporal gyrus and medial occipital cortex), and tools (posterior portion of inferior temporal gyrus and premotor cortex). A similar category-specific organization was observed in patients with lesions to these regions (H. Damasio et al., 1996); however, these patients had anomia (i.e., word retrieval deficits) rather than semantic knowledge deficits. Thus, the evidence for category-specific representations in studies of verbal fluency and picture naming may reflect principles of lexical organization rather than semantic organization.

The few studies that have examined category-specific differences with nonverbal tasks have reported mixed results. Perani and colleagues (1995, 1999) compared PET activation during same-different judgments about animals and tools. In one study they reported that tool judgments activated left frontal cortex (although not the same premotor region reported elsewhere), but animal judgments were associated with no consistent locus of activation (Perani et al., 1995). In a subsequent study, they identified common regions of activation for both pictures and words: across modalities, tool judgments were associated with middle temporal activation, whereas animal judgments were associated with left fusiform gyrus activation (Perani et al., 1999). Although this study might be seen as an improvement over strictly verbal studies, the extent to which semantic knowledge was required for these tasks is not clear (e.g., their word task required matching two stimuli presented in different fonts, which is arguably non-semantic).

Tyler and colleagues have conducted a series of experiments that have failed to find reliable category-specific activity during word comprehension: across three experiments, they observed activity during lexical decision and category judgments in a network of areas including the left inferior frontal lobe, left posterior temporal cortex, and the anterior temporal poles bilaterally (Devlin et al., 2002). While they did find category differences in some of the same regions as previous studies (i.e., the left anterior-medial temporal pole activated specifically for animals and the left posterior middle temporal gyrus specifically for tools), these effects were present only at lowered statistical thresholds. Utilizing the same category judgment task (i.e., Is the fourth item in a list of words from the same semantic category as the first three items?), Pilgrim et al. (2002) found no significant differences between artifact and natural kind concepts in an event-related fMRI study. The only significant activation difference between the two categories emerged in a region of interest analysis in the fusiform gyrus (artifacts greater than natural kinds—oddly, the reverse of other studies). Finally, in a third fMRI study, they repeated the experiment but restricted the object types to tools and animals (Tyler et al., 2003). Again, they failed to find category-specific effects at either a statistically corrected threshold or a lowered one.

In summary, attempts to find category-specific activation patterns using neuroimaging methods have had mixed success. In principle, the failure to find category-specific responses could result from neural category-specificity at a spatial resolution higher than that of our neuroimaging methods. However, in light of the relatively remote lesion sites that have been implicated in category-specific deficits, this is an unsatisfying explanation. More likely is the possibility that activation has been observed in areas which are not necessary for the performance of a task. Category judgments about animals, for example, might activate a widely distributed neural network, all of which represents information about animals, but only portions of which are necessary to perform the task. Clearly, additional work is necessary to discern what specializations exist within this rather extensive collection of regions that are recruited during semantic processing. In the next section, we consider one candidate organizing principle of a distributed semantic network.

Attribute Domains of Semantic Memory

At the outset of this chapter, we briefly introduced a model of semantic memory that describes object concepts as distributed mental representations implemented in functionally and physically distinct attribute domains (Allport, 1985). These attribute domains correspond to different sensory or motor domains of which they are also a part. In fact, according to Allport, these modules are the very same areas of the brain that are dedicated to processing sensorimotor information. Among the ideas discussed in this seminal paper, Allport suggested that (1) the class of attribute domains that pertain to any given object concept, and thus that serve to represent that concept, will vary across objects; (2) object concepts are less vulnerable to brain damage, by virtue of their widely distributed representation, than linguistic representations (e.g., word forms); (3) those object concepts which are defined over few attribute domains will be more vulnerable to brain damage than those which are defined over many attribute domains. We will revisit some of these claims, and implications of this model for understanding category-specificity, later in the chapter. For now, we turn to investigations of attribute domains—namely, what are they, and where are they?

The distinction between *visual* and *functional* attributes is the most common and perhaps also the coarsest division among attribute domains in the semantic memory literature. Research in several diverse areas, from language acquisition (e.g., Gentner, 1978; Nelson, 1974) to language dysfunction (e.g., Warrington & Shallice, 1984), from word reading (e.g., Schreuder et al., 1984) to object categorization (e.g., Rosch et al., 1976), indicates that semantic knowledge may be divided into visual and functional attributes. Now adding to these sources of evidence, a number of functional neuroimaging studies have reported neuroanatomical dissociations between visual and functional attributes (Cappa et al., 1998; Mummery et al., 1998; Thompson-Schill, Aguirre et al., 1999), or between abstract and concrete words, which, by definition, differ with regard to visual knowledge (Beauregard et al., 1997; D'Esposito et al., 1997; but see Kiehl et al., 1999). For example, retrieving the color of an object activates ventral temporal cortex bilaterally, while retrieving an associated action activates left middle temporal and prefrontal cortex (Martin et al., 1995). Note that the operationalization of "function" knowledge has varied widely across these studies (e.g., actions, uses, etc), so, to be more accurate, we organize the next two sections of the chapter around the principal neuroimaging findings relating to visual and *nonvisual* semantic knowledge.

Visual Attribute Domains One interpretation of the studies reviewed above is that knowledge about visual attributes of an object is represented differently from knowledge of nonvisual attributes. This conjecture is related to a central debate in cognitive science about the extent to which any type of conceptual knowledge relies on perceptual representations (for a review, see Barsalou, 1999). This controversy has perhaps been played out most thoroughly in the investigation of mental imagery. On one side of the imagery debate are those who maintain that mental images are propositional or symbolic, such as language, and therefore do not share representations with perception (e.g., Pylyshyn, 1981). On the other side of the debate are those who believe that mental images have a spatial format and share representations with those used during perception (e.g., Kosslyn, 1980). There is mounting support for the hypothesis that visual imagery and visual perception share common processes, including evidence from brain-damaged patients (Farah, 2000); transcranial magnetic stimulation (Kosslyn et al., 1999), ERP recordings (Farah, Peronnet et al., 1988); and now neuroimaging.

Numerous neuroimaging studies have found activation in visual cortex during mental imagery (e.g., Charlot et al., 1992; D'Esposito et al., 1997; Goldenberg et al., 1991; Goldenberg et al., 1987; Roland & Friberg, 1985), in extrastriate and occasionally striate cortex. Furthermore, images of different sizes produce different patterns of activation, consistent with what is known about the retinotopic mapping of visual cortex (Kosslyn et al., 1993). Across neuroimaging studies of mental imagery, there is some disagreement about whether the activation is confined to higher-order visual association cortex or whether it includes primary visual cortex. Despite this controversy, there is near agreement that visual imagery activates some retinotopically organized cortical regions, which supports the hypothesis that imagery and perception have common representations.

We have taken a slightly different approach recently (Kan et al., 2003), in which we examined activation in visual association cortex during a property verification task (e.g., Does a camel have a hump?). With no explicit imagery instructions, we observed activation in visual association cortex (i.e., fusiform gyrus) only under conditions in which conceptual knowledge was required (i.e., not when word association strength would suffice to make a correct response); this pattern indicates a specific reliance of conceptual knowledge on perceptual representations.

If one believes that knowledge of visual attributes depends on visual representations, then one might logically ask whether divisions that have been observed in visual perception exist in our representations of visual knowledge. For example, it is well known that regions of cortex are specialized for color perception, motion perception, and form perception. Recently, investigators have used functional neuroimaging to probe for similar distinctions within semantic knowledge.

Color Knowledge of color—and its relation to perception of color—has been investigated in more neuroimaging studies than any other visual attribute domain. Across a wide variety of tasks—including reporting the color of a pictured line drawing (Chao & Martin, 1999; Martin et al., 1995; Wiggs & Martin, 1998), verifying the color of a visually or auditorily named object (Kellenbach et al., 2001; Noppeney & Price, 2003), and making similarity judgments across a triad of object names (Mummery et al., 1998)—activation is typically observed in left or bilateral ventral temporal cortex, with a high degree of consistency across studies. Chao and Martin (1999) directly compared activation during color perception and color knowledge retrieval, and found activation during color naming just anterior to the areas responsible for processing color information. A similar finding was reported in a comparison of color perception and color imagery (Howard et al., 1998).

Unlike other regions that are active during a broad range of semantic retrieval tasks (e.g., PFC), ventral temporal cortex may be active *specifically* during color retrieval (e.g., in contrast to retrieval of object size knowledge (Kellenbach et al., 2001). However, contrary to this claim, Noppeney and Price (2003) reported *less*, not more, activation in left ventral temporal cortex during a color retrieval task ("Red?") for fruits compared with an "origin" retrieval task ("Tropical?"). Whether this anomalous finding is specific to the origin task remains to be determined.

Motion Several early neuroimaging studies of semantic memory reported that retrieval of action knowledge activates, among other areas (discussed more below), the left middle temporal gyrus (Martin et al., 1995; Warburton et al., 1996; Wise et al., 1991), anterior to the region associated with motion perception (MT/MST; e.g., Watson et al., 1993; Zeki et al., 1991). Similarly, Decety and colleagues reported activation in lateral temporal cortex while imagining actions or observing semantically meaningful actions (Decety et al., 1997; Ruby & Decety, 2001). Kable and colleagues (2002) observed increased activity in (or just anterior to) functionally defined MT/MST while subjects made semantic judgments about actions (relative to objects). Because of the coincidence of these locations, lateral temporal activation during retrieval of action attributes has been attributed to retrieval of motion knowledge (Martin et al., 2000).

In addition to object motion, the lateral temporal lobe has also been implicated in biological motion. Specifically, the superior temporal sulcus, which is slightly anterior and dorsal to MT, has been shown to be involved when subjects observe face and leg motion, mouth movements (e.g., Buccino et al., 2001; Buccino et al., 2004; Calvert et al., 1997; Calvert & Campbell, 2003; Campbell et al., 2001; Wheaton et al., 2004), eye movements (e.g., Pelphrey et al., 2003; Puce et al., 1998), and body movements (e.g., Bonda et al., 1996; Grezes et al., 2001; E. Grossman et al., 2000; Howard et al., 1996). Given the spatial separation and the consistency of the localization of these two types of motions, Martin and colleagues (Martin et al., 2000) proposed a dorsal-ventral divide in the representations of biological and nonbiological motion. Consistent with this hypothesis, Beauchamp et al. (2002, 2003) reported more activity during viewing of human movement (either videos or point-light displays) compared to tool movement in the superior temporal sulcus, and the reverse pattern in the middle temporal gyrus. To date, this putative distinction has not been tested during semantic retrieval tasks.

Size The findings of the few studies that specifically examined retrieval of size knowledge have been a bit more mixed than those which have looked at color or motion: when compared with other semantic retrieval tasks, retrieval of size knowledge has resulted in either no areas of selective activation (Vandenberghe et al., 1996), activation of medial parietal cortex (Kellenbach et al., 2001), or activation of lateral parietal cortex (Oliver & Thompson-Schill, 2003). Selective activation of medial parietal cortex during size retrieval (relative to color retrieval) was attributed to activation of spatial representations that encode relative size (Kellenbach et al., 2001). However, in our study, parietal activation (albeit lateral, not medial) was greater during retrieval of size, but also shape, relative to retrieval of color knowledge (Oliver & Thompson-Schill, 2003). We discuss the role of the dorsal visual processing stream in representing physical properties of objects, including size and shape, below.

Form Most of the studies that have probed the representation of form information have focused on the recognition of objects from pictures to explore the question of category differences in representation of form information in occipitotemporal cortex (Chao et al., 1999; Ishai et al., 2000; Ishai et al., 1999). Likewise, activation has been reported in ventral occipitotemporal cortex during mental imagery of object shape (e.g., De Volder et al., 2001; Ganis et al., 2004) or during semantic decisions based on object form (Cappa et al., 1998). Even in blind subjects, retrieval of shape knowledge activates occipitotemporal cortex, to the same extent as in sighted subjects (Noppeney et al., 2003; Pietrini et al., 2004). While results from blind subjects have been used to argue that ventral occipitotemporal representations of form are abstract and supramodal, this pattern may reflect reorganization of function in blind individuals (e.g., what may serve as a visual processing area in sighted individuals may operate as a spatial or tactile processing region in blind individuals).

Our investigations of shape retrieval highlighted the potential role of the *dorsal* visual processing stream in the representation of object concepts (Oliver & Thompson-Schill, 2003). When we compared shape retrieval to color retrieval, the most prominent selective activation was found in parietal cortex, in regions also activated (although less so) during size retrieval. The hypothesized involvement of parietal cortex in shape recognition is not without precedent (Murata et al., 2000; Peuskens et al., 2004), although the precise role of this region during semantic retrieval has not yet been determined. However, the field of visual perception suggests some avenues to explore in further research.

Extrastriate visual areas can be divided into a ventral stream running from occipital cortex through temporal cortex and a dorsal stream extending from occipital cortex through the parietal lobe (Ungerleider & Mishkin, 1982). It has been proposed that the ventral stream processes the identity of objects during perception, while the dorsal stream has been ascribed different roles, including spatial processing (Ungerleider & Mishkin, 1982) and processing performed during visually mediated actions (Goodale & Milner, 1992). By analogy, the dorsal stream may also be involved in *retrieval* of aspects of attributes that are acquired through spatial processing or through visually mediated actions. In other words, spatiomotor processing may provide another source of information about the shape and size of objects, at least for some categories of objects. In particular, objects that have a strong relationship between their form and their manner of manipulation (i.e., a strong affordance for action; Gibson, 1979) would be more likely to have motor representations that also carry information about their form. Below, we consider implications of this additional source of information when discussing vulnerability of semantic memory to brain damage.

Nonvisual Attribute Domains The term "functional knowledge," typically used to contrast with visual knowledge when talking about types of semantic memory, has been rendered almost meaningless through its abundance of uses. For example, the term has been used by some to denote any abstract property that is not physically defined (e.g., Schreuder et al., 1984), and by others to denote an attribute that is physically defined, but by motor properties rather than sensory properties (e.g., Farah & McClelland, 1991; Warrington & McCarthy, 1987). Abandoning this terminology completely, we focus here on action knowledge and how that knowledge may be further subdivided into function ("what for") knowledge and manipulation ("how") knowledge. Then, we briefly review investigations of other nonvisual (but sensory) attributes—sound, smell, and taste.

Action Dozens of neuroimaging studies have investigated the neural bases of action knowledge retrieval (e.g., Binkofski, Buccino, Posse, et al., 1999; Binkofski, Buccino, Stephan, et al., 1999; Buccino et al., 2001; Gerlach, Law, Gade, et al., 2002; Gerlach, Law, & Paulson, 2002; Grabowski et al., 1998; Grafton et al., 1996; Grafton et al., 1997; Kable et al., 2002; Kellenbach et al., 2003; Martin et al., 1995; Martin et al., 1996; Perani et al., 1999; Warburton et al., 1996; Wheaton et al., 2004). Across a variety of explicit retrieval tasks (e.g., verb generation, similarity judgments) and implicit retrieval tasks (e.g., tool identification, pleasantness ratings), a distributed network of brain regions including left ventral prefrontal, posterior temporal, and parietal areas has consistently been identified. In a recent meta-analysis of 24 neuroimaging studies of action knowledge retrieval, Grezes and Decety (2001) identified considerable overlap in the neural bases of action execution, simulation, observation, and verbalization.

In particular, the relation between action knowledge in premotor cortex has received considerable attention, fueled in part by parallel findings that neurons in monkey premotor cortex are involved in the recognition of motor actions (Rizzolatti et al., 1996). Differences within premotor cortex have been observed, depending on the body part involved in the retrieved action (e.g., Pulvermuller et al., 2001). An area of left ventrolateral premotor cortex that is activated by imagined grasping and other hand movements with the right hand (Decety, 1996; Decety et al., 1994; Stephan et al., 1995) is almost identical to the area activated during tool naming (Martin et al., 1996). Based on these results, Martin and colleagues have argued that knowledge of tool use is stored in this region (see also Chao & Martin, 2000; Grabowski et al., 1998; Grafton et al., 1997, for similar findings and interpretations).

There are two distinct meanings of tool use, and of action knowledge more generally: knowledge of the function of an object (e.g., a key opens a door) and knowledge of the manner of manipulation (e.g., using a key involves twisting and turning of the hand) have been doubly dissociated in neuropsychological investigations (e.g., Buxbaum & Saffran, 1998; Buxbaum et al., 2000; Sirigu et al., 1991). Kellenbach and colleagues (2003) reported that PET activation in frontal, middle temporal, and parietal cortex is linked to manipulation knowledge, not function knowledge. Similarly, Boronat and colleagues (2005) reported selective fMRI activation of the inferior parietal cortex during retrieval of manipulation information. Neither of these studies found reliable activation associated with retrieval of function knowledge; information about the function of an object (i.e., what it is used for) may depend on more abstract representations, which we will consider shortly.

Other Sensory Domains The few neuroimaging studies that have investigated retrieval of auditory knowledge (e.g., animal sounds) have found selective activity in the superior aspect of the temporal pole (Noppeney & Price, 2002), temporoparietal cortex near auditory association areas (Kellenbach et al., 2001), and the superior temporal gyrus (Adams & Janata, 2002; Wheeler et al., 2000). Overall, it appears that the temporal lobe, and in particular auditory association areas in the superior temporal lobe, may be selectively involved in the retrieval of auditory semantic information.

Several recent neuroimaging studies have examined selective activation during retrieval of information about smell and taste of objects; however, there are methodological issues (e.g., fMRI signal dropout in orbital regions) that make research in these areas difficult. Failures to find taste-specific activation (e.g., Noppeney & Price, 2003) may reflect these challenges. That said, at least one study has reported that taste imagery and taste perception activate common regions within frontal cortex (Levy et al., 1999). Research on odor knowledge has found that, in large part, the regions associated with olfactory perception, including orbitofrontal, pyriform, and insular cortex, are involved in identification of odors (Cerf-Ducastel & Murphy, 2003; Dade et al., 1998; Karaken et al., 2003). The tasks used in these studies are the olfactory equivalent of a picture-naming task (i.e., subjects must retrieve a name, given modality-specific input). To date, there have been no studies of olfactory retrieval that are not potentially confounded with effects of olfactory perception. Also, olfactory semantic studies that utilized an odor perception baseline task failed to find involvement of one or more of these regions (Karaken et al., 2003; Qureshy et al., 2000; Royet et al., 1999).

Abstract Semantic Representations

Thus far, our discussion of the representation of semantic memory has been confined to physical properties of concrete objects. When Allport articulated his theory of the representation of meanings, he limited himself, "for simplicity," to the domain of object concepts. Of course, any complete theory of semantic memory has a bit more work to do: there are abstract concepts (e.g., peace), abstract features of object concepts (e.g., "alive" as a feature of a plant), and abstract relations between concepts (e.g., the ways in which a "bat" is more similar to a "bear" than to a "bird").

There is ample neuropsychological evidence for a dissociation between the representation of abstract and concrete concepts (e.g., Breedin et al., 1994) that may reflect any number of qualitative differences in their acquisition and representational format. Neuroimaging comparisons of abstract and concrete words have identified an inconsistent array of regions associated with abstract concepts in the left superior temporal gyrus (Wise et al., 2000), right anterior temporal pole (Kiehl et al., 1999), and left posterior middle temporal gyrus (M. Grossman et al., 2002). Noppeney and Price (2004) compared fMRI activation while subjects made similarity judgments about triads of visual words, sound words, action words, and abstract words that were matched for difficulty. Relative to the three other conditions, retrieval of abstract concepts activated the left inferior frontal gyrus, middle temporal gyrus, superior temporal sulcus, and anterior temporal pole. The authors suggest that these differences reflect activation of areas involved in sentence comprehension, although this is clearly an area in need of more investigation.

There is, to date, even less work addressing abstract features. One particular problem with using functional neuroimaging to compare abstract and concrete features is that abstract semantic decisions typically take longer to resolve. The left inferior PFC has been implicated in extended or controlled semantic processing on the basis of studies that might confound effort with abstractness (Roskies et al., 2001); for example, PFC activity increased when subjects decided that "candle" and "halo" were similar, compared to deciding that "candle" and "flame" were similar

(Wagner et al., 2001), arguably a comparison that confounds effort with abstraction. To unconfound these processes, Goldberg and colleagues (2004) compared the effects of increasing semantic abstractness and increasing difficulty on activity in PFC while subjects verified perceptual or abstract facts about animals. fMRI activation in left PFC (BA 47) was specifically associated with an increased reliance on abstract properties but not increased semantic difficulty. This finding is consistent with recent evidence showing that neurons in a primate analogue of this region represent abstract rules (Wallis et al., 2001).

Many cognitive models of semantic memory have described hierarchical networks that reflect abstract relations between concepts (e.g., a tree is a plant and a plant is a living thing). This description is quite different from the distributed representation we have been describing thus far. However, Rogers and colleagues have articulated a formal model of semantic memory that includes units which 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, 206). The interaction between content-bearing perceptual representations and verbal labels produces a similarity space that is not captured in any single attribute domain; rather, they argue, it reflects abstract similarity (cf. Caramazza et al., 1990; A. R. Damasio, 1989; Plaut, 2002; Tyler et al., 2000). The cortical region they offer as a candidate for these abstract representations is the temporal pole, based both on the anatomical connectivity of this region and the degeneration of this region in semantic dementia.

The notion that interactions between perceptual and verbal representations lead to the emergence of new, abstract representations may be relevant for a puzzle that has emerged in neuroimaging tests of Allport's (1985) sensorimotor model of semantic memory: that there is a consistent trend for retrieval of a given physical attribute to be associated with activation of cortical areas 2–3 cm anterior to regions associated with perception of that attribute (Martin et al., 1995; Thompson-Schill, 2003). This pattern, which has been interpreted as coactivation of the "same areas" involved in sensorimotor processing, as Allport hypothesized, could alternatively be used as grounds to reject the Allport model. What does this anterior shift reflect? We believe the answer may lie in the ideas developed by Rogers and colleagues (2004). 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). The tasks that have been used to study conceptual retrieval of visual attributes have not consistently required the subject to retrieve perceptual information. For example, in order to recall that a banana is "yellow," activation of color representations that are more abstract than those necessary for perception could suffice. The conceptual similarity space in more anterior regions may depart a bit from the similarity space in the environment, perhaps moving in the direction of abstract relations. More work is needed to uncover the nature of the representations—and how the similarity space may gradually change across different cortical regions.

Categories of Semantic Memory—Redux

Thus far, we have presented two potentially orthogonal views about the organization of semantic memory. We initially considered the hypothesis that representations of specific categories of semantic knowledge are instantiated in spatially distinct neural regions. As we saw, there is ample support for this hypothesis from the neuropsychological literature, but only partial support from neuroimaging studies. Then, we reviewed neuroimaging studies that support models of distributed representations of semantic memory, where different attribute domains of object knowledge are represented in distinct sensorimotor systems. As the reader having even a passing familiarity with these literatures will know, these two hypotheses about the organization of semantic memory are intertwined, by virtue of the fact that the taxonomic category of an object and its associated attribute domains are not at all orthogonal. The confound between these two putative organizing principles has made it challenging to uncover the neural architecture of semantic memory.

Warrington and McCarthy (1983) first called attention to implications of this relation for the interpretation of category-specific deficits: whereas sensory attributes are important for discriminating between members of the category of living things, functional attributes are more important for discriminating between members of the category of nonliving things. Thus, category-specific deficits could result from the degradation of an attribute domain of semantic memory. Since the mid-1980s, this *sensory-functional theory* has persisted in a variety of accounts of category-specific deficits, all of which hold that semantic knowledge is stored in sensorimotor channels, and that the relative importance of information contained in these channels varies across items in different categories (e.g., Farah & McClelland, 1991; Martin et al., 2000; Saffran & Schwartz, 1994; Simmons & Barsalou, 2003).

Accordingly, one explanation of category-specific activation in neuroimaging studies is that these differences reflect the differential weighting of visual and functional knowledge across categories (e.g., Martin et al., 1996). In order to test this account, Patterson and colleagues have reported two PET studies that have unconfounded object category and attribute domain. In the first, subjects made similarity judgments about living or nonliving things on the basis of either visual or nonvisual information. With this fully crossed design, the authors compared the magnitude of category-specific effects and attribute-specific effects directly, and concluded that the latter were more prominent neurally (Mummery et al., 1998). In a second study, subjects generated visual or nonvisual features in response to an object name (Lee, Graham, et al., 2002). Although they found no category-specific effects, they did find an effect of attribute type: visual retrieval activated left posterior inferior temporal cortex, and nonvisual retrieval activated left middle temporal cortex and right fusiform cortex.

The relationship between visual processing demands and object category was elegantly demonstrated in a PET study by Rogers and colleagues (2005). Subjects categorized photographs of animals and vehicles at one of three levels of specificity (e.g., animal, bird, or robin; vehicle, boat, or ferry). Posterior fusiform activation was greater for animals than for vehicles *only* when subjects were categorizing pictures at an intermediate level (e.g., bird). The authors argued that the fusiform gyrus responds to the discrimination of items with similar visual representations, and that at the intermediate level of description only, animals have more overlapping visual properties than do vehicles. In addition, the modulation of the category effect by task demands provides a plausible explanation for the inconsistent pattern of category-specific effects described earlier.

The sensory-functional theory has been debated and refined as new observations have challenged the ability of this theory to parsimoniously account for the relevant neuropsychological data. Caramazza and colleagues have frequently called attention to some of the more problematic findings for the sensory-functional theory. An early objection was based on the observation that patients with living-things deficits have impairments across multiple attribute domains (Caramazza & Shelton, 1998). The sensory-functional theory, which presumes that living-things deficits result from loss of visual knowledge, would seem to predict normal nonvisual knowledge of living things. This objection was initially answered by Farah and McClelland (1991), who used a computational model to demonstrate the emergence of category-specific effects (across attributes) following damage to an interactive, attribute-specific systems. Key to the behavior of this model was the assumption that retrieval of a weakly represented attribute of a concept would depend on the activation of more strongly represented attributes, thus exhibiting a critical-mass effect. Thompson-Schill and colleagues (1999) sought physiological evidence for this assumption: for living things, retrieval of visual or nonvisual information should require activation of visual representations, because of the disproportionate weighting of visual information in the representations of living things. For nonliving things, no such dependence on visual knowledge should occur. As predicted, areas involved in visual knowledge retrieval were active during judgments about visual *and* nonvisual attributes of living things but only during judgments about visual attributes of nonliving things. These results lend credence to claims that category-specific activations actually reflect attribute-specific representations. (For a different interpretation of these data, see Caramazza, 2000).

A second criticism of Caramazza and colleagues' has proven more difficult to answer: the sensory-functional theory would seem to predict that patients with a degradation of the visual attribute domain would have impaired visual knowledge of all concepts, not just of living things. However, at least some patients with a living-things deficit have normal visual knowledge of nonliving things (Caramazza & Shelton, 1998). Here, we suggest a possible way to answer this objection, on the basis of some of the ideas that have emerged from the neuroimaging studies reviewed above. As we argued earlier, visual knowledge is most probably not a *single* attribute domain. Under this revised description of visual knowledge, in which visual knowledge itself is a distributed representation, a different set of predictions emerges: objects with multiple sources of knowledge about their appearance (e.g., vision, touch, actions) will be less susceptible to loss of any single source of visual knowledge (cf. Crutch & Warrington, 2003). We tend to have more sources of knowledge of the appearance of nonliving things, or at least of certain nonliving things. Thus, damage to ventral visual processing regions, which represent only one source of information, will not necessarily cause an impairment to other representations of appearance for these things. This idea was present in Allport's (1985) description of attribute domains (he used the example "cloud"), but it was not included in many sensory-functional theories that, in effect, collapsed across all types of visual knowledge. We argue here that the consideration of multiple sources of visual knowledge—and the way those sources vary across categories—may be crucial to our ability to explain category-specific phenomena.

There are some provocative data that lend credence to this conjecture: Borgo and Shallice (2001) described a patient with a living-things deficit who was also unable to identify nonliving things without a solid form (e.g., liquids). They argued that the affected attribute domains were purely visual qualities, such as color and texture, which are unrelated to object use. However, his knowledge—including visual knowledge—of artifacts presumed to have strong form-action links (i.e., affordances) was preserved (cf. De Renzi & Lucchelli, 1994; Tyler & Moss, 1997). Wolk and colleagues (2005) more directly examined the role of affordances in a patient with an apparent living-things deficit. They noted that this patient was impaired at recognizing not only animals but also artifacts that minimally afforded a particular action. In contrast, for artifacts that strongly afforded an action (e.g., piano), the patient could identify a line drawing of the object. The patient's ability to recognize shape, in the absence of a functional occipitotemporal representation of form, may have been mediated by action representations (for objects where the form affords the action). Subsequently, we demonstrated that this patient's knowledge of the *color* of objects was impaired (in contrast to his normal knowledge of both shape and size; Oliver et al., 2004).

In summary, the relationship between taxonomic categories and attribute domains, and the implications of that relationship for our understanding of phenomena such as category-specific deficits and activation patterns, is continuing to be informed by new neuroimaging studies of semantic memory. It is likely that at least some of the category-specific phenomena will be better understood as the result of processing within a distributed semantic system organized around a broad collection of sensorimotor attributes. However, refinements to the sensory-functional theory—perhaps beginning by abandoning the term "functional"—are clearly warranted by both the neuropsychological and the neuroimaging literature (figure 6.1). Finally, it is worth noting that evidence for attribute-specific representations does not necessarily refute the hypothesis that there are category-specific representations (and vice versa); it is possible that the organization of semantic representations has more than one governing principle. Several investigators have proposed the emergence of category representations as an intermediary between sensorimotor knowledge and language (e.g., Coltheart et al., 1998). The relationship of semantic memory to language, and the extent to which category-specific representations exist in either or both, should be the subject of future research.

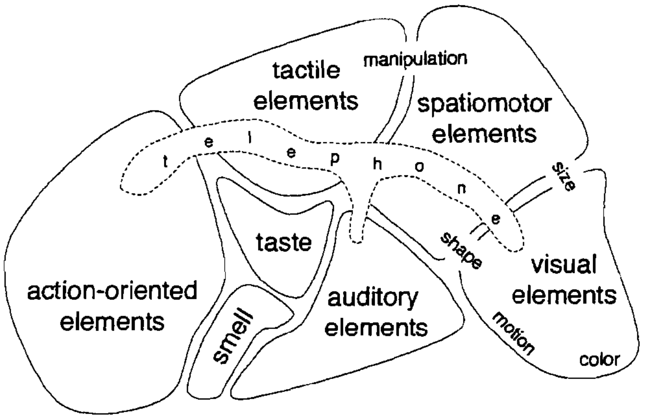

Figure 6.1
A revised version of Allport's (1985) influential model of distributed sensorimotor semantic representations, incorporating attribute domains that have been the subject of recent neuroimaging investigations.

Semantic Memory Retrieval

In the preceding section, we argued that semantic memory comprises, at least in part, a distributed set of representations that are tied to sensorimotor channels. Now we turn to the question of how these distributed representations are retrieved when one accesses semantic memory. In particular, we focus on two questions: First, we consider the relationship between the input modality and the process of semantic retrieval. Second, we discuss evidence that regions of PFC, in certain contexts, function to bias activity across distributed representations in semantic memory.

Accessing Semantic Memory from Words and Pictures

In neuropsychological investigations of semantic memory impairments, striking dissociations have been noted between visual and verbal input modalities. For example, patients with optic aphasia are unable to name visually presented objects, despite relatively spared perception of stimulus surface structure (Beauvois, 1982; Riddoch & Humphreys, 1987), and other patients perform significantly better with pictures than with words (e.g., Bub et al., 1988; Lambon Ralph & Howard, 2000; Saffran et al., 2003). These dissociations have led researchers to examine whether information from different input modalities may have differential access to different content within the conceptual system (see also Paivio, 1971; Shallice, 1988).

Many of the neuroimaging studies examining modality differences have reported regions of common activation and regions of modality-specific activations. For example, Vandenberghe and colleagues (1996) reported that semantic judgments of both words and pictures activated common regions in inferior temporal and frontal cortex, but also that a few areas were uniquely activated only by pictures (left posterior inferior temporal sulcus) or only by words (left anterior middle temporal gyrus and left inferior frontal sulcus). Similarly, Postler and colleagues (2003) observed common areas of activation across verbal and visual modalities (left inferior frontal gyrus and middle temporal gyrus) along with modality-specific areas (see also Bright et al., 2004 for a meta-analysis and report of similar findings).

Across various neuroimaging studies, a few regions have emerged as candidate regions for an amodal semantic system: left inferior frontal gyrus, middle temporal areas, and ventral temporal lobe, centered on the fusiform gyrus (see also Bookheimer et al., 1995; Moore & Price, 1999; Perani et al., 1999). Since activity in these common regions is invariant to input modality, these data seem to provide support for a unitary semantic system, such as that described by Caramazza and colleagues (1990). However, one must be cautious in interpreting "common activation" as "common representations." Given the limited spatial resolution of fMRI and PET, it is difficult to determine whether commonly activated brain regions indicate involvement of the same network of neurons or involvement of different networks of neurons existing in the same regions. One possible way to sidestep this limitation is discussed in "Issues" (below).

Neuroimaging evidence for input modality-specific activations proves equally problematic to interpret. One possibility is that these patterns reflect the existence of separate visual and verbal semantic systems (cf. Warrington & Shallice, 1984). Under this account, there is a redundant representation of semantic information in two different formats. A second possibility is that modality-specific activation patterns reflect differences in presemantic processing (Bright et al., 2004). This account might explain why the locations of putative modality-specific regions have been inconsistent across studies. We favor a third explanation: different input modalities may be preferentially associated with (or have preferential access to) different attribute domains in the distributed semantic system. By this logic, modality-specific effects do not reveal differences in the format of the representations accessed by different modalities, nor do they indicate redundant representations of the same semantic information. Rather, under this account, modality-specific effects reflect relations across attribute domains. For example, consider the relationship between form and manipulation knowledge (described in the Form section): Pictorial stimuli, which contain form information, may have preferential access to manipulation knowledge compared with word stimuli. Consistent with this claim, Chainay and Humphreys (2002) reported that normal subjects were faster at making action decision (e.g., pour or twist?) about picture stimuli than word stimuli. Also, using a free association task, Saffran et al. (2003) observed that subjects generated more action words (i.e., verbs) in response to pictures of objects than to written names of objects. Thus, activation patterns that appear specific to pictures could instead be pointing to areas specialized to represent action information. These three accounts of modality-specific activations have yet to be distinguished within the neuroimaging literature.

Selection of Semantic Representations

Consider the task of deciding whether a cherry is more similar to a rose or to a banana: On the one hand, cherries and bananas are both the fruits of a tree, both are edible, and both taste sweet. On the other hand, cherries and roses (at least the canonical ones) are red and approximately (in the case of the rose) spherical. If the attribute domains representing these three items were "polled" to assess similarity, conflict would occur. In order to answer the question, presuming you were not content simply to choose randomly, you might try to pay attention to some sources of information more than others. The process of resolving this sort of conflict is the subject of this section of the chapter.

In any model in which information is represented as a distributed pattern across multiple units, there exists the possibility for the partial activation of multiple, incompatible representations. The process of resolving this conflict and arriving at a stable representation can be referred to by the term *selection*: In any step along an information-processing stream, an appropriate representation must be selected for further processing. In some cases, selection of a representation may proceed successfully based entirely on local constraints (e.g., bottom-up inputs to a system). However, in other cases, conflict among competing representations may require top-down modulation of the selection process. We suggest that this intervention comes in the form of a modulatory signal from PFC that aids in the selection of an appropriate representation (cf. Fletcher et al., 2000; Miller & Cohen, 2001).

One example of variation in selection demands can be seen in the verb generation task: In response to the probe "cat," the activation of many weakly associated actions (e.g., "scratch," "purr") and/or of a strongly associated non-action (e.g., dog) might fail to produce sufficient activation to select any action representation. Both of these situations (underdetermined representations and prepotent representations) can induce conflict among active representations in working memory that requires top-down intervention (Botvinick et al., 2001). In contrast, in response to the probe "scissors," the strongly associated action "cut" might be activated from the input without additional demands for conflict resolution. The process of generating a verb related to "cat" and "scissors" thus differs in the selection demands.

Systematic manipulation of selection demands during semantic processing effectively modulates the fMRI response in the posterior left inferior frontal gyrus (pLIFG; Thompson-Schill et al., 1997). Subsequent studies have shown that this effect is specific to PFC (Thompson-Schill, D'Esposito, et al., 1999); is not limited to production tasks or to certain stimulus types, such as verbs (Thompson-Schill et al., 1997); is not an effect of response conflict (which has been linked to the anterior cingulate; Barch et al., 2000); and is not simply a reflection of task difficulty (Thompson-Schill, D'Esposito, et al., 1999). Rather, it appears that activity in the pLIFG is modulated by increasing demands to select a representation among competing sources of information (for a more detailed review, see Thompson-Schill, 2003). This conclusion is bolstered by evidence that patients with lesions to the pLIFG have impairments in word retrieval under high selection demands that are proportional to the extent of their lesion in the left frontal operculum (Thompson-Schill et al., 1998).

There are, naturally, other hypotheses about the role of ventrolateral PFC in semantic retrieval. Early observations of pLIFG activation during semantic retrieval led to consideration of the specific role this area may play in semantic memory (Petersen et al., 1988; Tulving et al., 1994) because the one region that is most consistently activated during semantic retrieval, across categories, attributes, and modalities, is the pLIFG. Our hypothesis that pLIFG is necessary for the selection of semantic information from competing alternatives, and not semantic retrieval per se, was motivated in part by the observation that naming pictures and making semantic comparisons do not consistently lead to pLIFG activation, despite the prima facie involvement of semantic knowledge in these tasks (e.g., Wise et al., 1991), and in part by the absence of converging evidence from lesion studies of the necessity of pLIFG for semantic retrieval. For example, Price and colleagues (1999) described a patient with pLIFG damage who was able to make semantic similarity judgments; PET activation in this patient revealed temporal, not frontal, activation associated with semantic processing.

Another, more specific, hypothesis about the role of pLIFG in semantic processing came from reports of increased activation in this region during semantic tasks involving tools. As was discussed above, knowledge about tool use has been hypothesized to depend on regions at or near ventral premotor cortex (adjacent to hand representations in motor cortex), typically including the region of pLIFG described above but extending more posteriorally into premotor cortex. To examine whether the left frontal response to tools can be further dissociated, we systematically manipulated object category (animals vs. tools) and selection demands (based on name agreement measures, cf. Kan & Thompson-Schill, 2004) in a picture-naming task. We identified two distinct neural components that jointly contribute to the previously reported tool-specific response: a posterior region, centered in left ventrolateral premotor cortex, that responds to motor knowledge retrieval, and an anterior region, centered in the left frontal operculum, that responds to selection among competing alternatives (Kan et al., 2006).

Other accounts of the role of the ventrolateral PFC in semantic retrieval draw a clear distinction between areas that represent semantic memory and areas that serve to maintain or manipulate those representations. One such proposal is that PFC is involved in temporary maintenance of semantic attributes in working memory (Gabrieli et al., 1998). Another alternative proposal is that activity in PFC reflects "controlled semantic retrieval" (Wagner et al., 2001). One key difference between these hypotheses and our own (see also Barch et al., 2000; Fletcher et al., 2000) is that we have described a potentially general-purpose mechanism that is not specific to semantic processing, whereas proposals of semantic working memory or controlled semantic retrieval are clearly specific to semantic retrieval. A mechanism that guides selection among competing representations may be necessary not only for some semantic retrieval tasks, but also for the successful performance of many tasks, including the ability to identify a color type instead of reading a word (i.e., the Stroop task; Milham, 2001; Perret, 1974), to reduce interference during working memory, or to maintain fixation instead of making a saccade to a target (i.e., the anti-saccade task; Guitton et al., 1985). For example, we have discussed the relation between the putative selection mechanism and working memory (Thompson-Schill et al., 2002), language processing (Novick et al., 2005; Thompson-Schill, in press) and visual selective attention (Kan & Thompson-Schill, 2004).

One reason to favor a more general account is that numerous lines of evidence suggest that PFC is not organized by stimulus content or domain but rather by processing type (for a review, see D'Esposito et al., 1998; Owen, 1997). Although many of these studies have compared visual and spatial forms of working memory, we have reported a similar lack of material specificity in pLIFG in a comparison of semantic and phonological working memory (Barde & Thompson-Schill, 2002). At least one other study also has failed to find differences between phonological and semantic processing (Gold & Buckner, 2002). However, these two studies exist alongside many reports of increased pLIFG activation during phonological processing (relative to semantic processing; e.g., Poldrack et al., 1999). What accounts for this discrepancy? We believe that the so-called phonological activation may actually reflect increased selection demands in response to representational conflict during the phonological tasks. These tasks typically require subjects to make judgments about the syllable structure or vowel sounds of words, as in the cherry-rose-banana example above. Such a comparison will likely involve ignoring other forms of similarity (e.g., similarity in various semantic attribute domains) in order to focus solely on phonological similarity. It is noteworthy that the two studies which have failed to find differences between phonological and semantic tasks in pLIFG (Barde & Thompson-Schill, 2002; Gold & Buckner, 2002) are the only two reported comparisons of semantic processing of words to phonological processing of *non-words* (where conflicting semantic similarity would not be a problem).

Summary

In this review of neuroimaging studies of semantic memory, we have presented evidence for a semantic memory system in which concept representations are distributed across sensorimotor domains. Expanding on previous descriptions of these sensorimotor representations, the model we have depicted in figure 6.1 includes putative subdivisions that are emerging from neuropsychological and neuroimaging studies of perception, action, and semantic retrieval. For example, we argue for multiple representations of visual knowledge attributes that parallel distinctions made in visual neuroscience. We also propose a subdivision of action knowledge across motor domains and abstract domains of knowledge. These modifications provide a more complete description of the many sources of information that we have about concepts, and may prove useful in understanding selective breakdowns in semantic memory. We have argued that activation of information represented across these various sensorimotor domains will depend on the nature of the specific concept being retrieved (i.e., what is known about it), the input modality (i.e., what part of the distributed pattern is determined by the input), and biasing mechanisms that guide competitive interactions between representations. Consideration of these factors can be crucial for the interpretation of neuroimaging patterns across the wide variety of tasks and stimuli that we have described here. Finally, we have described how interactions between different domains (e.g., linguistic and perceptual) may alter sensorimotor representations and allow for the emergence of abstract semantic representations.

Issues

Tulving titled his 1986 response to the commentaries on his précis on the organization of memory "Episodic and semantic memory: Where should we go from here?" We might ask the same question today. And more precisely, for this volume, we ask, "Where should neuroimaging studies go from here?" Throughout this chapter, we have tried to highlight areas of inquiry that are still in need of clarification. Here, we outline a few new directions in which we believe the field is (or should be) moving. These are our predictions for three general questions about semantic memory that will be covered in the third edition of this volume.

Adapting to Change

One way to characterize the kind of information that is represented by a population of neurons is with a description of the similarity space of neural responses. Just as one can discern the function of an individual neuron by determining what stimulus variations affect its firing rate and what variations do not, so the description of a population of neurons can be informed by an understanding of the factors that determine overlap in firing patterns. In a distributed representation of some aspect of semantic memory, the similarity of two patterns will reflect the similarity between two concepts along some dimension: If you can figure out the organizing principles behind the similarity space, you will understand what properties the area represents.

Until recently, attempts to determine the population code of a region using functional neuroimaging methods seemed well beyond any hoped-for resolution of these methods. However, several investigators have made arguments about representational similarity using a technique that is referred to as "fMRI adaptation" (Grill-Spector & Malach, 2001). The logic of the approach depends on the assumption that the integrated fMRI response to a sequentially presented pair of stimuli that are representationally similar will be less than to a pair of stimuli that are representationally distinct, because in the former case, the repeated activation of the same set of neurons will produce a reduced (i.e., adapted) response (Muller et al., 1999).

This logic has been applied to studies of object and space representations in occipital and temporal cortex (Epstein et al., 2003; Grill-Spector et al., 1999; Kourtzi & Kanwisher, 2001).

There are a number questions that could be addressed using this technique. An obvious place to begin would be to characterize the similarity space of regions hypothesized to function as attribute domains in semantic memory. For example, as illustrated in figure 6.2, a region that represents color knowledge should show weaker (i.e., adapted) responses during retrieval of concepts that are the same color than it does for concepts that vary in color (but are similar in other ways). Likewise, the technique could also be used to investigate the similarity space of anterior temporal cortex, which has been described as the repository of more abstract representations. Finally, fMRI adaptation could be used to understand the phenomenon that we have referred to as the "anterior shift" in semantic representations. If this shift represents the gradual transformation from sensorimotor to abstract representa-

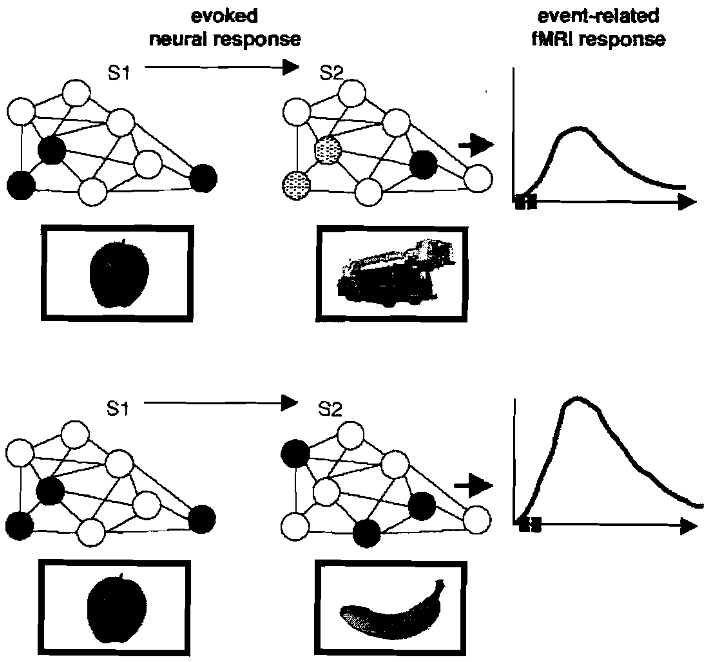

Figure 6.2
A hypothetical example of the application of fMRI adaptation to the study of semantic memory representations. In the example shown here, the fMRI response in an area that represents color knowledge (e.g., V4) should be less to a pair of stimuli with similar colors than to a pair with different colors, regardless of other similarities and differences. In contrast, the reverse pattern should be expected in an area that represents more abstract properties of objects. Figure courtesy of Russell Epstein.

tions, as we have hypothesized, the similarity space (and thus the adaptation effects) should reflect this shift.

Connecting the Dots

In the opening pages of his book on networks, Albert-Lászlő Barabási considers the effect of reductionism on scientific progress: "The assumption is that once we understand the parts, it will be easy to grasp the whole. Divide and conquer; the devil is in the details. Therefore for decades we have been forced to see the world through its constituents. . . . Now we are close to knowing just about everything there is to know about the pieces. But we are as far as we have ever been from understanding nature as a whole" (Barabási, 2002, 6).

For much of this chapter, we have been taking apart semantic memory. Although we are not quite in the position to say we know "just about everything there is to know" about the pieces that make up our semantic memory networks, the contributions of neuroimaging to that enterprise are on the rise. The next step—or a parallel venture—will be to study the network properties of semantic memory, including how it develops and how it degrades. We have already seen the influence of "network thinking" on cognitive models of semantic memory; one such example is the work of McClelland and Rogers described earlier (McClelland & Rogers, 2003), and there are many others. However, most neuroimaging studies of semantic memory are still largely reductionist, even if the results describe "networks of activation." This will change.

Emerging neuroimaging methods are making it easier to describe the structural networks that provide the scaffolding for semantic memory and the correlated patterns that emerge: Studies that invasively trace anatomical projections in monkeys (Petrides & Pandya, 2002) can now be approximated in humans using diffusion tensor imaging (DTI) and functional connectivity analyses. For example, DTI-derived estimates of white matter density can be used to predict the magnitude of the fMRI response in adjacent gray matter during working memory tasks (Olesen et al., 2003). Patterns of task-dependent correlated activity between anterior and posterior cortical regions have been used to describe functions of PFC (Bokde et al., 2001). These methods are beginning to be used to describe networks that could give rise to the sorts of computational principles proposed by cognitive theorists (McClelland & Rogers, 2003). Perhaps these inquiries will lead to the discovery that semantic networks—like networks that describe the Internet, the economy, and the cell—have the same "hublike" properties that govern many evolving networks and that give those networks both resilience and vulnerability in predictable ways (Barabási, 2002). Networks are everywhere, and we will be hearing more about them in the functional neuroimaging of semantic memory.

Embracing Differences

Psychologists can be divided into those who treat subject variability as noise and those who treat it as data. In the short history of functional neuroimaging, subject variability has been treated almost exclusively as noise. We hate it. We try to get rid of it. Anything to get those random-effects t-values higher!

Of course, as the "other half" could tell us, variability is noise only if you can't explain it. And, as cognitive neuroscientists have started making attempts to explain subject variability in activation patterns, they are discovering that, in many cases, it can be explained. We are now witnessing the gradual emergence of a cognitive neuroscience of individual differences: variation in V1 activation is related to contrast discrimination thresholds (Boynton et al., 1999); variation in parahippocampal cortex activation is related to navigational competence (Epstein et al., 2005); variation in amygdala activation is related to baseline mood (Schaefer et al., 2002) and personality variables (Canli et al., 2002); and variation in PFC activation is related to fluid intelligence (Gray et al., 2003). Closer to the topic of this chapter, Farah and Peronnet (1989) observed that ERP patterns evoked during mental imagery varied as a function of self-reported skill in imagery, and Kosslyn and colleagues (1996) reported PET activation in V1 that correlated with response time on a visualization task. But, by and large, investigators using neuroimaging to study semantic memory have not yet jumped on the "individual differences" bandwagon. Perhaps this is because many define semantic memory as *shared* knowledge, to distinguish it from the individual experiences that form our episodic memory. But semantic memories are shared only to the extent that our experiences are shared.

There have been occasional attempts to explain variation in behavioral category-specific effects (in normal subjects and brain-damaged patients) in terms of individual experience (Laws, 2000). For example, Wilson and colleagues (1995) described the living-things deficit of a professional musician (Patient C) who, unlike many patients with living-things deficits, displayed preserved knowledge of musical instruments; one explanation of the variation in this pattern is that a musician has more sources of information (e.g., tactile, motor) about instruments than others do, leaving the category of musical instruments less susceptible to degradation following focal damage. There are also reports of the effects of *extreme* variation in experience on neuroimaging patterns, such as that observed in comparisons of blind and sighted individuals (e.g., Burton et al., 2003; Roder et al., 2002). For example, Noppeney and colleagues (2003) compared activation during semantic retrieval in sighted and early-blind subjects. Interestingly (relevant to the point about networks above), they found similar profiles of activation but different patterns of functional connectivity within those networks that the authors attribute to an abnormal pruning process.

We observed variation during semantic retrieval that may result from slightly *less* extreme variations in experience: left- and right-handed tool use. We found that naming photographs of manipulable objects was, as expected, associated with increased activity in left inferior frontal cortex, extending from the frontal operculum to ventrolateral premotor cortex (Kan et al., 2006). Crucial to the interpretation of the premotor response, individual variation in motor experience with these objects was highly correlated with the magnitude of the response in ventrolateral premotor cortex, but not in the frontal operculum. These results provide the first demonstration of a domain-specific response in premotor cortex during retrieval of stored knowledge that is both linked to motor experience and distinguishable from domain-general cognitive control functions of prefrontal cortex.

A complete theory of the neural bases of semantic memory not only will describe the "average" semantic network but also will be able to predict individual variation around that average. It is easy to talk about the role of sensorimotor experience in the formation of a semantic network, but it is another matter to measure it, to manipulate it, and to quantify its effects. We anticipate seeing efforts to do just that in the neuroimaging of semantic memory, such as What factors predict the developmental progression to mature semantic activation patterns? How does motor experience affect object representations in dorsal and ventral visual areas? How are activation patterns during semantic retrieval related to other visuomotor competencies?

Returning to *An Essay Concerning Human Understanding*, Locke argued that individuals "come to be furnished with fewer or more simple ideas from without, according as the objects they converse with afford greater or less variety; and from the operations of their minds within, according as they more or less reflect on them" (p. 61). Variations both in our experiences with the world and in the way in which those experiences are represented should have profound, and perhaps predictable, effects on the organization and retrieval of semantic memory. A complete understanding of the representation of "shared knowledge" may depend on our ability to describe aspects of these representations that aren't shared, to characterize variations in the neural bases of semantic memory.

Acknowledgments

We would like to thank the individuals who have contributed in various ways to the ideas we have discussed in this chapter. We've talked about all of these ideas in some form or another with members of the Thompson-Schill lab, including Laura Barde, Marina Bedny, Rob Goldberg, Dawn Morales, Stacey Schaefer, Tatiana Schnur, Geeta Shivde, and numerous undergraduate research assistants. We are continually appreciative of frequent discussions and active collaborations with our colleagues at Penn, including Geoff Aguirre, David Brainard, Anjan Chatterjee, Andy Connolly, Branch Coslett, Marc Egeth, Russell Epstein, Martha Farah, Lila Gleitman, Amishi Jha, Joe Kable, Jared Novick, Marianna Stark, and John Trueswell. From farther away, we acknowledge the contributions of our collaborators, including Larry Barsalou, Laurel Buxbaum, Mark D'Esposito, John Jonides, Bob Knight, Myrna Schwartz, Ed Smith, Diane Swick, and Lynette Tippett. Finally, we are grateful to the National Institutes of Health, the Searle Scholars Program, and the University of Pennsylvania Research Foundation for the generous support of our research program.

References

Adams, R. B., & Janata, P. (2002). A comparison of neural circuits underlying auditory and visual object categorization. *NeuroImage* 16(2), 361–377.

Allport, D. A. (1985). Distributed memory, modular subsystems and dysphasia. In S. K. Newman & R. Epstein (Eds.), *Current Perspectives in Dysphasia*, 32–60. Edinburgh: Churchill Livingstone.

Barabási, A. (2002). *Linked: How Everything Is Connected to Everything Else and What It Means for Business, Science, and Everyday Life.* New York: Plume.

Barch, D. M., Braver, T. S., Sabb, F. W., & Noll, D. C. (2000). Anterior cingulate and the monitoring of response conflict: Evidence from an fMRI study of overt verb generation. *Journal of Cognitive Neuroscience* 12(2), 298–309.

Barde, L. H., & Thompson-Schill, S. L. (2002). Models of functional organization of the lateral prefrontal cortex in verbal working memory: Evidence in favor of the process model. *Journal of Cognitive Neuroscience* 14(7), 1054–1063.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral Brain Science* 22, 577–660.

Basso, A., Capitani, E., & Laiacona, M. (1988). Progressive language impairment without dementia: A case with isolated category specific semantic defect. *Journal of Neurology, Neurosurgery & Psychiatry* 51(9), 1201–1207.

Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2002). Parallel visual motion processing streams for manipulable objects and human movements. *Neuron* 34(1), 149–159. (See comment.)

Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2003). FMRI responses to video and point-light displays of moving humans and manipulable objects. *Journal of Cognitive Neuroscience* 15(7), 991–1001.

Beauregard, M., Chertkow, H., Bub, D., Murtha, S., Dixon, R., & Evans, A. (1997). The neural substrate for concrete, abstract, and emotional word lexica: A positron emission tomography study. *Journal of Cognitive Neuroscience* 9, 441–461.

Beauvois, M. F. (1982). Optic aphasia: A process of interaction between vision and language. *Philosophical Transactions of the Royal Society of London*, B298, 35–47.

Binkofski, F., Buccino, G., Posse, S., Seitz, R. J., Rizzolatti, G., & Freund, H. (1999). A fronto-parietal circuit for object manipulation in man: Evidence from an fMRI-study. *European Journal of Neuroscience* 11(9), 3276–3286.

Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J., & Freund, H. J. (1999). A parieto-premotor network for object manipulation: Evidence from neuroimaging. *Experimental Brain Research* 128(1–2), 210–213.

Bokde, A. L., Tagamets, M. A., Friedman, R. B., & Horwitz, B. (2001). Functional interactions of the inferior frontal cortex during the processing of words and word-like stimuli. *Neuron* 30(2), 609–617.

Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *Journal of Neuroscience* 16(11), 3737–3744.

Bookheimer, S. Y., Zeffiro, T. A., Blaxton, T., Gaillard, W., & Theodore, W. (1995). Regional cerebral blood flow during object naming and word reading. *Human Brain Mapping* 3, 93–106.

Borgo, F., & Shallice, T. (2001). When living things and other "sensory quality" categories behave in the same fashion: A novel category specificity effect. *Neurocase* 7, 201–220.

Boronat, C. B., Buxbaum, L. J., Coslett, H. B., Tang, K., Saffran, E. M., Kimberg, D. Y., & Detre, J. A. (2005). Distinctions between manipulation and function knowledge of objects: Evidence from functional magnetic resonance imaging. *Cognitive Brain Research* 23, 361–373.

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review* 108(3), 624–652.

Boynton, G. M., Demb, J. B., Glover, G. H., & Heeger, D. J. (1999). Neuronal basis of contrast discrimination. *Vision Research* 39(2), 257–269.

Breedin, S. D., Saffran, E. M., & Coslett, H. B. (1994). Reversal of the concreteness effect in a patient with semantic dementia. *Cognitive Neuropsychology* 11, 617–660.

Bright, P., Moss, H., & Tyler, L. K. (2004). Unitary vs multiple semantics: PET studies of word and picture processing. *Brain and Language* 89, 417–432.

Bub, D., Black, S., Hampson, E., & Kertesz, A. (1988). Semantic encoding of pictures and words: Some neuropsychological observations. *Cognitive Neuropsychology* 5(1), 27–66.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience* 13(2), 400–404.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *Journal of Cognitive Neuroscience* 16(1), 114–126.

Buckner, R. L., Petersen, S. E., Ojemann, J. G., Miezin, F. M., Squire, L. R., & Raichle, M. E. (1995). Functional anatomical studies of explicit and implicit memory retrieval tasks. *Journal of Neuroscience* 15(1), 12–29.

Burton, H., Diamond, J. B., & McDermott, K. B. (2003). Dissociating cortical regions activated by semantic and phonological tasks: A fMRI study in blind and sighted people. *Journal of Neurophysiology* 90(3), 1965–1982.

Buxbaum, L. J., & Saffran, E. M. (1998). Knowing "how" vs. "what for": A new dissociation. *Brain and Language* 65, 73–86.

Buxbaum, L. J., Veramonti, T., & Schwartz, M. F. (2000). Function and manipulation tool knowledge in apraxia: Knowing "what for" but not "how." *Neurocase* 6, 83–97.

Calvert, G. A., Bullmore, E. T., Brammer, M. J., Campbell, R., Williams, S. C., McGuire, P. K., et al. (1997). Activation of auditory cortex during silent lipreading. *Science* 276(5312), 593–596.

Calvert, G. A., & Campbell, R. (2003). Reading speech from still and moving faces: The neural substrates of visible speech. *Journal of Cognitive Neuroscience* 15(1), 57–70.

Campbell, R., MacSweeney, M., Surguladze, S., Calvert, G., McGuire, P., Suckling, J., et al. (2001). Cortical substrates for the perception of face actions: An fMRI study of the specificity of activation for seen speech and for meaningless lower-face acts (gurning). *Cognitive Brain Research* 12(2), 233–243.

Canli, T., Sivers, H., Whitfield, S. L., Gotlib, I. H., & Gabrieli, J. D. (2002). Amygdala response to happy faces as a function of extraversion. *Science* 296(5576), 2191.

Capitani, E., Laiacona, M., Mahon, B., & Caramazza, A. (2003). What are the facts of semantic category-specific deficits? A critical review of the evidence. *Cognitive Neuropsychology* 20, 213–261.

Cappa, S. F., Perani, D., Schnur, T., Tettamanti, M., & Fazio, F. (1998). The effects of semantic category and knowledge type on lexical-semantic access: A PET study. *NeuroImage* 8(4), 350–359.

Caramazza, A. (2000). Minding the facts: A comment on Thompson-Schill et al.'s "A neural basis for category and modality specificity of semantic knowledge." *Neuropsychologia* 38(7), 944–949. (comment.)

Caramazza, A., Hillis, A. E., Rapp, B. C., & Romani, C. (1990). The multiple semantics hypothesis: Multiple confusions? *Cognitive Neuropsychology* 7, 161–189.

Caramazza, A., & Shelton, J. R. (1998). Domain-specific knowledge systems in the brain: The animate-inanimate distinction. *Journal of Cognitive Neuroscience* 10(1), 1–34.

Cerf-Ducastel, B., & Murphy, C. (2003). fMRI brain activation in response to odors is reduced in primary olfactory areas of elderly subjects. *Brain Research* 986(1–2), 39–53.

Chainay, H., & Humphreys, G. W. (2002). Privileged access to action for objects relative to words. *Psychonomic Bulletin & Review* 9(2), 348–355.

Chao, L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience* 2, 913–919.

Chao, L., & Martin, A. (1999). Cortical regions associated with perceiving, naming, and knowing about colors. *Journal of Cognitive Neuroscience* 11(1), 25–35.

Chao, L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *NeuroImage* 12, 478–484.

Charlot, V., Tzourio, N., Zilbovicius, M., Mazoyer, B., & Denis, M. (1992). Different mental imagery abilities result in different regional cerebral blood flow activation patterns during cognitive tasks. *Neuropsychologia* 30, 565–580.

Coltheart, M., Inglis, L., Cupples, L., Michie, P., Bates, A., & Budd, B. (1998). A semantic subsystem of visual attributes. *Neurocase* 4, 353–370.

Crutch, S. J., & Warrington, E. K. (2003). The selective impairment of fruit and vegetable knowledge: A multiple processing channels account of fine-grain category specificity. *Cognitive Neuropsychology* 20, 355–372.

D'Esposito, M., Aguirre, G. K., Zarahn, E., Ballard, D., Shin, R. K., & Lease, J. (1998). Functional MRI studies of spatial and nonspatial working memory. *Cognitive Brain Research* 7(1), 1–13.

D'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. J., et al. (1997). A functional MRI study of mental image generation. *Neuropsychologia* 35(5), 725–730.

Dade, L. A., Jones-Gotman, M., Zatorre, R. J., & Evans, A. C. (1998). Human brain function during odor encoding and recognition. A PET activation study. *Annals of the New York Academy of Sciences* 855, 572–574.

Dalla Barba, G., Parlato, V., Jobert, A., Samson, Y., & Pappata, S. (1998). Cortical networks implicated in semantic and episodic memory: Common or unique? *Cortex* 34(4), 547–561.

Damasio, A. R. (1989). The brain binds entities and events by multiregional activation from convergence zones. *Neural Computation* 1, 123–132.

Damasio, A. R., McKee, J., & Damasio, H. (1979). Determinants of performance in color anomia. *Brain & Language* 7(1), 74–85.

Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D., & Damasio, A. R. (1996). A neural basis for lexical retrieval. *Nature* 380(6574), 499–505. (See comments.) Published erratum appears in *Nature* 381(6595) (1996), 810.

De Renzi, E., & Lucchelli, F. (1994). Are semantic systems separately represented in the brain? The case of living category impairment. *Cortex* 30, 3–25.

De Volder, A. G., Toyama, H., Kimura, Y., Kiyosawa, M., Nakano, H., Vanlierde, A., et al. (2001). Auditory triggered mental imagery of shape involves visual association areas in early blind humans. *NeuroImage* 14(11), 129–139.

Decety, J. (1996). Do imagined and executed actions share the same neural substrate? *Cognitive Brain Research* 3(2), 87–93.

Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., et al. (1997). Brain activity during observation of actions: Influence of action content and subject's strategy. *Brain* 120(10), 1763–1777.

Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., et al. (1994). Mapping motor representations with positron emission tomography. *Nature* 371, 600–602.

Dennis, M. (1976). Dissociated naming and locating of body parts after left anterior temporal lobe resection: An experimental case study. *Brain and Language* 3, 147–163.

Devlin, J. T., Russell, R. P., Davis, M. H., Price, C. J., Moss, H. E., Fadili, M. J., et al. (2002). Is there an anatomical basis for category-specificity? Semantic memory studies in PET and fMRI. *Neuropsychologia* 40(1), 54–75.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science* 293(5539), 2470–2473. (See comment.)

Epstein, R., Graham, K. S., & Downing, P. E. (2003). Viewpoint-specific scene representations in human parahippocampal cortex. *Neuron* 37(5), 865–876.

Epstein, R., Higgins, J. S., & Thompson-Schill, S. L. (2005). Learning places from views: Variation in scene processing as a function of experience and navigational ability. *Journal of Cognitive Neuroscience* 17, 73–83.

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature* 392(6676), 598–601.

Farah, M. J. (2000). *The Cognitive Neuroscience of Vision.* Malden, MA: Blackwell.

Farah, M. J., & McClelland, J. L. (1991). A computational model of semantic memory impairment: Modality specificity and emergent category specificity. *Journal of Experimental Psychology: General* 120(4), 339–357.

Farah, M. J., McMullen, P. A., & Meyer, M. M. (1991). Can recognition of living things be selectively impaired? *Neuropsychologia* 29, 185–193.

Farah, M. J., & Peronnet, F. (1989). Event-related potentials in the study of mental imagery. *Journal of Psychophysiology* 3, 99–109.

Farah, M. J., Peronnet, F., Gonon, M. A., & Giard, M. H. (1988). Electrophysiological evidence for a shared representational medium for visual images and visual percepts. *Journal of Experimental Psychology: General* 117(3), 248–257.

Fletcher, P. C., Shallice, T., & Dolan, R. J. (2000). "Sculpting the response space"—an account of left prefrontal activation at encoding. *NeuroImage* 12(4), 404–417.

Gabrieli, J. D., Cohen, N. J., & Corkin, S. (1988). The impaired learning of semantic knowledge following bilateral medial temporal-lobe resection. *Brain and Cognition* 7(2), 157–177.

Gabrieli, J. D., Poldrack, R. A., & Desmond, J. E. (1998). The role of left prefrontal cortex in language and memory. *Proceedings of the National Academy of Sciences USA* 95(3), 906–913.

Galton, C. J., Patterson, K., Graham, K., Lambon-Ralph, M. A., Williams, G., Antoun, N., et al. (2001). Differing patterns of temporal atrophy in Alzheimer's disease and semantic dementia. *Neurology* 57(2), 216–225.

Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: An fMRI study. *Cognitive Brain Research* 20, 226–241.

Gentner, D. (1978). On relational meaning: The acquisition of verb meaning. *Child Development* 49(4), 988–998.

Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (2002). The role of action knowledge in the comprehension of artefacts—a PET study. *NeuroImage* 15(1), 143–152.

Gerlach, C., Law, I., & Paulson, O. B. (2002). When action turns into words: Activation of motor-based knowledge during categorization of manipulable objects. *Journal of Cognitive Neuroscience* 14(8), 1230–1239.

Gibson, J. J. (1979). *The Ecological Approach to Visual Perception.* Boston: Houghton Mifflin.

Gold, B. T., & Buckner, R. L. (2002). Common prefrontal regions coactivate with dissociable posterior regions during controlled semantic and phonological tasks. *Neuron* 35(4), 803–812.

Goldberg, R. F., Perfetti, C. A., & Schneider, W. (2004). *The role of left inferior prefrontal cortex in semantic processing.* Paper presented at the Eleventh Annual Meeting of the Cognitive Neuroscience Society, San Francisco.

Goldenberg, G., Podreka, I., Steiner, M., Franzen, P., & Deecke, L. (1991). Contributions of occipital and temporal brain regions to visual and acoustic imagery—a spect study. *Neuropsychologia* 29(7), 695–702.

Goldenberg, G., Podreka, I., Steiner, M., & Willmes, K. (1987). Patterns of regional cerebral blood flow related to memorizing of high and low imagery words: An emission computer tomography study. *Neuropsychologia* 25(3), 473–485.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences* 15, 20–25.

Goodglass, H., Klein, B., Carey, P., & Jones, K. J. (1966). Specific semantic word categories in aphasia. *Cortex* 2, 74–89.

Grabowski, T. J., Damasio, H., & Damasio, A. R. (1998). Premotor and prefrontal correlates of category-related lexical retrieval. *NeuroImage* 7, 232–243.

Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Experimental Brain Research* 112(1), 103–111.

Grafton, S. T., Fadiga, L., Arbib, M. A., & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *NeuroImage* 6, 231–236.

Graham, K. S., Simons, J. S., Pratt, K. H., Patterson, K., & Hodges, J. R. (2000). Insights from semantic dementia on the relationship between episodic and semantic memory. *Neuropsychologia* 38(3), 313–324.

Gray, J. R., Chabris, C. F., & Braver, T. S. (2003). Neural mechanisms of general fluid intelligence. *Nature Neuroscience* 6(3), 316–322. (See comment.)

Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping* 12(1), 1–19.

Grèzes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., & Decety, J. (2001). Does perception of biological motion rely on specific brain regions? *NeuroImage* 13(5), 775–785.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron* 24(1), 187–203.

Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychologica* (Amsterdam), 107(1–3), 293–321.

Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., et al. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience* 12(5), 711–720.

Grossman, M., Koenig, P., DeVita, C., Glosser, G., Alsop, D., Detre, J., et al. (2002). The neural basis for category-specific knowledge: An fMRI study. *NeuroImage* 15(4), 936–948.

Guitton, D., Buchtel, H. A., & Douglas, R. M. (1985). Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal-directed saccades. *Experimental Brain Research* 58, 455–472.

Hart, J., Berndt, R. S., & Caramazza, A. (1985). Category-specific naming deficit following cerebral infarction. *Nature* 316, 439–440.

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293(5539), 2425–2430. (See comment.)

Hodges, J. R., Patterson, K., & Tyler, L. K. (1994). Loss of semantic memory: Implications for the modularity of mind. *Cognitive Neuropsychology* 11(5), 505–542.

Howard, R. J., Brammer, M., Wright, I., Woodruff, P. W., Bullmore, E. T., & Zeki, S. (1996). A direct demonstration of functional specialization within motion-related visual and auditory cortex of the human brain. *Current Biology* 6(8), 1015–1019.

Howard, R. J., ffytche, D. H., Barnes, J., McKeefry, D., Ha, Y., Woodruff, P. W., et al. (1998). The functional anatomy of imagining and perceiving colour. *NeuroReport* 9, 1019–1023.

Ishai, A., Ungerleider, L. G., Martin, A., & Haxby, J. V. (2000). The representation of objects in the human occipital and temporal cortex. *Journal of Cognitive Neuroscience* 12(supp. 2), 35–51.

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences USA* 96(16), 9379–9384.

Kable, J. W., Lease-Spellmeyer, J., & Chatterjee, A. (2002). Neural substrates of action event knowledge. *Journal of Cognitive Neuroscience* 14(5), 795–805.

Kan, I. P., Barsalou, L. W., Solomon, K. O., Minor, J. K., & Thompson-Schill, S. L. (2003). Role of mental imagery in a property verification task: fMRI evidence for perceptual representations of conceptual knowledge. *Cognitive Neuropsychology* 20, 525–540.

Kan, I. P., Kable, J. W., Van Scoyoc, A., Chatterjee, A., & Thompson-Schill, S. L. (2006). Fractionating left frontal response to tools: Dissociable effects of selection and action. *Journal of Cognitive Neuroscience* 18.

Kan, I. P., & Thompson-Schill, S. L. (2004). Effect of name agreement on prefrontal activity during overt and covert picture naming. *Cognitive, Affective, & Behavioral Neuroscience* 4, 43–57.

Kan, I. P., & Thompson-Schill, S. L. (2004). Selection from perceptual and conceptual representations. *Cognitive, Affective, & Behavioral Neuroscience* 4, 466–482.

Kanwisher, N., & Duncan, J. (Eds.). (2003). *Attention and Performance XX: Functional Neuroimaging of Visual Cognition.* Oxford: Oxford University Press.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience* 17(11), 4302–4311.

Karaken, D. A., Mosnik, D. M. M., Doty, R. L., Dzemidzic, M., & Hutchins, G. D. (2003). Functional anatomy of human odor sensation, discrimination, and identification in health and aging. *Neuropsychology* 17(3), 482–495.

Kellenbach, M. L., Brett, M., & Patterson, K. (2001). Large, colorful or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge. *Cognitive, Affective, & Behavioral Neuroscience* 1(3), 207–221.

Kellenbach, M. L., Brett, M., & Patterson, K. (2003). Actions speak louder than functions: The importance of manipulability and action in tool representation. *Journal of Cognitive Neuroscience* 15(1), 30–46.

Kiehl, K. A., Liddle, P. F., Smith, A. M., Mendrek, A., Forster, B. B., & Hare, R. D. (1999). Neural pathways involved in the processing of concrete and abstract words. *Human Brain Mapping* 7(4), 225–233.

Konorski, J. (1967). *Integrative Activity of the Brain.* Chicago: University of Chicago Press.

Kosslyn, S. M. (1980). *Image and Mind.* Cambridge, MA: Harvard University Press.

Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Maljkovic, V., Weise, S., Chabris, C. F., et al. (1993). Visual mental imagery activates topographically organized visual cortex: PET investigations. *Cognition* 5, 139–181.

Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J. P., Thompson, W. L., et al. (1999). The role of area 17 in visual imagery: Convergent evidence from PET and rTMS. [erratum appears in Science 1999 May 7;284(5416):197]. *Science* 284(5411), 167–170. (See comment.) Erratum appears in *Science* 284(5416) (1999), 197.

Kosslyn, S. M., & Thompson, W. L. (2000). Shared mechanisms in visual imagery and visual perception: Insights from cognitive neuroscience. In M. S. Gazzaniga (Ed.), *The New Cognitive Neurosciences*, 2nd ed., 975–985. Cambridge, MA: MIT Press.

Kosslyn, S. M., Thompson, W. L., Kim, I. J., Rauch, S. L., & Alpert, N. M. (1996). Individual differences in cerebral blood flow in area 17 predict the time to evaluate visualized letters. *Journal of Cognitive Neuroscience* 8, 78–82.

Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science* 293(5534), 1506–1509.

Lambon-Ralph, M. A., & Howard, D. (2000). Gogi aphasia or semantic dementia? Simulating and assessing poor verbal comprehension in a case of progressive fluent aphasia. *Cognitive Neuropsychology* 17, 437–465.

Laws, K. R. (2000). Category-specific naming errors in normal subjects: The influence of evolution and experience. *Brain & Language* 75(1), 123–133.

Lee, A. C., Graham, K. S., Simons, J. S., Hodges, J. R., Owen, A. M., & Patterson, K. (2002). Regional brain activations differ for semantic features but not categories. *NeuroReport* 13(12), 1497–1501.

Lee, A. C., Robbins, T. W., Graham, K. S., & Owen, A. M. (2002). "Pray or Prey?" Dissociation of semantic memory retrieval from episodic memory processes using positron emission tomography and a novel homophone task. *NeuroImage* 16(3, pt 1), 724–735.

Levy, L. M., Henkin, R. I., Lin, C. S., Finley, A., & Schellinger, D. (1999). Taste memory induces brain activation as revealed by functional MRI. *Journal of Computer Assisted Tomography* 23(4), 499–505.

Lewis, C. S. (1989). *A Grief Observed.* New York: HarperCollins.

Locke, J. (1690/1995). *An Essay Concerning Human Understanding.* New York: Prometheus Books.

Maguire, E. A., & Frith, C. D. (2004). The brain network associated with acquiring semantic knowledge. *NeuroImage* 22(1), 171–178.

Margolis, E., & Laurence, S. (Eds.). (1999). *Concepts: Core Readings.* Cambridge, MA: MIT Press.

Martin, A. (2001). Functional neuroimaging of semantic memory. In R. Cabeza & A. Kingstone (Eds.), *Handbook of Functional Neuroimaging of Cognition*, 153–186. Cambridge, MA: MIT Press.

Martin, A., & Caramazza, A. (2003). Neuropsychological and neuroimaging perspectives on conceptual knowledge: An introduction. *Cognitive Neuropsychology* 20, 195–212.

Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* 270(5233), 102–105.

Martin, A., Ungerleider, L. G., & Haxby, J. V. (2000). Category-specificity and the brain: The sensory-motor model of semantic representations of objects. In M. S. Gazzaniga (Ed.), *The Cognitive Neurosciences*, 2nd ed. Cambridge MA: MIT Press.

Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature* 379, 649–652.

Mayes, A. R., Montaldi, D., Spencer, T. J., & Roberts, N. (2004). Recalling spatial information as a component of recently and remotely acquired episodic or semantic memories: An fMRI study. *Neuropsychology* 18(3), 426–441.

McClelland, J. L., & Rogers, T. T. (2003). The parallel distributed processing approach to semantic cognition. *Nature Reviews Neuroscience* 4(4), 310–322.

McKenna, P., & Warrington, E. K. (1980). Testing for nominal dysphasia. *Journal of Neurology, Neurosurgery & Psychiatry* 43(9), 781–788.

Milham, M. P., Banich, M. T., Webb, A., Barad, V., Cohen, N. J., Wszalek, T., & Kramer, A. F. (2001). The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Cognitive Brain Research* 12, 467–473.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience* 24, 167–202.

Moore, C. J., & Price, C. (1999). Three distinct ventral occipitotemporal regions for reading and object naming. *NeuroImage* 10, 181–192.

Muller, J. R., Metha, A. B., Krauskopf, J., & Lennie, P. (1999). Rapid adaptation in visual cortex to the structure of images. *Science* 285(5432), 1405–1408.

Mummery, C. J., Patterson, K., Hodges, J. R., & Price, C. J. (1998). Functional neuroanatomy of the semantic system: Divisible by what? *Journal of Cognitive Neuroscience* 10(6), 766–777.

Mummery, C. J., Patterson, K., Hodges, J. R., & Wise, R. J. (1996). Generating "tiger" as an animal name or a word beginning with T: Differences in brain activation. *Proceedings of the Royal Society of London* B263(1373), 989–995. Erratum published in *Proceedings of the Royal Society of London* B263(1377) (1996), 1755–1756.

Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *Journal of Neurophysiology* 83(5), 2580–2601.

Nelson, K. (1974). Concept, word, and sentence: Interrelations in acquisition and development. *Psychological Review* 81(4), 267–285.

Nielsen, J. M. (1936). *Agnosia, Apraxia, and Aphasia: Their Value in Cerebral Localization.* New York: Paul Hoeber.

Noppeney, U., Friston, K. J., & Price, C. J. (2003). Effects of visual deprivation on the organization of the semantic system. *Brain* 126(7), 1620–1627.

Noppeney, U., & Price, C. J. (2002). Retrieval of visual, auditory, and abstract semantics. *NeuroImage* 15(4), 917–926.

Noppeney, U., & Price, C. J. (2003). Functional imaging of the semantic system: Retrieval of sensory-experienced and verbally learned knowledge. *Brain & Language* 84(1), 120–133.

Noppeney, U., & Price, C. J. (2004). Retrieval of abstract semantics. *NeuroImage* 22(1), 164–170.

Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Toward the neural basis of parsing: Prefrontal cortex and the role of selectional processes in language. *Cognitive, Affective, & Behavioral Neuroscience* 5, 263–281.

Nyberg, L., Marklund, P., Persson, J., Cabeza, R., Forkstam, C., Petersson, K. M., et al. (2003). Common prefrontal activations during working memory, episodic memory, and semantic memory. *Neuropsychologia* 41(3), 371–377.

Olesen, P. J., Nagy, Z., Westerberg, H., & Klingberg, T. (2003). Combined analysis of DTI and fMRI data reveals a joint maturation of white and grey matter in a fronto-parietal network. *Cognitive Brain Research* 18(1), 48–57.

Oliver, R. T., Coslett, H. B., Wolk, D., Geiger, E. J., & Thompson-Schill, S. L. (2004). *What does the parietal lobe know about objects?* Paper presented at the Annual Meeting of the Cognitive Neuroscience Society, San Francisco.

Oliver, R. T., & Thompson-Schill, S. L. (2003). Dorsal stream activation during retrieval of object size and shape. *Cognitive, Affective & Behavioral Neuroscience* 3(4), 309–322.

Owen, A. (1997). The functional organization of working memory processes within human lateral frontal cortex: The contribution of functional neuroimaging. *European Journal of Neuroscience* 9, 1329–1339.

Paivio, A. (1971). *Imagery and Verbal Processes.* New York: Holt, Rinehart, and Winston.

Pelphrey, K. A., Singerman, J. D., Allison, T., & McCarthy, G. (2003). Brain activation evoked by perception of gaze shifts: The influence of context. *Neuropsychologia*, 41(2), 156–170. Erratum appears in *Neuropsychologia* 41(11) (2003), 1561–1562.

Perani, D., Cappa, S. F., Bettinardi, V., Bressi, S., Gorno-Tempini, M., Matarrese, M., et al. (1995). Different neural systems for the recognition of animals and man-made tools. *NeuroReport* 6(12), 1637–1641.

Perani, D., Schnur, T., Tettamanti, M., Gorno-Tempini, M., Cappa, S. F., & Fazio, F. (1999). Word and picture matching: A PET study of semantic category effects. *Neuropsychologia* 37, 293–306.

Perret, E. (1974). The left frontal lobe of man and the suppression of habitual responses in verbal categorical behavior. *Neuropsychologia* 12, 323–330.

Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* 331(6157), 585–589.

Petrides, M., & Pandya, D. N. (2002). Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey. *European Journal of Neuroscience* 16(2), 291–310.

Peuskens, H., Claeys, K. G., Todd, J. T., Norman, J. F., Van Hecke, P., & Orban, G. A. (2004). Attention to 3-D shape, 3-D motion, and texture in 3-D structure from motion displays. *Journal of Cognitive Neuroscience* 16(4), 665–682.

Pietrini, P., Furey, M. L., Ricciardi, E., Gobbini, M. I., Wu, W. H., Cohen, L., et al. (2004). Beyond sensory images: Object-based representation in the human ventral pathway. *Proceedings of the National Academy of Sciences USA* 101(15), 5658–5663.

Pilgrim, L. K., Fadili, J., Fletcher, P., & Tyler, L. K. (2002). Overcoming confounds of stimulus blocking: An event-related fMRI design of semantic processing. *NeuroImage* 16(3, pt 1), 713–723.

Platel, H., Baron, J. C., Desgranges, B., Bernard, F., & Eustache, F. (2003). Semantic and episodic memory of music are subserved by distinct neural networks. *NeuroImage* 20(1), 244–256.

Plaut, D. C. (2002). Graded modality-specific specialization in semantics: A computational account of optic aphasia. *Cognitive Neuropsychology* 19, 603–639.

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage* 10(1), 15–35.

Postler, J., De Bleser, R., Cholewa, J., Glauche, V., Hamzei, F., & Weiller, C. (2003). Neuroimaging of the semantic system(s). *Aphasiology* 17(9), 799–814.

Price, C. J., Mummery, C. J., Moore, C. J., Frakowiak, R. S., & Friston, K. J. (1999). Delineating necessary and sufficient neural systems with functional imaging studies of neuropsychological patients. *Journal of Cognitive Neuroscience* 11(4), 371–382.

Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience* 18(6), 2188–2199.

Pulvermuller, F., Harle, M., & Hummel, F. (2001). Walking or talking? Behavioral and neurophysiological correlates of action verb processing. *Brain & Language* 78(2), 143–168.

Pylyshyn, Z. W. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychological Review* 88, 16–45.

Qureshy, A., Kawashima, R., Imran, M. B., Sugiura, M., Goto, R., Okada, K., et al. (2000). Functional mapping of human brain in olfactory processing: A PET study. *Journal of Neurophysiology* 84(3), 1656–1666.

Riddoch, M. J., & Humphreys, G. W. (1987). A case of integrative visual agnosia. *Brain* 110, 1431–1462.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research* 3(2), 131–141.

Roder, B., Stock, O., Bien, S., Neville, H., & Rosler, F. (2002). Speech processing activates visual cortex in congenitally blind humans. *European Journal of Neuroscience* 16(5), 930–936.

Rogers, T. T., Hocking, J., Mechelli, A., Patterson, K., & Price, C. (2005). Fusiform activation to animals is driven by the process, not the stimulus. *Journal of Cognitive Neuroscience* 17, 434–445.

Rogers, T. T., Lambon-Ralph, M. A., Garrard, P., Bozeat, S., McClelland, J. L., Hodges, J. R., et al. (2004). Structure and deterioration of semantic memory: A neuropsychological and computational investigation. *Psychological Review* 111(1), 205–235.

Roland, P. E., & Friberg, L. (1985). Localization of cortical areas activated by thinking. *Journal of Neurophysiology* 53, 1219–1243.

Rosch, E., Mervis, C. B., Gray, W., Johnson, D., & Boyes-Braem, P. (1976). Basic objects in natural categories. *Cognitive Psychology* 8, 382–439.

Roskies, A. L., Fiez, J. A., Balota, D. A., Raichle, M. E., & Petersen, S. E. (2001). Task-dependent modulation of regions in the left inferior frontal cortex during semantic processing. *Journal of Cognitive Neuroscience* 13(6), 829–843.

Royet, J. P., Koenig, O., Gregoire, M. C., Cinotti, L., Lavenne, F., Le Bars, D., et al. (1999). Functional anatomy of perceptual and semantic processing for odors. *Journal of Cognitive Neuroscience* 11(1), 94–109.

Ruby, P., & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: A PET investigation of agency. *Nature Neuroscience* 4(5), 546–550.

Saffran, E. M., Coslett, H. B., & Keener, M. T. (2003). Differences in word associations to pictures and words. *Neuropsychologia* 41, 1541–1546.

Saffran, E. M., & Schwartz, M. F. (1994). Of cabbages and things: Semantic memory from a neuropsychological perspective—A tutorial review. In C. M. M. Umiltà (Ed.), *Attention and Performance XV: Conscious and Nonconscious Information Processing*, 507–536. Cambridge, MA: MIT Press.

Schaefer, S. M., Jackson, D. C., Davidson, R. J., Aguirre, G. K., Kimberg, D. Y., & Thompson-Schill, S. L. (2002). Modulation of amygdalar activity by the conscious regulation of negative emotion. *Journal of Cognitive Neuroscience* 14(6), 913–921.

Schreuder, R., Flores D'Arcais, G. B., & Glazenborg, G. (1984). Effects of perceptual and conceptual similarity in semantic priming. *Psychological Research* 45, 339–354.

Shallice, T. (1988). *From Neuropsychology to Mental Structure.* New York: Cambridge University Press.

Silveri, M. C., & Gainotti, G. (1988). Interaction between vision and language in category-specific semantic impairment. *Cognitive Neuropsychology* 5, 677–709.

Simmons, W. K., & Barsalou, L. W. (2003). The similarity-in-topography principle: Reconciling theories of conceptual deficits. *Cognitive Neuropsychology* 20, 451–486.

Sirigu, A., Duhamel, J. R., & Poncet, M. (1991). The role of sensorimotor experience in object recognition. A case of multimodal agnosia. *Brain* 114(6), 2555–2573. Erratum appears in *Brain* 115(2) (1992), 645.

Spitzer, M., Kischka, U., Guckel, F., Bellemann, M. E., Kammer, T., Seyyedi, S., et al. (1998). Functional magnetic resonance imaging of category-specific cortical activation: Evidence for semantic maps. *Cognitive Brain Research* 6(4), 309–319.

Spitzer, M., Kwong, K. K., Kennedy, W., Rosen, B. R., & Belliveau, J. W. (1995). Category-specific brain activation in fMRI during picture naming. *NeuroReport* 6, 2109–2112.

Stefanacci, L., Buffalo, E. A., Schmolck, H., & Squire, L. R. (2000). Profound amnesia after damage to the medial temporal lobe: A neuroanatomical and neuropsychological profile of patient E. P. *Journal of Neuroscience* 20(18), 7024–7036.

Stephan, K. M., Fink, G. R., Passingham, R. E., Silbersweig, D., Ceballos-Baumann, A. O., Frith, C. D., et al. (1995). Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *Journal of Neurophysiology* 73, 373–386.

Tarr, M. J., & Gauthier, I. (2000). FFA: A flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience* 3(8), 764–769.

Thompson-Schill, S. L. (2003). Neuroimaging studies of semantic memory: Inferring "how" from "where." *Neuropsychologia* 41(3), 280–292.

Thompson-Schill, S. L. (in press). Dissecting the language organ: A new look at the role of Broca's area in language processing. In A. Cutler (Ed.), *Twenty-first Century Psycholinguistics: Four Cornerstones.* Hillsdale, NJ: Erlbaum.

Thompson-Schill, S. L., Aguirre, G. K., D'Esposito, M., & Farah, M. J. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia* 37(6), 671–676.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences USA* 94(26), 14792–14797.

Thompson-Schill, S. L., D'Esposito, M., & Kan, I. P. (1999). Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron* 23(3), 513–522.

Thompson-Schill, S. L., Jonides, J., Marshuetz, C., Smith, E. E., D'Esposito, M., Kan, I. P., et al. (2002). Effects of frontal lobe damage on interference effects in working memory. *Cognitive, Affective, and Behavioral Neuroscience* 2(2), 109–120.

Thompson-Schill, S. L., Swick, D., Farah, M. J., D'Esposito, M., Kan, I. P., & Knight, R. T. (1998). Verb generation in patients with focal frontal lesions: A neuropsychological test of neuroimaging findings. *Proceedings of the National Academy of Sciences USA* 95, 15855–15860.

Tippett, L. J., Glosser, G., & Farah, M. J. (1996). A category-specific naming deficit after temporal lobectomy. *Neuropsychologia* 34, 139–146.

Tulving, E. (1972). Episodic and semantic memory. In E. Tulving & W. Donaldson (Eds.), *Organization of Memory*. New York: Academic Press.

Tulving, E. (1984). Précis of *Elements of episodic memory. Behavioral and Brain Sciences* 7, 223–268.

Tulving, E. (1986). Episodic and semantic memory: Where should we go from here? *Behavioral & Brain Sciences* 9, 573–577.

Tulving, E., Kapur, S., Craik, F. I. M., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Sciences USA* 91(6), 2016–2020.

Tyler, L. K., & Moss, H. E. (1997). Functional properties of concepts: Studies of normal and brain-damaged patients. *Cognitive Neuropsychology* 14, 511–545.

Tyler, L. K., Moss, H. E., Durrant-Peatfield, M. R., & Levy, J. P. (2000). Conceptual structure and the structure of concepts: A distributed account of category-specific deficits. *Brain & Language* 75(2), 195–231.

Tyler, L. K., Stamatakis, E. A., Dick, E., Bright, P., Fletcher, P., & Moss, H. (2003). Objects and their actions: Evidence for a neurally distributed semantic system. *NeuroImage* 18(2), 542–557.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of Visual Behavior*, 549–586. Cambridge, MA: MIT Press.

Vandenberghe, R., Price, C., Wise, R., Josephs, O., & Frackowiak, R. S. J. (1996). Functional anatomy of a common semantic system for words and pictures. *Nature* 383(6597), 254–256.

Vargha-Khadem, F., Gadian, D. G., & Mishkin, M. (2001). Dissociations in cognitive memory: The syndrome of developmental amnesia. *Philosophical Transactions of the Royal Society of London*, B356(1413), 1435–1440.

Wagner, A. D., Pare-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. *Neuron* 31(2), 329–338.

Wallis, J. D., Anderson, K. C., & Miller, E. K. (2001). Single neurons in prefrontal cortex encode abstract rules. *Nature* 411(6840), 953–956.

Warburton, E., Wise, R. J., Price, C. J., Weiller, C., Hadar, U., Ramsay, S., et al. (1996). Noun and verb retrieval by normal subjects. Studies with PET. *Brain* 119(1), 159–179.

Warrington, E. K. (1975). The selective impairment of semantic memory. *Quarterly Journal of Experimental Psychology* 27, 635–657.

Warrington, E. K., & McCarthy, R. (1983). Category specific access dysphasia. *Brain* 106, 859–878.

Warrington, E. K., & McCarthy, R. A. (1987). Categories of knowledge: Further fractionations and an attempted integration. *Brain* 110(5), 1273–1296.

Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain* 107, 829–854.

Watson, J. D. G., Myers, R., Frackowiak, R. S. J., Hajnal, J. V., Woods, R. P., Mazziotta, J. C., et al. (1993). Area V5 of the human brain: Evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cerebral Cortex* 3(2), 79–94.

Wheaton, K. J., Thompson, J. C., Syngeniotis, A., Abbott, D. F., & Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *NeuroImage* 22(1), 277–288.

Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: Vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences USA* 97(20), 11125–11129. Erratum appears in *Proceedings* 101(14) (2004), 5181.

Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology* 8(2), 227–233.

Wiggs, C. L., Weisberg, J., & Martin, A. (1999). Neural correlates of semantic and episodic memory retreival. *Neuropsychologia* 37(1), 103–118.

Wilson, B. A., Baddeley, A. D., & Kapur, N. (1995). Dense amnesia in a professional musician following herpes simplex virus encephalitis. *Journal of Clinical & Experimental Neuropsychology* 17(5), 668–681.

Wise, R. J., Chollet, F., Hadar, U., Friston, K., Hoffner, E., & Frackowiak, R. (1991). Distribution of cortical neural networks involved in word comprehension and word retrieval. *Brain* 114(4), 1803–1817.

Wise, R. J., Howard, D., Mummery, C. J., Fletcher, P., Leff, A., Buchel, C., et al. (2000). Noun imageability and the temporal lobes. *Neuropsychologia* 38(7), 985–994.

Wolk, D. A., Coslett, H. B., & Glosser, G. (2005). The role of sensory-motor information in object recognition: Evidence from category-specific visual agnosia. *Brain and Language* 94, 131–146.

Yamadori, A., & Albert, M. L. (1973). Word category aphasia. *Cortex* 9, 112–125.

Zeki, S., Watson, J. D., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience* 11(3), 641–649.