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6 Functional Neuroimaging of Semantic Memory

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INTRODUCTION

It is now well recognized that memory is not a single, all-purpose, monolithic system, but rather is composed of multiple systems. Prominent among these systems is semantic memory (e.g., Tulving, 1983). "Semantic memory" refers to a broad domain of cognition composed of knowledge acquired about the world, including facts, concepts, and beliefs. In comparison to episodic or autobiographical memory, it consists of memories that are shared by members of a culture rather than those which are unique to an individual and are tied to a specific time and place. For example, whereas remembering what you had for breakfast yesterday is dependent on episodic memory, knowing the meaning of the word "breakfast" is dependent on semantic memory. Thus one component of semantic memory is the information stored in our brains about the meanings of objects and words.

Meaning, however, has proved to be a fairly intractable problem, especially regarding the meaning of words. One important reason why this is so is that words have multiple meanings. To cite one extreme example, the *Oxford English Dictionary* lists 96 entries for the word "run." The specific meaning of a word is determined by context, and comprehension is possible because we have contextual representations (see Miller, 1999, for a discussion of lexical semantics and context). One way to begin to get traction on the problem of meaning in the brain is to limit inquiry to concrete objects as represented by pictures and by their names (in which case the names are presented in a context that makes the reference clear (e.g., that "dog" refers to a four-legged animal, not a contemptible person).

Consider, for example, the most common meaning of two concrete objects, a camel and a wrench. Camel is defined as "either of two species of large, domesticated ruminants (genus camelus) with a humped back, long neck, and large cushioned feet"; wrench is defined as "any number of tools used for holding and turning nuts, bolts, pipes, etc." (*Webster's New World Dictionary*, 1988). Two things are noteworthy about these definitions. First, they are largely about features: camels are large and have a humped back, and wrenches hold and turn things. Second, different types of features are emphasized for different types of objects. The definition of the camel consists of information about its visual appearance, whereas the definition of the wrench emphasizes how it is used. I will return to this difference later in this chapter. For now, it should be noted that differences in the types of features that define different objects have played, and continue to play, a central role in thinking about disorders of semantic memory and in models of how semantic memory is organized in the human brain.

Another point about these brief definitions is that they include only part, perhaps only a small part, of the information we may possess about these objects. For example, we may know that camels are found primarily in Asia and Africa, that they are known as the "ships of the desert," and that the word "camel" can refer to a color as well as to a brand of cigarettes. Similarly, we also know that camels are larger than a bread box and weigh less than a 747 jumbo jet. Clearly, this information is also part of semantic memory. Unfortunately, little, if anything, is known about the brain bases of these associative and inferential processes. We are, however, beginning to gain insights into the functional neuroanatomy associated with our ability to identify objects and to retrieve information about specific object features and attributes. These topics will be the central focus of this review.

The chapter is divided into four main sections. In the first, I define semantic representations and review data from patients with selective but global (i.e., nonspecific) impairments of semantic memory. In the second, I review studies which show that many semantic tasks activate a broad network of cortical regions, most of which are lateralized to the left hemisphere. Prominent components of this network are the ventral and lateral surfaces of the temporal lobes. The third section concentrates on studies on retrieving information about specific features and attributes of objects. The results of these studies suggest that different regions of temporal cortex are active depending on the nature of the information retrieved. The final section concentrates on object category specificity, especially studies contrasting activity associated with animals and tools as represented by pictures and words. These studies suggest that object semantic representations consist of networks of discrete cortical regions ranging from occipital to left premotor cortices. The organization of these sites seems to parallel the organization of sensory and motor systems in the human brain. These networks may provide neurobiologically plausible mechanisms that function in the service of referential meaning.

Background

A semantic representation of an object is defined as the information stored in our brains which defines that object as a distinct entity (i.e., as a specific animal, food, item of furniture, tool, etc.). This information will include information shared by other category members, as well as information that makes it distinct from other exemplars of the same category. Thus the semantic representation of a particular object would include information about the object's typical shape. In addition, depending on the object, the semantic representation could include information about other visual attributes, such as color and motion, as well as features derived through other sensory modalities, and through visuomotor experience with the object. Finally,

activation of these representations is dependent on an item's meaning, not on the physical format of the stimulus denoting that object. For example, the semantic representation of "dog" would be activated by a picture of a dog, the written word "dog," the heard name "dog," the sound of a dog's bark, or simply thinking about dogs. It is this claim that defines the representation as semantic. Thus, central to this model are the claims that there is a single semantic system which is accessed through multiple sensory channels, and that activation of at least part of the semantic representation of an object is automatic and obligatory.

A central question for investigators interested in the functional neuroanatomy of semantic memory is to determine where this information is represented in the brain. One particularly influential idea, and one that has guided much of my own work on this topic, is that the features and attributes which define an object are stored in the perceptual and motor systems active when we first learned about that object. Thus, for example, information about the visual form of an object, its typical color, its unique pattern of motion, would be stored in or near regions of the visual system that mediate perception of form, color, and motion. Similarly, knowledge about the sequences of motor movements associated with the use of an object would be stored in or near the motor systems active when that object was used. This idea, which I have referred to elsewhere as the sensory-motor model of semantic representations (Martin, 1998; Martin et al., 2000), has a long history in behavioral neurology. Indeed, many neurologists in the late nineteenth century assumed that the concept of an object was composed of the information about that object learned through direct sensory experience and stored in or near sensory and motor cortices (e.g., Broadbent, 1878; Freud, 1891; Lissauer, 1890/1988).

The modern era of the study of the organization of semantic memory in the human brain began with Elizabeth Warrington's seminal paper "The Selective Impairment of Semantic Memory" (Warrington, 1975). Warrington reported three patients with progressive dementing disorders that appeared to provide neurological evidence for Tulving's concept of a semantic memory system. (Pick's disease was later verified by autopsy for two of these patients.) There were three main components of the disorder. First, it was selective. The disorder could not be accounted for by general intellectual impairment, sensory or perceptual problems, or an expressive language disorder. Second, it was global rather than material-specific. Object knowledge was impaired regardless of whether objects were represented by pictures or by their written or spoken names. Third, the disorder was graded. Knowledge of specific object attributes (e.g., does a camel have two, four, or six legs?) was much more impaired than knowledge of superordinate category information (i.e., is a camel a mammal, bird, or insect?).

Following Warrington's report, similar patterns of semantic memory dysfunction have been reported. These have included patients with progressive dementias such as Alzheimer's disease (e.g., Martin & Fedio, 1983) and semantic dementia (e.g., Hodges et al., 1992), with herpes encephalitis (e.g., Pietrini et al., 1988), and with stroke (e.g., Hart & Gordon, 1990). In addition to the properties established by Warrington, these reports showed that these patients typically have a marked deficit in producing object names under a variety of circumstances, including difficulty naming pictures of objects, naming from the written descriptions of objects, and generating the names of objects that belong to a specific category (e.g., animals, fruits and vegetables, furniture, etc.). In addition, the deficits were primarily associated with damage to the left temporal lobe (see Martin et al., 1986, for evidence in patients with Alzheimer's disease; Hodges & Patterson, 1996, for semantic dementia; and Hart & Gordon, 1990, for focal brain injury cases).

FUNCTIONAL NEUROIMAGING OF SEMANTIC MEMORY

Object Naming and Word Reading

Difficulties in naming objects is a cardinal symptom of a semantic impairment. This is as expected. There is abundant evidence from the cognitive literature that semantic representations are automatically activated when objects are named, and even when they are simply viewed. When we see an object we cannot help but identify it. And in order to identify it, we must access previously stored information about that class of objects (e.g., Glaser, 1992; Humphreys et al., 1988).

Consistent with the clinical literature, functional neuroimaging studies of object naming suggest that semantic processing may be critically dependent on the left temporal lobe. Several studies have investigated silent object naming (Bookheimer et al., 1995; Martin et al., 1996) and object viewing (which also likely elicited silent naming, Zelkowicz et al., 1998) relative to viewing nonsense objects. The rationale behind this comparison is that both real and nonsense objects will activate regions which mediate perception of object shape, whereas only real objects will engage semantic, lexical, and phonological processes. Direct comparison of real object and nonsense object conditions revealed activity in a network of regions that included left inferior frontal cortex (Broca's area). Activation of left inferior frontal cortex was consistent with the clinical literature and with what is now a relatively large body of functional brain imaging studies, documenting the prominent role of this region in word selection and retrieval (see Caplan, 1992, for review of clinical literature; and Poldrack et al., 1999, for a review of brain-imaging studies). The other prominent site of activity was the

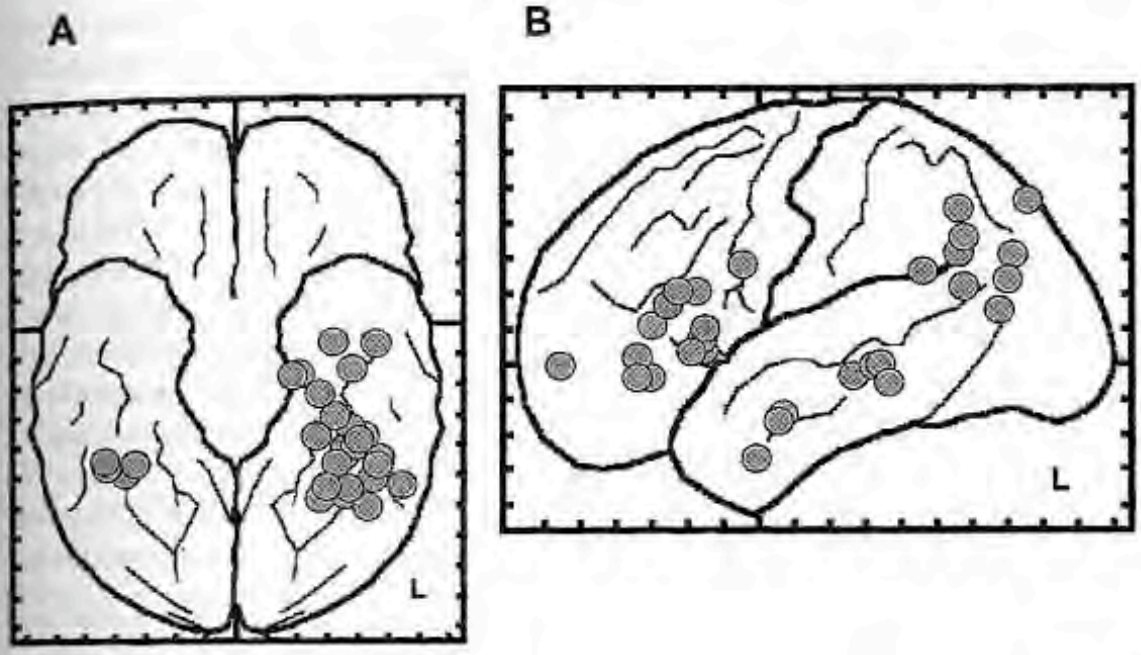

Figure 6.1
Schematic representation of the location of the main activations in temporal, left temporoparietal, and left prefrontal cortices, reported in object-naming, word-reading, semantic category fluency, semantic decision, and association tasks. Note the large number of activations in left ventral temporal cortex, clustered along fusiform and inferior temporal gyri (*A*), and left middle temporal gyrus (*B*).

posterior temporal lobes. These activations were centered on the fusiform gyrus, located on the ventral surface of the temporal lobes. The activity was bilateral in the Bookheimer et al. (1995) and Martin et al. (1996) studies, and on the left in Zelkowicz et al. (1998). Kiyosawa and colleagues (1996) also reported bilateral activation of this region when overt object naming was contrasted to rest, and to a counting condition to control for speech output (figure 6.1A).

Importantly, both real objects and nonsense objects produced equivalent activation of more posterior regions in ventrolateral occipital cortex, bilaterally (e.g., Malach et al., 1995; Martin et al., 1996). In contrast, the fusiform activations that were significantly greater for real, than for nonsense, objects were located further downstream in the ventral object-processing pathway. Because posterior temporal lobe lesions, especially to the left hemisphere, cause semantic deficits (including impaired object naming), the most likely explanation is that these temporal lobe activations reflect lexical and/or semantic processing.

If that is so, then this region should be active when single words are read in comparison to a baseline that presents physically similar stimuli devoid of semantic

meaning. A number of studies have investigated this issue by comparing single-word reading to consonant strings. This baseline may be more appropriate than using nonsense words because the latter are often phonologically similar to real words, or contain legal words, and thus may produce unintended semantic processing. Price and colleagues (Price, Wise, et al., 1996) showed that reading words, relative to viewing consonant strings (and also relative to false font stimuli), activated the left fusiform gyrus of the temporal lobe slightly anterior to the regions active in the object-naming studies. A similar finding was reported by Herbster et al. (1997). In addition, and of particular relevance for the present discussion, Büchel and colleagues (1998) reported that this region of the left fusiform gyrus was active not only when normal individuals read words but also when congenitally blind subjects, and individuals blinded later in life, read Braille (Büchel et al., 1998). Based on these studies, it is apparent that both naming objects and reading words activate the ventral region of the posterior temporal lobes centered on the fusiform gyrus; this effect is greater on the left than on the right, especially during word reading. The data also suggest that activation of this region is independent of the physical form of the stimulus presented to the subjects.

Semantic Fluency

The findings from object naming and word reading are consistent with the view that the ventral region of the temporal lobes, in particular the fusiform gyrus, is engaged by lexical and/or semantic processing. One way to test whether these activations are purely lexical is to contrast word retrieval under conditions that emphasize semantic constraints (for example, asking subjects to generate a list of words denoting objects that belong to a specific semantic category) with conditions that emphasize lexical and phonological constraints (e.g., asking subjects to generate a list of words that begin with the same letter). If ventral temporal lobe activity reflects only lexical/phonological processes, then both of these tasks should activate this region to an equivalent degree. However, if activity in this region reflects semantic processes, then this region should be more active when word retrieval is driven by semantic, than by lexical, constraints.

Evidence in support of the semantic interpretation has been reported by Shaywitz et al. (1995) and Mummery et al. (1996). These studies were motivated by the findings that whereas lesions of the frontal lobes, especially of left lateral frontal cortex, disrupt word retrieval on both semantic and letter fluency tasks (e.g., Baldo & Shimamura, 1998), temporal lobe lesions produce greater impairment of semantic than of letter fluency (for a discussion of this issue, see Martin et al., 1994; Hodges et al., 1999). Mummery et al. (1996) compared semantic category fluency tasks to letter fluency tasks and reported that the semantically driven tasks produced greater activ-

ity of the left temporal lobe than lexically driven tasks, even though subjects produced a similar number of words under both retrieval conditions. The activations included both posterior and anterior regions of the inferior temporal gyrus and the anteromedial region of the left temporal lobe. Similarly, using fMRI, Shaywitz et al. (1995) reported that a semantic category fluency task produced greater activation of left posterior temporal cortex than a rhyme fluency task (generating words that rhymed with a target word). (Because fMRI is extremely sensitive to movement artifact, subjects generated words silently. As a result, output could not be monitored. Also, a "region of interest" analysis was employed that may have missed other activations.) Thus these findings suggest that activity in left ventral temporal cortex is modulated by semantic factors, and does not simply reflect lexical retrieval. As will be reviewed below, the importance of the temporal lobes, especially the posterior region of the left temporal lobe, has been confirmed by a number of studies directly aimed at evaluating the functional neuroanatomy of semantic processes.

Semantic Decision and Semantic Association Tasks

In one of the earliest functional brain-imaging studies of semantic processing, Sergent and colleagues (1992) asked subjects to make an overt semantic decision (living versus nonliving) about pictures of objects. Consistent with the reports reviewed above, this task produced activation of the left posterior fusiform gyrus, relative to a letter-sound decision task using visually presented letters. Using written words, Price and colleagues (1997) also reported activation of the left temporal lobe when a living/nonliving semantic judgment task was contrasted to a phonological decision task (two versus one or three syllables), using the same stimuli employed in the semantic decision condition. The activations included ventral temporal cortex, but were considerably anterior to those reported in the studies reviewed so far. The lack of activity in posterior regions of the ventral temporal lobe may have been due to the automatic engagement of semantic processing during the syllable decision baseline task (as had been demonstrated by these authors; Price, Wise, et al., 1996). Nevertheless, using a similar design, Chee et al. (1999) reported activation of the posterior left fusiform gyrus, as well as of the left middle temporal gyrus, when subjects made concrete/abstract decisions regarding aurally presented words, compared to a one- versus multiple-syllable decision task.

Activation of the left temporal lobe has also been found across a number of studies that have used more effortful and complex semantic decision tasks. Démonet and colleagues (1992) presented subjects with an adjective-noun word pair monitoring task. Subjects were instructed to monitor word pairs for a positive affect and a small animal (i.e., respond to "kind mouse" but not to "kind horse" or "horrible mouse.") The study was noteworthy because the stimuli were delivered aurally rather than visually

(as in most of the previously reviewed studies), and the task required a rather detailed analysis of meaning. It also had some drawbacks, including the use of a highly unusual and complex task and limitation of words to two categories (animals and affective states). Nevertheless, relative to a task requiring subjects to monitor the order of phonemes in syllables (respond to /b/ when preceded by /d/), the semantic monitoring task activated the posterior region of the left ventral temporal cortex (fusiform and inferior temporal gyri). Other prominent regions of activity were in left posterior temporoparietal cortex (supramarginal and angular gyri), medial posterior parietal cortex (precuneus), posterior cingulate, and left prefrontal cortex.

This broad pattern of left hemisphere activation, including ventral and lateral regions of posterior temporal lobe, inferior parietal, and prefrontal cortices, has been replicated in nearly all studies using tasks that required effortful retrieval of semantic information. For example, Binder et al. (1997, 1999) used a semantic monitoring task similar to one employed by Démonet et al. (1992) (animals that are "native to the US and are used by people"). Relative to a tone detection task, the semantic decision task activated left ventral temporal cortex (including parahippocampal, fusiform, and inferior temporal gyri), left lateral temporal cortex (including middle and superior temporal gyri), left posterior parietal, and prefrontal regions. When these data were reanalyzed relative to a difficult phoneme monitoring task, the peak of the left ventral temporal lobe activation was located more medially in the parahippocampal gyrus (Binder et al. 1999; this study also demonstrated that the network active during the semantic monitoring task was also active when subjects were simply instructed to "rest" with eyes closed, i.e., when engaged in internally generated thought and daydreams).

Semantic association tasks requiring subjects to make subtle, within-category decisions have revealed a similar network of areas as well. Vandenberghe et al. (1996) tested subjects on a modified version of a semantic task, *The Pyramids and Palms Trees Test*, developed by Howard and Patterson (1992). In contrast to the semantic decision tasks reviewed above, this task was directly derived from the clinical literature. For example, patients with semantic dementia perform poorly on this test, whereas patients with nonfluent progressive aphasia do not (Hodges & Patterson, 1996). Subjects were shown triplets of pictures of objects with the target item on the top and two choice items below it to the left and right. Subjects indicated which of the two objects on the bottom was more similar to the object on top. For most trials, the objects were from the same semantic category, but one choice was more related to the target than the other choice. For example, the target may be a wrench and the choices pliers and a saw. Performance on this task activated a network of regions similar to those reported by Démonet et al. (1992), in comparison to a task that required

subjects to make subtle visual distinctions (judging which object was more similar in size, as displayed on the screen, to the target object; Vandenberghe et al., 1996). Active regions included left posterior (fusiform gyrus) and anterior (inferior temporal gyrus) regions of ventral temporal cortex, left posterior lateral temporal cortex (middle temporal gyrus), left prefrontal, and left posterior parietal cortices. Importantly, these regions were also active when the objects were represented by their written names, thus providing evidence for a single semantic system engaged by pictures and words. Similar findings with *The Pyramids and Palms Trees Test* have been reported by Ricci et al. (1999; only pictures were used) and Mummery et al. (1999; for pictures and words).

The study by Mummery and colleagues (1999) is particularly noteworthy because it included patients with semantic dementia as well as normal individuals. The patients had prominent atrophy of the anterior temporal lobes, greater for the left than for the right hemisphere, as determined by volumetric analysis of the MRIs. Atrophy was not detected in more posterior temporal regions. Analysis of the PET data revealed activation of left anterior temporal lobe for the normal subjects during the semantic processing task (more strongly for words than for pictures). The dementia patients also showed activity in this region, but more variably than in normal individuals. This was not surprising, given that this was the area of greatest atrophy. However, whereas normal subjects also showed robust activation of posterior temporal cortex, the patients did not. One explanation for the patients' failure to activate left posterior temporal cortex was that this region was damaged, but the pathology was not detectable with present imaging technology. Alternatively, this region was intact, but inactive because of an absence of top-down influences from anterior temporal cortex. If that is the case, then this finding suggests that the effect of a lesion on task performance may be due not only to a disruption of processes normally performed by the damaged cortex but also to a disruption of processes performed at more distant sites within a processing network.

In summary, the studies reviewed to this point indicate a strong association between performance on a variety of semantic processing tasks and activation of a broad network of cortical regions, especially in the left hemisphere. This network includes prefrontal cortex, posterior temporoparietal cortex, and the ventral and lateral regions of the temporal lobes (fusiform, inferior, and middle temporal gyri; see figure 6.1A, B).

These temporal lobe sites accord well with the clinical literature reviewed previously that documented a strong association between semantic deficits and left temporal lobe pathology including, but certainly not limited to, posterior cortex. Studies of patients also have provided compelling evidence that semantic memory has a struc-

ture, and that this structure may, therefore, have anatomical boundaries. The goal of most of the studies reviewed above was to isolate "semantic processing regions" from brain areas that support perceptual and other language processes, not to reveal its structure. The studies considered next have direct bearing on the structure of semantic representations, from both a cognitive and a neuroanatomic perspective.

The Structure of Semantic Memory: Retrieving Information about Object Attributes

In 1988, Petersen and colleagues reported the first study of the functional neuroanatomy of semantic processing in the normal human brain. A word retrieval task was employed. However, unlike the previously discussed studies of semantic fluency that averaged brain activity across multiple retrieval cues (e.g., generating names of mammals and car parts; Shaywitz et al., 1995), the words generated in this study were all of the same type (action verbs). Subjects were presented with single words denoting concrete nouns (e.g., "cake") and asked to generate a single word denoting a use associated with the noun (e.g., "eat"). Comparison of activity recorded during this scan with activity recorded while the subjects simply read the words revealed activity in left lateral prefrontal cortex. Left prefrontal cortical activity was also found when the words were presented aurally, thus strengthening the authors' conclusion of an association between left prefrontal cortex and semantics.

There were two problems with this conclusion. First, many semantic models view meaning as compositional rather than unitary (e.g., Fodor & Lepore, 1996). As such, meaning in the brain has been viewed as a distributed system, involving many brain regions (e.g., Damasio, 1989). Second, even if semantic networks were confined to a single region, the neuropsychological evidence suggests that the critical area would be the left temporal, not the left frontal, lobe. As noted previously, damage to left prefrontal cortex often results in impaired word retrieval, thereby providing one explanation for the Petersen et al. finding (and see Thompson-Schill et al., 1997, 1998, for evidence of left prefrontal involvement in the selection of a specific word among competing alternatives). Alternatively, the left prefrontal site reported by Petersen and colleagues (1988) may have been associated with retrieval of verbs, relative to other word types (if that is the case, it would remain to be determined whether this was tied to the grammatical or to the semantic function of verbs). In support of this possibility, patients have been described with selective verb retrieval deficits (e.g., Caramazza & Hillis, 1991; Damasio & Tranel, 1993), and their lesions typically included left prefrontal cortex. (However, the damage often extended posteriorally to include much of the perisylvian region. See Gainotti et al., 1995, for review.)

We addressed some of these issues by comparing verb retrieval to retrieval of another object-associated feature, color (Martin et al., 1995). We decided on color

and action because of evidence that the perception of these features, as well as knowledge about them, could be differentially impaired following focal damage to the human brain. Color blindness, or achromatopsia, is associated with lesions of the ventral surface of the occipital lobes (e.g., Damasio et al., 1980; Vaina, 1994). PET and fMRI studies of normal individuals had identified regions in ventral occipital cortex active during color perception (specifically, the fusiform gyrus and collateral sulcus in the occipital lobe) (e.g., Corbetta et al., 1990; McKeefry & Zeki, 1997; Sakai et al., 1995; Zeki et al., 1991). In contrast, impaired motion perception, or akinetopsia, is associated with a more dorsally located lesion at the border of occipital, temporal, and parietal lobes (e.g., Zihl et al., 1991; Vaina, 1994). This location has also been confirmed by imaging studies of normal subjects (e.g., Corbetta et al., 1990; A. Smith et al., 1998; Zeki et al., 1991; Watson et al., 1993) (see figure 6.2A, B).

In addition, focal lesions can result in selective deficits in retrieving information about object-associated color and object-associated motion. Patients have been de-

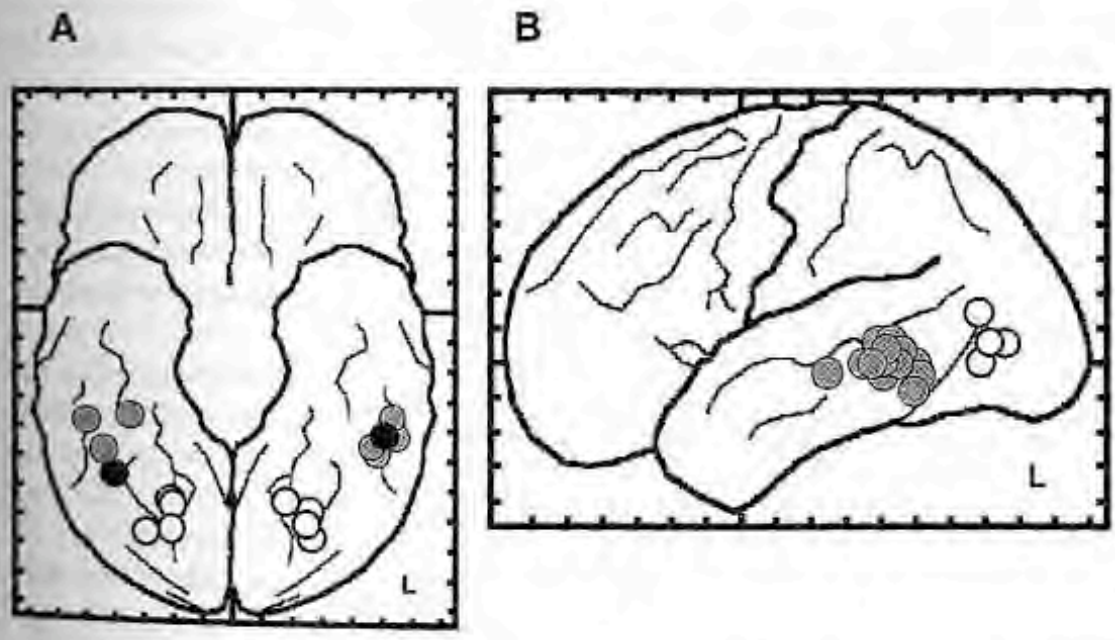

Figure 6.2
Schematic representation of the location of activations associated with perceiving and retrieving information about color and actions. (*A*) Ventral view of the left and right hemispheres showing occipital regions that responded to color (white circles), and temporal regions active when color information was retrieved (gray circles). Black circle on the left hemisphere shows location of the region active when color-word synethetes experienced color imagery. Black circle on the right hemisphere shows location of the region active in normal subjects during a color imagery task. (*B*) Lateral view of the left hemisphere showing sites at the junction of the occipital, temporal, and parietal lobes that responded to visual motion (white circles), and the region of the middle temporal gyrus active when verbs were retrieved (gray circles).

scribed with color agnosia who, for example, can neither retrieve the name of a color typically associated with an object nor choose from among a set of colors the one commonly associated with a specific object (e.g., De Vreese, 1991; Luzzati & Davidoff, 1994). And, as noted above, others have been described with selective verb comprehension and production impairments.

In our study, subjects were presented with black-and-white line drawings of objects. During one PET scan they named the object, during another scan they retrieved a single word denoting a color commonly associated with the object, and during a third scan they retrieved a single word denoting an action commonly associated with the object (Petersen et al's. verb generation condition). For example, subjects were shown a picture of a child's wagon and would respond "wagon," "red," and "pull" during the different scanning conditions (Martin et al., 1995).

In agreement with Petersen et al. (1988), retrieving object attribute information activated the left lateral prefrontal cortex, over and above that seen for object naming. However, this prefrontal activity did not vary with the type of information that subjects retrieved. Rather, the activation was similar for both the color and the action retrieval conditions, and thus consistent with the idea that left lateral prefrontal cortex is critically involved in retrieval from semantic memory (e.g., Gabrieli et al., 1998). In contrast, other brain regions were differentially active, depending on the type of information retrieved. Importantly, behavioral data collected during the scans (voice response times) confirmed that the color and action retrieval tasks were equally difficult to perform. As a result, differences in patterns of cortical activity associated with these tasks could be attributed to differences in the type of information retrieved rather than to differences in the ease of information retrieval.

Relative to action verbs, generating color words activated the ventral region of the temporal lobes bilaterally, including the fusiform and inferior temporal gyri, approximately 2 to 3 cm anterior to regions known to be active during color perception (figure 6.2A). In contrast, action word generation was associated with a broader pattern of activation that included left inferior frontal cortex (Broca's area), the posterior region of the left superior temporal gyrus (Wernicke's area), and the posterior region of the left middle temporal gyrus (figure 6.2B). Activation of the middle temporal gyrus was located approximately 1 to 2 cm anterior to the regions active during the motion perception, based on previous functional brain imaging findings. Thus, retrieving information about specific object attributes activated brain regions proximal to the areas that mediate perception of those attributes.

Given the claims of the sensory-motor model of semantic representations, it may be surprising that regions close to primary motor cortex were not active during action word generation. As we suggested in our initial report, this failure may have been

related to our choice of objects. Few tools, or other small manipulable objects such as kitchen utensils, were presented because of their limited range of color associations (tools invariably elicit silver, black, and brown as color responses; Martin et al., 1995). However, as we will discuss later, left premotor cortex is indeed active when subjects generate action verbs exclusively to tools (Grafton et al., 1997).

Finally, a similar pattern of differential engagement of the fusiform gyrus (greater for color word generation than for action word generation) and left middle temporal gyrus (greater for action word generation than for color word generation) was seen when subjects responded to the written names of the objects rather than to pictures (Martin et al., 1995). Taken together, these results provided additional evidence that activity in these regions is related to meaning rather than to the physical characteristics of the stimuli.

It is also noteworthy that the activation in the ventral temporal cortex associated with retrieving color words, and the activation in the left middle temporal gyrus associated with retrieving action words, overlap with the regions active during performance of many of the semantic processing tasks reviewed previously (compare figures 6.1 and 6.2). Thus, the color/action word generation studies suggest that these posterior temporal regions may not serve a uniform function in the service of "semantics." Rather, temporal cortex may be segregated into distinct areas that serve different functions. Specifically, qualitatively different types of information are stored in ventral temporal and lateral temporal cortices.

We have now reported two additional studies of color word generation that provide supportive evidence for an association between retrieving information about object color and activity in posterior ventral temporal cortex. One experiment addressed whether activation of the ventral temporal lobe when color words are retrieved was specifically tied to retrieving information from semantic memory. Subjects generated the names of typical object colors in one condition (retrieval from semantic memory), and generated the names of recently taught object-color associations in another condition (retrieval from episodic memory). For example, subjects responded "red" to an achromatic picture of a child's wagon in one condition and "green" in another condition. (However, no subject saw the same objects in the semantic and episodic memory conditions. See Wiggs et al., 1999, for details.) In a second study, retrieving color information from semantic memory was evaluated in relation to color naming and color perception in order to more precisely map the functional neuroanatomy engaged by these processes (Chao & Martin, 1999). The results of these studies replicated our initial finding. Retrieving object-color information from semantic memory activated a region of ventral temporal cortex, bilaterally in Chao and Martin (1999) and lateralized to the left in Wiggs et al. (1999), that was

located anterior to the occipital areas active during color perception (figure 6.2A). Thus, we interpreted these findings as identifying a region where object-associated color information is stored.

Additional evidence in support of this claim comes from functional brain-imaging studies of individuals with color-word synesthesia (Paulesu et al., 1995) and color imagery in normal individuals (Howard et al., 1998). Color-word synesthetes are individuals who claim that hearing words often triggers the experience of vivid color imagery. Using PET, Paulesu and colleagues reported that listening to words activated a site in the left ventral temporal lobe in color-word synesthetes, but not in the normal individuals. The region active in the synesthetes when they heard words and experienced colors was the same area active when normal subjects retrieved object-color information (figure 6.2A). Howard et al. (1998) also reported fusiform activity, but on the right rather than the left, when normal subjects answered questions designed to elicit color imagery (e.g., "Is a raspberry darker red than a strawberry?"). Thus, the vivid experience of color imagery automatically elicited in the synethestes —the effortful and conscious generation of color imagery, and effortful retrieval of verbal, object-color information—activated similar regions of the ventral temporal lobes (see figure 6.2A).

Interestingly, although the word-color synesthesia subjects experienced color when they heard words, they did not show activation of sites in ventral occipital cortex typically active during color perception. This finding is in accord with the Chao and Martin (1999) study of color word generation and color perception, and with the Howard et al. (1998) study of color imagery and color perception. In those reports, neither color word retrieval nor color imagery activated occipital regions that were active during color perception. These negative findings are consistent with clinical reports which suggest that color perception and color knowledge can be doubly dissociated. For example, Shuren et al. (1996) reported intact color imagery in an achromatopsic patient, while De Vreese (1991) reported impaired color imagery in a patient with intact color perception (case II). Taken together, the functional brain imaging and clinical literature provide converging evidence that information about object color is stored in the ventral temporal lobe, and that the critical site is close to, but does not include, more posterior occipital sites that respond to the presence of color.

In contrast to these reports on retrieving color information from semantic memory, there is now considerable evidence that retrieving a different type of object-associated information (as represented by action verbs) is associated with activity in a different region of the posterior temporal lobe; specifically, the left middle temporal gyrus. To date, there are at least 26 functional brain-imaging studies in the literature that have used the action word generation task. In addition to the studies discussed above (one in Petersen et al., 1988; and two in Martin et al., 1995), these include one study

reported in Wise et al. (1991), one in Raichle et al. (1994), four reported in Warburton et al. (1996), 12 studies (from 12 different laboratories) in Poline et al. (1996), four studies (from different laboratories) in Tatsumi et al. (1999), and one in Klein et al. (1999). (All used PET. McCarthy et al., 1993, studied verb generation using fMRI, but only the frontal lobes were imaged.)

The stimuli used in these studies have included pictures of objects (Martin et al., 1995), words presented visually (Martin et al., 1995; Petersen et al., 1988; Raichle et al., 1994), and words presented aurally (the remaining studies). Stimulus presentation rates ranged from one per sec (Petersen et al., 1988) to one per 6 sec (Poline et al., 1996; Tatsumi et al., 1999). Subjects responded aloud in some studies (Klein et al., 1999; Martin et al., 1995; Petersen et al., 1988; Raichle et al., 1994) and silently in the others, and produced a single response to each item in some studies (Klein et al., 1999; Martin et al., 1995; Petersen et al., 1988; Raichle et al., 1994) and multiple responses to each item in the others. Finally, subjects have been tested in a variety of native languages, including English, German, French, Italian, Dutch, Danish, Swedish, Chinese, and Japanese. Given these and numerous other differences between studies (including baseline comparison tasks), the findings have been remarkably consistent. In particular, retrieving information about object-associated actions activated the left middle temporal gyrus in 19 of 25 studies that imaged this region. Two of the remaining studies reported peak activity at a slightly more superior location in the superior temporal gyrus (Wise et al., 1991, and one study in Warburton et al., 1996; superior temporal activity was also observed in several data sets analyzed in Poline et al., 1996). The locations of the left middle temporal gyrus activations relative to regions active during motion perception are illustrated in figure 6.2B.

Taken together, the findings provide clear and compelling evidence against the idea that information about object attributes and features is stored in a single region of the brain, and thus within an undifferentiated semantic system. Rather, the color/action word retrieval data suggest that information is distributed throughout the cerebral cortex. In addition, the locations of the sites appear to follow a specific plan that parallels the organization of sensory systems and, as will be reviewed below, motor systems, as well. Thus, within this view, information about object features and attributes, such as form, color, and motion, would be stored within the processing streams active when that information was acquired, but downstream from (i.e., anterior to) regions in occipital cortex that are active when these features are physically present.

The Structure of Semantic Memory: Object Category-Specific Representations

Background Investigations of the functional neuroanatomy engaged by different categories of objects provide additional evidence for this view. As with many of the studies reviewed above, these investigations were motivated by the clinical literature.

Specifically, patients have been described with relatively selective deficits in recognizing, naming, and retrieving information about different object categories. The categories that have attracted the most attention are animals and tools. This is because of a large and growing number of reports of patients with greater difficulty naming and retrieving information about animals (and often other living things) than about tools (and often other man-made objects). Reports of the opposite pattern of dissociation (greater for tools than animals) are considerably less frequent. However, enough carefully studied cases have been reported to provide convincing evidence that these categories can be doubly dissociated as a result of brain damage. The impairment in these patients is not limited to visual recognition. Deficits occur when knowledge is probed visually and verbally, and therefore are assumed to reflect damage to the semantic system or systems (see Forde & Humphreys, 1999, for a review).

While it is now generally accepted that these disorders are genuine, their explanation, on both the cognitive and the neural level, remains controversial. Two general types of explanations have been proposed. The most common explanation focuses on the disruption of stored information about object features. Specifically, it has been proposed that knowledge about animals and tools can be selectively disrupted because these categories are dependent on information about different types of features stored in different regions of the brain. As exemplified by the definitions provided in the introduction to this chapter, animals are defined primarily by what they look like. Functional attributes play a much smaller role in their definition. In contrast, functional information—specifically, how an object is used—is critical for defining tools. As a result, damage to areas where object form information is stored leads to deficits for categories that are overly dependent on visual form information, whereas damage to regions where object use information is stored leads to deficits for categories overly dependent on functional information. The finding that patients with category-specific deficits for animals also have difficulties with other visual form-based categories, such as precious stones, provides additional support for this view (e.g., Warrington & Shallice, 1984; and see Bunn et al., 1998, for a reevaluation of this patient).

This general framework for explaining category-specific disorders was first proposed by Warrington and colleagues in the mid-to-late 1980s (e.g., Warrington & McCarthy, 1983, 1987; Warrington & Shallice, 1984). Influential extensions and re-formation of this general idea have been provided by a number of investigators, including Farah (e.g., Farah & McClelland, 1991), Damasio (1990), Caramazza (Caramazza et al., 1990), and Humphreys (Humphreys & Riddoch, 1987), among others (see Forde & Humphreys, 1999, for an excellent discussion of these models).

The second type of explanation focuses on much broader semantic distinctions (e.g., animate versus inanimate objects), rather than on features and attributes, as the

key to understanding category-specific deficits. A variant of this argument has been strongly presented by Caramazza and Shelton (1998) to counter a number of difficulties with feature-based formulations. Specifically, Caramazza and Shelton note that a central prediction of at least some feature-based models is that patients with a category-specific deficit for animals should have more difficulty answering questions that probe knowledge of visual information about animals (does an elephant have a long tail?) than about function information (is a elephant found in the jungle?). As Caramazza and Shelton show, at least some patients with an animal-specific knowledge disorder (and, according to their argument, all genuine cases) have equivalent difficulty with both visual and functional questions about animals. As a result of these and other findings, Caramazza and Shelton argue that category-specific disorders cannot be explained by feature-based models. Instead, they propose that such disorders reflect evolutionary adaptations for animate objects, foods, and, perhaps by default, tools and other man-made objects (the "domain-specific hypothesis").

We now turn to functional brain-imaging studies to see if they provide information that may help in sorting out these issues. Currently, there are 14 studies that have investigated object category specificity. Studies contrasting animals and tools (and other manipulable, man-made objects, such as kitchen utensils) have employed a variety of paradigms. Object naming has been investigated using detailed line drawings (Martin et al., 1996), silhouettes (Martin et al., 1996), and photographs (Chao, Haxby, et al., 1999; Damasio et al., 1996). Subjects responded silently, except in Damasio et al. Object comparison tasks have also been used in which subjects judged whether pairs of objects were different exemplars of the same object or different objects in the same category. Objects were represented by line drawings (Perani et al., 1995) and by written names (Perani et al., 1999). Other paradigms have included delayed match-to-sample using photographs (Chao, Haxby, et al., 1999), passive viewing of rapidly presented photographs (Chao, Haxby, et al., 1999), presentation of written yes/no questions probing knowledge of visual and associative features (objects represented by their written names; Cappa et al., 1998), and written yes/no questions about where objects are typically found (objects represented by their written names; Chao, Haxby, et al., 1999).

Other studies have investigated category specificity by averaging across multiple categories of living things and artifacts. These have employed verbal fluency tasks (land animals, sea animals, fruits, and vegetables, versus toys, tools, weapons, and clothes; Mummery et al., 1996); written yes/no questions about visual and nonvisual features (objects were represented by their written names; categories included, but were not limited to, animals, flowers, vegetables, versus clothing, furniture, kitchen utensils; Thompson-Schill et al., 1999); object comparisons based on similarity in color and similarity in location (place typically found), using visually presented word

triads (living things versus artifacts, not further specified; Mummery et al., 1998); and naming and word-picture matching tasks using colored and black-and-white line drawings (animals, fruits, and vegetables versus vehicles, appliances, tools, and utensils; Moore and Price, 1999; only activations common to both the naming and the matching tasks were reported). All of the studies used PET except Chao, Haxby, et al. (1999) and Thompson-Schill et al. (1999), which used fMRI.

Category-Related Activations of Occipital Cortex The first studies to directly compare functional brain activity associated with animals versus tools were reported by Perani et al. (1995) and Martin et al. (1996). Both studies found greater activation of occipital cortex for animals relative to tools. These activations were lateralized to the left hemisphere and were located medially (Perani et al., 1995; Martin et al., 1996) and in ventrolateral cortex (fusiform gyrus and inferior occipital cortex; Perani et al., 1995). Using a naming task, Damasio et al. (1996) also reported greater medial occipital activity for animals, but lateralized to the right and superior to those in the above noted studies. Direct comparisons of animals and tools were not reported. Unlike the Martin and Perani studies, the tasks were not equated for difficulty, thus requiring the stimuli to be presented at different rates (see Grabowski et al., 1998, for details). Presentation rate, however, can influence the pattern of cortical activations (Price, Moore, et al., 1996). Moreover, the baseline comparison task consisted of judging whether photographs of faces were upright or inverted. As a result, the findings of Damasio et al. are difficult to interpret, especially in light of more recent data indicating substantial overlap in the network of regions activated by pictures of animals and human faces (Chao, Haxby, et al., 1999; Chao, Martin, et al., 1999).

Patients with category-specific deficits for living things most often have damage to the temporal lobes, usually as a result of herpes encephalitis (e.g., Pietrini et al., 1988). Thus, the finding that the occipital cortex was the main region activated for animals, relative to tools, was surprising and problematic. One possibility is that this heightened occipital activity simply reflected differences in the visual complexity of the stimuli. In this view, pictures of animals are visually more complex (e.g., Snodgrass & Vanderwart, 1980), and therefore require more visual processing than do pictures of tools (e.g., Gaffan & Heywood, 1993). This interpretation was weakened by the results of a study that used silhouettes of animals and tools, thereby eliminating stimulus differences with regard to internal visual detail. Naming animal silhouettes was associated with greater left medial occipital activity, relative to naming tool silhouettes, even though the stimuli were equated for naming speed and accuracy (Martin et al., 1996).

Recent reports have all but eliminated the visual complexity argument by showing greater occipital activity for animals, relative to tools, when the objects were repre-

sented by their written names rather than by pictures. Perani et al. (1999) reported greater left inferior occipital activity for animals than for tools using a same/different word-matching task, and Chao, Haxby, et al. (1999) reported greater bilateral inferior occipital activity for reading and answering questions about animals than about tools. Both of these studies also found greater animal-related than tool-related activity in inferior occipital cortex using object picture tasks (same/different judgments in Perani et al., 1999; viewing, delayed match-to-sample, and naming in Chao, Haxby, et al., 1999). However, Perani and colleagues also reported bilateral activation of the medial occipital region (lingual gyrus) for tools, relative to animals, in their reading task (but not in their object picture task). This exception notwithstanding, most of the evidence suggest that occipital cortex, especially around calcarine cortex and the inferior occipital gyrus, is more active when stimuli represent animals than when they represent tools (figure 6.3). Further support for this possibility is provided by a study of patients with focal cortical lesions. Tranel and colleagues identified 28 patients with impaired recognition and knowledge of animals, relative to tools, and famous people. All had posterior lesions that included medial occipital cortex, 14 on the right and 14 on the left (Tranel et al., 1997).

Given that occipital activity is unlikely to be due to differences in visual complexity, an alternative explanation is that it reflects top-down activation from more anterior sites (Martin et al., 1996, 2000). This may occur whenever retrieval of detailed information about visual features or form is needed to identify an object. However, if this were the case, then category-related differentiation should be found anteriorally in the ventral object-processing stream to drive this process. In addition, although, as noted above, there have been reports of patients with occipital lesions that had category-specific impairment for animals and other animate or living objects (Tranel et al., 1997), most cases have had lesions confined to the temporal lobes (see Gainotti et al., 1995, for review). Thus, one would expect to find animal-related activity farther downstream in the ventral object-processing pathway.

Ventral Temporal Cortex and the Representation of Visual Form As reviewed previously, many studies of semantic processing have reported activity centered on the fusiform gyrus in posterior temporal cortex. For example, the naming studies reported by Martin et al. (1996) found bilateral fusiform activity for both animals and tools, relative to a lower-level baseline condition. However, these activations were not seen when the categories were directly contrasted, thus suggesting that category-related differences were not represented in this region of the brain. More recent studies, however, suggest that this failure may have been due to the limited spatial resolution of PET. Using fMRI, Chao, Haxby, et al. (1999) reported multiple, category-related sites in the ventral region of the posterior temporal lobes. These

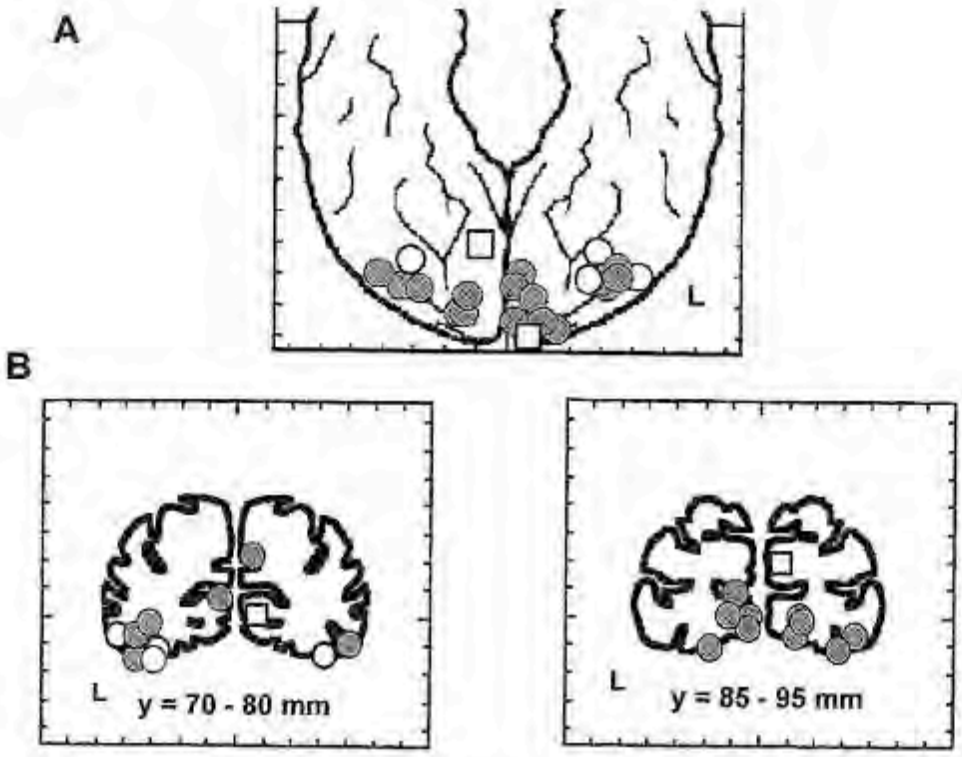

Figure 6.3
Schematic representation of category-related activations in occipital cortex reported by Perani et al. (1995), Martin et al. (1996), Damasio et al. (1996), Perani et al. (1999), and Chao, Haxby, et al. (1999). Circles represent sites more active for animals than for tools or other object categories; squares represent region more active for tools than for animals. Gray circles indicate tasks that employed pictures, and white circles indicate tasks that used words. Nearly all sites were activated more by animal than by tool stimuli. See text for description of paradigms. (*A*) Location of activations, represented as a see-through ventral view of the left and right hemispheres. (*B*) Coronal sections showing location of the same activations shown in A. Section on left depicts activations that were located approximately 70–80 mm posterior to the anterior commissure. Section on the right depicts activations located approximately 85–95 mm posterior to the anterior commissure.

ventral activations were located in the same region identified in many of the previously reviewed semantic tasks (fusiform gyrus, ~4.5–6.5 cm posterior to the anterior commissure) (figure 6.4 and color plate 6).

The location of these category-related activations was highly consistent across individual subjects, and different paradigms with pictures (passive viewing, delayed match-to-sample, and naming) and the written names of objects (Chao, Haxby, et al., 1999). In addition to animals and tools, the stimuli for the viewing and delayed match-to-sample tasks included pictures of human faces and houses. Faces and houses were included because previous studies had shown that these objects elicit highly consistent patterns of activation in ventral temporal cortex. Viewing faces has

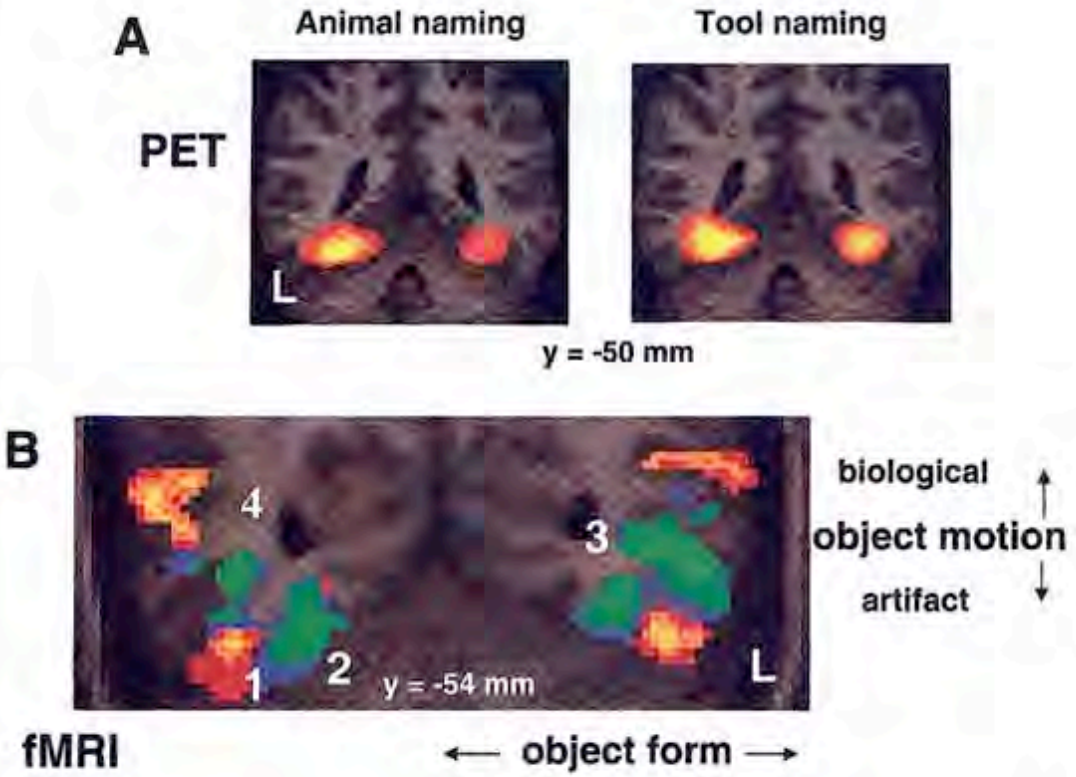

Figure 6.4
Coronal sections showing locations of animal- and tool-related activations in posterior temporal lobes. (*A*) Results from a study using PET (adapted from Martin et al., 1996). Both categories were associated with bilateral activity centered on the fusiform gyri. The only category-related activity seen with PET in this region was in the left middle temporal gyrus, greater for tools than for animals (not visible here because it was below the threshold used to make this picture, $p < .001$). (*B*) Category-related activity revealed by fMRI in the same region of the posterior temporal cortex shown in (*A*) (adapted from Chao, Haxby, et al., 1999). Regions depicted in the red-yellow color spectrum responded more to animals than to tools; regions in the blue-green spectrum responded more to tools than to animals. 1. lateral fusiform; 2. medial fusiform; 3. middle temporal gyrus; 4. superior temporal sulcus (see text and Chao, Haxby, et al., 1999, for details). The location of these activations in relation to the functions of more posterior regions leads to the suggestion that information about object form may be stored in ventral temporal cortex, and information about object-associated motion may be stored in lateral temporal cortex. (See color plate 6.)

been associated with activation of the more lateral portion of the fusiform gyrus (Haxby et al., 1999; Ishai et al., 1999; Kanwisher et al., 1997; McCarthy et al., 1997, Puce et al., 1996), whereas viewing houses and landmarks has activated regions medial to face-responsive cortex, including the medial aspect of the fusiform gyrus (Haxby et al., 1999; Ishai et al., 1999), lingual gyrus (Aguirre et al., 1998), and parahippocampal cortex (Epstein & Kanwisher, 1998).

In addition to the bilateral inferior occipital activation discussed above, Chao, Haxby, et al. (1999) found bilateral activation centered on the lateral half of the fusiform gyri for animals relative to tools (see figure 6.4B). This region could thus pro-

vide the purported top-down modulation of occipital cortex. In addition, consistent with reports cited above, this region also responded strongly to human faces. The peaks of the activation for animals and for human faces were essentially identical, even when the faces of the animals were completely obscured (Chao, Martin, et al., 1999). However, the animal- and face-related activations were not identical in all respects. Specifically, the neural response to faces was more focal than that to animals. This finding suggests that while recognition of animals and faces may be dependent, at least partially, on a common neural substrate, faces may be processed by a more discretely organized system. This finding, in turn, may explain why some patients may have selective deficit for faces (e.g., McNeil & Warrington, 1993), and also why impaired recognition of animals may be the most common co-occurring category-related deficit in prosopagnosic patients (Farah, 1990).

In contrast, the medial fusiform region responded more strongly to tools than to animals (see figure 6.4B). This region also responded strongly to houses, as previously reported. However, as was the case for the animals and faces, direct comparison of houses and tools revealed finer-grained distinctions between these object categories as well. The peak activity associated with processing tool stimuli was consistently lateral to the peak activation associated with houses (although still in the more medial section of the fusiform gyrus). These findings suggest that the pattern of response to different object categories varies continuously across the posterior ventral temporal cortex. For this reason, we suggested that the ventral temporal cortex may be organized according to object features that cluster together (Chao, Haxby, et al., 1999; Ishai et al., 1999; Martin et al., 2000). The nature of these features remains to be determined. However, because the fusiform gyrus is part of the ventral object vision pathway, this region may be tuned to the features of object form shared by members of a category.

Lateral Temporal Cortex and the Representation of Object-Related Visual Motion

Animal stimuli were also associated with activation of the lateral surface of the posterior temporal cortex centered on the superior temporal sulcus (STS). Again, the location of activity was consistent across individuals and tasks. However, in contrast to the fusiform activity, which was found in every subject, significant STS activity was found in only half the subjects for the picture-processing tasks, and only one quarter of the subjects (two of eight) for the word-reading task (Chao, Haxby, et al., 1999). Finally, as was the case for the lateral region of the fusiform gyrus, pictures of human faces also activated STS in approximately half the subjects, as previously reported by Kanwisher and colleagues (1997). Again, the peaks of the activations for animals and faces were essentially identical, but faces evoked a more focal pattern of activity in STS than did animals.

Single-cell recording studies in monkeys have shown activity in STS when viewing faces or face components, and when observing motion of people and other monkeys (see Desimone, 1991, for review). Consistent with these findings, human brain-imaging studies have revealed STS activity when viewing faces (Chao, Haxby, et al., 1999; Haxby et al., 1999; Ishai et al., 1999; Kanwisher et al., 1997), viewing mouth and eye movements (Puce et al., 1998), and observing human movements (Bonda et al., 1996; Rizzolatti, Fadiga, Matelli, et al., 1996). Thus, as we have suggested previously (Chao, Haxby, et al., 1999; Martin et al., 2000), STS may be involved not only in perception of biological motion but also in storing information about biological motion, perhaps in different parts of this region. If that is so, then the fact that viewing animals activates a portion of STS suggests that this information may be necessary, or at least available, to aid in identifying these stimuli.

In summary, the findings of the fMRI studies reported by Chao, Haxby, et al. (1999) revealed several category-related activations in the posterior region of the temporal lobes that were not seen in previous studies using PET. These included greater activation of the lateral portion of the fusiform gyrus and STS for animals (and human faces) than for tools (and houses), and greater activation of the medial fusiform region for tools (and houses) than for animals (and faces). In addition, these studies confirmed a finding that had been reported multiple times using PET: greater activity in the left posterior middle temporal gyrus for tools than for animals.

Activation of the left middle temporal gyrus in response to tools has been reported across a large number of paradigms using pictures of objects and their written names. These have included object naming of line drawings (Martin et al., 1996), silhouettes (Martin et al., 1996), and photographs (Chao, Haxby, et al., 1999); viewing rapidly presented pictures (Chao, Haxby, et al., 1999); delayed match-to-sample (Chao, Haxby, et al., 1999); answering written questions about object locations (Chao, Haxby, et al., 1999); verbal fluency (inanimate versus animate categories; Mummery et al., 1996); and answering written questions about visual and associative object features (Cappa et al., 1998). Other studies have employed a word triad task in which subjects judged the similarity of objects on different attributes (nonliving versus living categories; Mummery et al., 1998) and a same/different word-matching task (Perani et al., 1999). In addition, Perani and colleagues reported greater left middle temporal gyrus activity for a picture-matching task with tools, but not animals, relative to a low-level visual baseline task, and Moore and Price (1999) reported greater left middle temporal gyrus activity for tools versus a variety of other object categories using a picture-matching task (figure 6.5).

It is noteworthy that the location of these activations overlaps with the locations reported in verb generation studies reviewed previously (compare figures 6.2B and

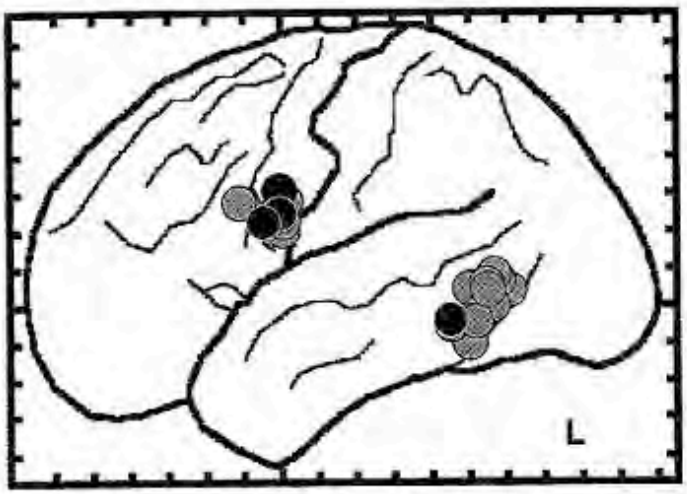

Figure 6.5
Schematic representation of the location of activations in the left middle temporal gyrus and left premotor cortex associated with tools, relative to animals or other object categories, across a variety of different paradigms (gray circles). Black circles indicate location of activations associated with imagined object grasping and imagined object manipulation (see text for details).

6.5). In addition, damage to this region has been linked to a selective loss of knowledge about tools (Tranel et al., 1997). These findings are consistent with the idea that information about object-associated motion is stored in the posterior region of the middle temporal gyrus.

As we suggested for the ventral region of the temporal lobe, the lateral region of the temporal lobes may also be tuned to different object features that members of a category share. The nature of these features remains to be determined. However, given the functional properties of posterior STS and middle temporal gyrus, one possibility may be that the lateral temporal cortex is tuned to the features of object motion. In the studies of Chao et al., biological objects (animals and faces) were associated with heightened activity in STS, whereas in Chao, Haxby, et al. (1999) and the studies listed above, tools were associated with heightened activity in the middle temporal gyrus. Objects, which by definition are stationary (houses), produced negligible activity in both regions. This pattern of activation suggests a superior-to-inferior gradient that may be tuned to the yet-to-be-determined features which distinguish biological motion from motion associated with the use of manipulable, man-made objects (see figure 6.4).

Left Premotor Cortex and the Representation of Object-Related Motor Sequences In the view taken here, semantic representations of objects are assumed to include information about their defining attributes, and are automatically active when objects are

identified. If that is so, one would expect to find selective activity near motor cortex for objects that we routinely manipulate manually (tools and utensils). Activation of one such area has been reported. Greater activation of the ventral region of left premotor cortex for tools than for animals has been reported for silent object naming of line drawings (Martin et al., 1996) and silhouettes (Martin et al., 1996). In addition, Grafton and colleagues (1997) reported left prefrontal activation for silently naming tools and tool-associated actions. Finally, Grabowski et al. (1998) reported that although left premotor and left prefrontal regions were active for naming animals and faces, as well as tools, an isolated region of left premotor cortex responded selectively to tools (this was a reanalysis of data from Damasio et al., 1996) (see figure 6.5).

These findings provide some support for an association between recognition of tools and activity in left premotor cortex. Tool-related activation of left premotor cortex, however, has not been nearly as consistent a finding as the association between tools and the left middle temporal gyrus. One possibility is that selective activity in left premotor cortex is difficult to identify with PET because many of the tasks employed have typically activated adjoining anterior sites in left lateral prefrontal cortex. In this regard, it may be noteworthy that the clearest findings have come from studies that used silent naming (Grafton et al., 1997; Martin et al., 1996) and silent verb generation (Grafton et al., 1997). Recent data from our laboratory using fMRI have replicated this finding. These studies have shown selective activation of left ventral premotor cortex for silent naming of tools relative to naming animal photographs and for viewing rapidly presented pictures of tools, but not of animals, faces, or houses (Chao & Martin, 2000). It is also noteworthy that activity in this region of premotor cortex has been found when subjects imagined grasping objects with their right hand (Decety et al., 1994; Grafton et al., 1997), and imagined performing a sequence of joystick movements with their right hand (Stephan et al., 1995) (figure 6.5).

Selective activation of left premotor cortex in response to manipulable objects is consistent with single-cell recording studies in monkeys. Rizzolatti and colleagues have identified neurons in the inferior region of monkey premotor cortex (area F5) that respond both during the execution of a movement and when observing the movement performed by others. Moreover, some cells that responded during movement execution also responded when the animals simply viewed objects they had previously manipulated (Murata et al., 1997). These and related findings have led to the suggestion that these neurons represent observed action, and form the basis for the understanding of motor events (see Jeannerod et al., 1995; Rizzollati, Fadiga, Gallese, et al., 1996). Thus, it may be that the left premotor region identified in the above noted functional brain-imaging studies carries out a similar function, specifically, storing infor-

mation about the patterns of motor movements associated with the use of an object. If that is so, then the fact that naming tools, but not animals, activates this region further suggests that this information is automatically accessed when manipulable objects are identified.

Summary and Implications of Category-Specific Activations Functional neuroimaging studies suggest that different types or classes of objects, such as animals and tools, are associated with different networks of discrete cortical regions. Tasks dependent on identifying and naming pictures of animals are associated with activity in the more lateral aspect of the fusiform gyrus, medial occipital cortex, and STS. These activations may be related to the automatic activation of stored information about object form, visual detail, and biological motion, respectively. In contrast, identifying and processing pictures of tools are associated with activation of the more medial aspect of the fusiform gyrus, left middle temporal gyrus, and left premotor cortex. These sites may be related to the automatic activation of stored information about object form, nonbiological motion, and object use-associated motor movements, respectively.

There is also evidence that reading the names of, and answering questions about, animals and tools produces category-related activity in some of the regions identified by the picture-processing tasks. This correspondence provides strong evidence that activity in temporal cortex reflects stored information about an object, not just the physical features of the material presented for processing. Moreover, in the Chao et al. study, the strongest activation was in the fusiform gyrus (a region assumed to represent object form) when answering questions about animals, and in the middle temporal gyrus (a region assumed to represent object motion) when answering questions about tools (see Chao, Haxby, et al., 1999, for details). Taken together with the studies of object picture-processing, these findings suggest that thinking about a particular object may require activation of the critical features that define that object. Thus, thinking about any characteristic of a particular animal would require activation of visual feature information. This finding could explain why some patients with a category-specific disorder for recognizing living things have difficulty answering questions that probe both visual and nonvisual information. In this view, these patients have damage to regions of the brain that store information about the visual form of animals, and activation of these representations may be necessary to gain access to other types of information about animals, assumed to be stored elsewhere. Consistent with this idea, Thompson-Schill and colleagues (1999) found increased activity in the left fusiform gyrus when subjects retrieved visual and nonvisual information about animals.

Viewed in this way, the evidence presented here appears to provide considerable support for feature-based models of semantic representation. However, some of the findings could be interpreted as evidence for Caramazza and Shelton's "domain-specific" hypothesis (1998) as well. For example, the clustering of activations associated with animals and faces, on the one hand, and tools and houses, on the other hand, reported by Chao, Haxby, et al. (1999) may be viewed as consistent with this interpretation. However, there is evidence to suggest that the representations of all nonbiological objects do not cluster together. For example, we have reported that the peak of activity associated with a category of objects of no evolutionary significance (chairs) was located laterally to the face-responsive region (in the inferior temporal gyrus) rather than medially (Ishai et al., 1999). Moreover, the domain-specific hypothesis does not make any predictions about where information about biological and nonbiological objects is represented in the brain. Clearly, different categories of objects activate different cortical networks. There does not seem to be a single region that maps onto whole categories. Nevertheless, it could be that there is a broader organization of these networks that reflects evolutionarily adapted, domain-specific knowledge systems for biological and nonbiological kinds. This possibility remains to be explored.

ISSUES

The evidence reviewed here suggests that we are beginning to make progress in understanding the neural substrate of some aspects of meaning. It is equally clear that we are only beginning to scratch the surface. Although I have tried to highlight agreements among studies, those familiar with this area of research may object that my focus has been overly narrow, and thus I have glossed over many puzzling discrepancies and contradictions in the literature. This is true. Time will tell whether the activations I chose to focus on, and the interpretations I have offered, are reasonable or not. Below I offer a brief list of some of the questions that may be worth pursuing in the future.

1. What is the role of the occipital lobes in object semantics? Specifically, does category-related activity in medial and ventral occipital cortex reflect top-down influences from more anterior regions in temporal cortex? If this activity is related to retrieving visual feature information, then why isn't occipital cortex active when information about color is retrieved? Integration of fMRI and MEG should help to sort out the temporal dynamics of activity within these networks.

2. How are category-related activations modified by experience? For example, what is the role played by expertise (e.g., Gauthier et al., 1999)? Will experience with motion and manipulation of novel objects result in the emergence of posterior middle temporal activity, and left premotor activity, respectively?

3. How is the lexicon organized? And how are lexical units linked to the networks of semantic primitives discussed in this chapter?

4. Similarly, where do we store associative information that comprises the bulk of semantic memory? How is this information linked to the networks of semantic primitives described here?

5. What neural structures mediate other aspects of meaning, such as the understanding of metaphor (e.g., Bottini et al., 1994)?

6. Do different structures within the medial temporal lobe declarative memory system (i.e., hippocampus, and entorhinal, perirhinal, and parahippocampal cortices) play different roles in the acquisition and/or retrieval of semantic and episodic memories (e.g., Maguire & Mummery, 1999)?

7. What brain structures are involved in categorizing objects? E. E. Smith and colleagues have shown that exemplar-based and rule-based categorizations activate different neural structures (E. E. Smith et al., 1999). Their study is an excellent example of how functional neuroimaging data can provide evidence germane to long-standing disputes in cognitive psychology.

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