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71 Category Specificity and the Brain: The Sensory/Motor Model of Semantic Representations of Objects

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ABSTRACT The semantic representation of an object is composed of stored information about the features and attributes defining that object, including its typical form, color, motion, and the motor movements associated with its use. Evidence from functional brain imaging studies of normal individuals indicates that this information is represented in the brain as a distributed network of discrete cortical regions. Within this network the features that define an object are stored close to the primary sensory and motor areas that were active when information about that object was acquired. Thus, the organization of semantic information parallels the organization of the sensory and motor systems in the primate brain. This organizational scheme provides a basis for understanding category-specific disorders of knowledge resulting from focal brain damage based on the premise that the distinction between members of different categories of objects, such as animals and tools, is dependent on access to information about different types of features. Storage of information about such features as form, color, motion, and object use-associated motor movements in separate regions of the brain may provide innately determined, neurobiologically plausible mechanisms that function in the service of referential meaning.

One of the most puzzling and intriguing consequences of focal brain injury is a category-specific disorder of knowledge—a selective difficulty naming and retrieving information about objects from a single semantic category. Reports of such patients have appeared in the clinical literature for more than 100 years (for review see Nielsen, 1958), but it is mostly in the past 10 to 15 years that significant progress has been made in understanding these category-specific effects. This progress is due largely to the seminal work of Elizabeth Warrington and her colleagues in the mid-1980s (Warrington and McCarthy, 1983, 1987; Warrington and Shallice, 1984), the ever-increasing number of careful case studies and theoretical analyses that followed (e.g., Allport, 1985; Damasio, 1989, 1990; Farah and McClelland, 1991; Farah, Mc-

Mullen, and Meyer, 1991; Hillis and Caramazza, 1991; Humphreys and Riddoch, 1987; Saffran and Schwartz, 1994; Shallice, 1988), and, more recently, functional brain-imaging studies of normal individuals.

This chapter focuses on functional brain-imaging studies of semantic object processing and on category-specific effects using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). Although these studies are in their infancy, the available evidence suggests that the study of object recognition and object naming can provide us with a window into the much broader issue of how information is stored and organized in the cerebral cortex.

In 1988, Petersen, Posner, Raichle, and colleagues published the first report on the functional neuroanatomy of semantic processing in the normal human brain (Petersen et al., 1988). Using PET, they presented single words (concrete nouns; e.g., “cake”) and asked their subjects to generate a 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 (Brodmann area, BA 47). Activation of left prefrontal cortex was found regardless of whether the words were presented visually or auditorily (in which case the subjects orally repeated the presented nouns to serve as the baseline), thus strengthening the authors’ conclusion of an association between left prefrontal cortex and semantics.

This was an extremely important study because it demonstrated the power of O15 PET and the subtraction method for isolating distinct regions of the brain associated with specific cognitive processes. However, there were two main problems with their conclusion concerning semantics. First, linguistic and cognitive models posit that the meaning of a concrete noun is not unitary, but rather is composed of parts—specifically, knowledge about the physical and functional properties of the object. As such, meaning in the brain has been viewed as a

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distributed system, involving many brain regions (e.g., Damasio, 1989). Second, even if semantic networks were confined to a single region, the neuropsychological evidence suggested that the critical area would be the left temporal, not the left frontal, lobe (e.g., Cappa, Cavallotti, and Vignolo, 1981; Hart and Gordon, 1990).

Thus, motivated by these issues, we began to explore the functional neuroanatomy of object semantics in the normal brain using PET. Specifically, we sought to determine whether information about the attributes and features that define an object is stored in the sensory and motor systems that were active during initial learning about that object. This hypothesis, which we call the *sensory/motor model of semantic knowledge* (Martin, 1998), has a long history in behavioral neurology. In fact, turn-of-the-century neurologists commonly assumed that the concept of an object (i.e., its representation) was composed of information about that object learned through direct sensory experience (e.g., Broadbent, 1878; Lissauer, 1890; Freud, 1891; Lewandowsky, 1908, translated in Davidoff and Fodor, 1989).

Retrieving information about object attributes

Given this framework, the critical question was: What object features should be studied? We decided on color and action because there is considerable evidence suggesting that the perception of these features, and knowledge about these features, can be differentially impaired following focal damage to the human brain. For example, acquired color blindness, or achromatopsia, can occur from a lesion of the ventral surface of the occipital lobes (e.g., Damasio et al., 1980; Vaina, 1994; Zeki, 1990), and PET and fMRI studies of normal individuals have confirmed selective activation of this region (specifically, the fusiform gyrus and collateral sulcus in the occipital lobe) during color perception (e.g., Corbetta et al., 1990; Sakai et al., 1995; Zeki et al., 1991). In contrast, a more dorsally located lesion, in the region of the lateral occipital gyrus (located at the border of occipital, temporal, and parietal lobes), can result in impaired motion perception, or akinetopsia (e.g., Zeki, 1991; Zihl et al., 1991; Vaina, 1994), and this location was subsequently confirmed by functional brain-imaging studies of normal subjects (e.g., Beauchamp, Cox, and DeYoe, 1997; Corbetta et al., 1990; Zeki et al. 1991; Watson et al., 1993).

In addition, focal lesions can result in selective deficits in retrieving information about object-associated color and object-associated motion. There are, for example, patients with color agnosia who 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; Luzzatti and Davidoff, 1994), and other patients have been described with a selective deficit in retrieving verbs (e.g., Caramazza and Hillis, 1991; Damasio and Tranel, 1993). Although the behavioral dissociations exhibited by these patients could be remarkably focal, their brain lesions were not. As a result, the locations of the regions which, when damaged, produced these deficits could not be precisely defined, aside from the suggestion that color agnosias were most commonly associated with damage to the posterior region of the left temporal lobe (see Damasio, Tranel, and Damasio, 1989, for review), whereas verb-generation deficits most commonly were seen in association with damage in and around Broca's area. However, the lesions in these patients often extended posteriorly to include perisylvian cortex (see Gainotti et al., 1995, for review).

The paradigm we used was straightforward. 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. For example, subjects shown a picture of a child's wagon would respond "wagon," "red," and "pull" during the different PET scanning conditions. This last condition is the same as the verb-generation task developed by Petersen, Posner, and colleagues, discussed above.

In agreement with Petersen and co-workers (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 as a function of the type of information subjects retrieved. Rather, the activation was similar for the color and action retrieval conditions, and hence consistent with the idea that left lateral prefrontal cortex is critically involved in retrieval from semantic memory (e.g., Gabrieli, Poldrack, and Desmond, 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 pattern of cortical activity associated with these tasks could be attributed to differences in the type of information that the subjects retrieved, rather than to differences in the ease of retrieving the information.

Relative to action verbs, generating color words activated the ventral region of the temporal lobes bilaterally, including the fusiform and inferior temporal gyri, approximately 2–3 cm anterior to regions known to be active during color perception (figure 71.1A; see also color plate

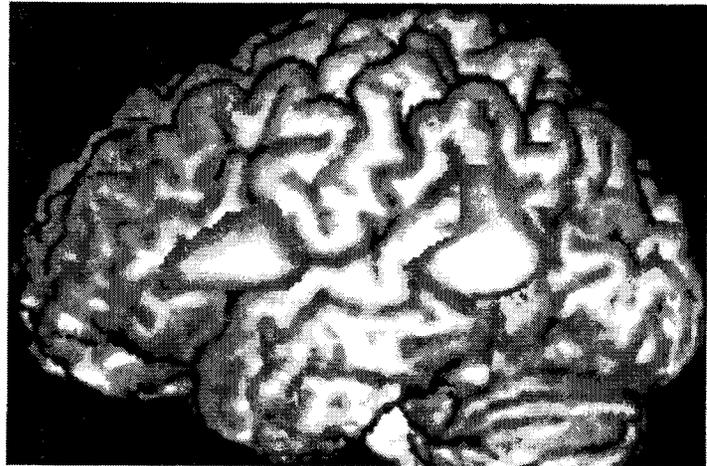
A.**B.**

FIGURE 71.1 (A) Ventral view of the brain showing regions in the temporal lobe more active when subjects retrieved information about object-associated color than object-associated action. (B) Lateral view of the left hemisphere showing regions

more active when subjects retrieved information about object-associated action than object-associated color. (Adapted from Martin et al., 1995.)

45). In contrast, action word generation was associated with a broader pattern of activation that included the classic language zones (left inferior frontal cortex—Broca's area—and the posterior aspect of the left superior temporal gyrus—Wernicke's area) and the posterior region of the left middle temporal gyrus (figure 71.1B; see also color plate 45).¹ The middle temporal activation was located approximately 1–2 cm anterior to the regions active during the motion perception, based on previous PET findings. Thus, retrieving information about specific object attributes activated brain regions proximal to the areas that mediate perception of those attributes.

Replication and converging evidence

COLOR There are now three additional studies reporting an association between the retrieval of object color information and activation of the ventral region of the posterior temporal lobes. In one experiment, subjects generated color words in response to written names of objects, rather than to object pictures (Martin et al., 1995). In

another study, color word generation to pictures of objects was contrasted with generating a color word based on a recently learned, novel, object–color association (Wiggs, Weisberg, and Martin, in press). In a third study, color word generation was evaluated in relation to color naming and color perception (Chao and Martin, 1999). In each study, generating the name of a color commonly associated with an object activated the same region of the ventral temporal cortex, bilaterally in three of the four investigations, located anterior and lateral to the occipital areas active during color perception (figure 71.2A).

Additional evidence that this region may be the site where object-associated color information is stored comes from a PET study of individuals with color-word synesthesia (Paulesu et al., 1995). These individuals, who experience vivid colors when hearing words, showed activity in the left ventral temporal lobe when listening to single words (concrete nouns), whereas normal subjects did not. Moreover, the region active in the synesthetes when they heard words and experienced colors was the same area active when normal subjects retrieved object

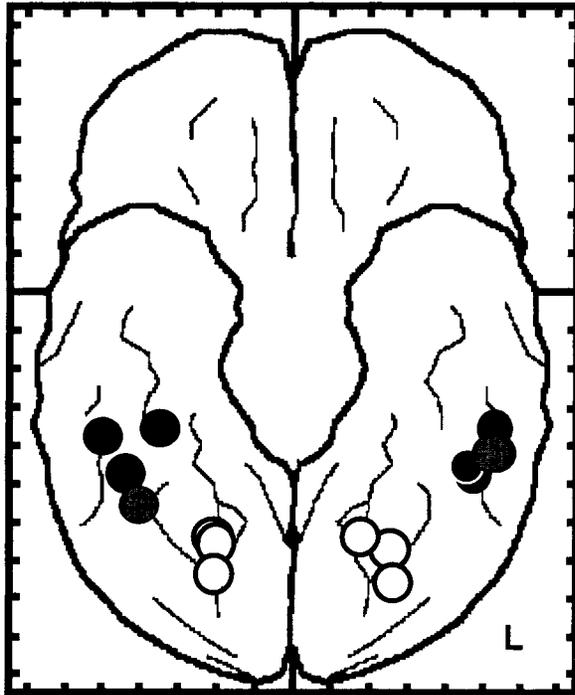
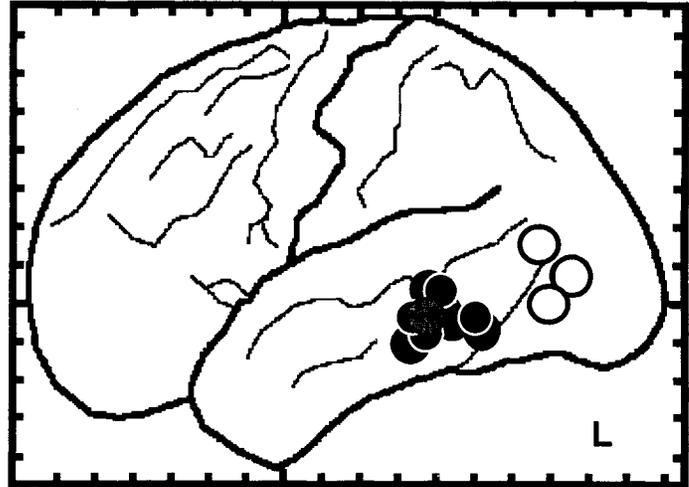
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FIGURE 71.2 (A) Summary of findings suggesting that color information is stored in the ventral temporal lobe, anterior to the regions that mediate color perception. White circles show the location of regions active during color perception (Corbetta et al., 1990; Sakai et al., 1995; Zeki et al., 1991); black circles show the location of regions in the ventral temporal lobes active when subjects generated color words (Martin et al., 1995, two studies; Wiggs, Weisberg, and Martin, 1999; Chao and Martin, 1999); the gray circle on the left hemisphere shows the location of the region active when color-word synesthetes experienced color imagery (Paulesu et al., 1995); the gray circle on the right hemisphere shows the location of the region active in normal subjects during a color imagery task

color information (figure 71.2A). Thus, the vivid experience of color imagery automatically elicited by auditory stimulation in the synesthetes and the effortful retrieval of information about object color by normal individuals activated a similar region of ventral temporal cortex.

Interestingly, although the word-color synesthesia subjects experienced color when they heard words, they did not show activation in ventral occipital cortex. This finding is in accord with studies in normal subjects of color perception that also evaluated color word (Chao and Martin, 1999) and color imagery generation (Howard et al., 1998)—studies that found activation in the ventral temporal lobe, but not in regions of the occipital cortex active when colors were perceived. These findings, coupled with reports of intact color imagery in an achromatopsic patient (Shuren et al., 1996) and impaired color

B

(Howard et al., 1998). (B) Summary of findings suggesting that motion information is stored in the middle temporal gyrus, anterior to the regions that mediate motion perception. White circles show the location of regions active during motion perception (Corbetta et al., 1990; Watson et al., 1993; Zeki et al., 1991); black circles show the location of the area in the left middle temporal gyrus active when subjects generated action words (Fiez et al., 1996; Martin et al., 1995, two studies; Warburton et al., 1996, four studies; Wise et al., 1991); the gray circle shows the location of activity in the left middle temporal gyrus from an analysis of the pooled data from verb generation experiments conducted at 12 centers participating in the European Union collaborative study (Poline et al., 1996).

imagery in a patient with intact color perception (De Vreese, 1991; case II), suggest that information about object color is stored in the ventral temporal lobe, and that the critical site is close to, but does not include, the areas in occipital cortex that selectively respond to the presence of color.

ACTION There are at least a dozen studies in the literature that have used the action word generation task. As with studies of color word generation, the results have been remarkably consistent. The stimuli used in these studies have included pictures of objects, words presented visually, and words presented auditorily. Subjects have responded aloud in some studies, and silently in others; and they have been required to produce a single response to each item in some studies, and multiple re-

sponses to each item in others. Nevertheless, retrieving information about object-associated action has consistently activated the left middle temporal gyrus, anterior to the region commonly activated during motion perception (figure 71.2B). Moreover, direct electrical stimulation of this region produced greater disruption of action naming than object naming (Corina et al., 1998). Thus, the posterior region of the left middle temporal gyrus appears to be a critical site for storing information about object-associated motion.

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. Rather, these data suggest that this information is distributed throughout the cerebral cortex, and that information about different features is stored in different regions. In addition, the locations of the sites are not distributed randomly, but rather follow a specific plan that parallels the organization of sensory systems, and perhaps 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) the regions that mediate perception of those attributes.

Automatic activation of semantic object representations

In requiring subjects to focus attention on their knowledge (i.e., stored information) about different object attributes, these findings showed an association with activity in different regions of the posterior temporal lobe. These findings were therefore similar to studies showing modulation of activity in different regions of occipital cortex when subjects attended to different, physically present, features of a stimulus such as its color and motion (e.g., Corbetta et al., 1990). The difference was that in the word generation and imagery studies, attention was paid to stored information about these attributes, rather than to visual properties of the stimulus.

However, as noted earlier, a defining characteristic of patients with category-specific deficits is that they have trouble naming particular types of objects. This finding, in turn, is in accord with models of object naming in which access to stored information about the object is necessary to name it (e.g., Glaser, 1992; Humphreys, Riddoch, and Quinlan, 1988). Simply put, there is no way to get from the lower-order processing of the physically presented object to the object's name without activating prior knowledge about that object. Therefore, a number of investigators have asked whether one could

find evidence for automatic activation of semantic representations during object naming.

The strategy used in these investigations was similar to the word-generation studies reviewed above. The main idea was to try to identify different patterns of activation by pitting different categories against each other. Now, however, instead of focusing attention on information about different attributes, subjects simply named objects from different categories during different brain-imaging scans.

The categories most commonly investigated have been animals (primarily four-legged mammals) and manipulable man-made objects such as tools and utensils. As with the choice of color and action attributes, this choice was motivated by the clinical literature. Specifically, some patients have been described with selective deficits in naming and retrieving information about animals (and often other living things) and others with selective deficits concerning tools (and often other man-made objects), and these are the most common categories affected in patients with category-specific disorders (see Saffran and Schwartz, 1994, for review). One idea as to why this dissociation occurs is based on an argument initially advanced by Warrington and her colleagues (Warrington and McCarthy, 1987): Recognition and naming of individual animals may depend on access to stored information about visual form, whereas recognition and naming of individual tools may depend on access to stored information about function. In fact, as demonstrated by Farah and McClelland (1991), these relationships are evident in standard dictionary definitions. For example, the word *camel* is defined by what it looks like—specifically, as being large, having a humped back, a long neck, and large feet; the word *wrench*, however, is defined by its function—specifically as being used for holding and turning other objects (cf. *Webster's New World Dictionary*, 3d edition, 1988).

Thus the central idea is that we need to utilize information about relatively subtle differences in visual form to distinguish one four-legged animal from another. We know animals, and we distinguish among them by their physical features—primarily shape and, to a lesser extent, color and pattern (consider, for example, the difference between a leopard, a tiger, and a jaguar, or between a horse, a donkey, and a zebra). But tools are different. Although tools clearly have different shapes, and there is certainly a relationship between their form and function, the relationship between a tool's physical shape and its name is simply not as tightly constrained as the relationship between the physical shape of an animal and its name. Thus, for animals, there is an invariant relationship between name and form, whereas for tools there is an invariant relationship between name and function.

An important point to be addressed, then, is the meaning of “function” in the present context. In some formulations the term *function* is used to designate a large number of characteristics concerned with an object’s use. As such, the information is characterized as more “abstract,” “conceptual,” “verbal,” and “semantic” than the visual form-based information needed to distinguish among animals (e.g., Riddoch and Humphreys, 1987; and see discussion in Tyler and Moss, 1997). In contrast, the position proposed here is that the information about object function needed to support tool recognition and naming is information about the patterns of visual motion and patterns of motor movements associated with the actual use of the object. As such, this information is as dependent on sensory experience as is information about the visual form. The difference is that functional information is derived from motor movements, and visual processing of motion, rather than visual processing of form.

In our first study we asked subjects to silently name line drawings of real objects, each presented for a brief period of time (180 ms) (Martin et al., 1996). For one scan the objects were four-legged animals, and for another the objects were common tools and utensils. Subjects also attended to visual noise patterns, and stared at novel, nonsense objects during other scans to provide baselines. First, as expected, relative to viewing nonsense objects, naming real objects was associated with activity in the left inferior frontal lobe (i.e., Broca’s area), thus indicating that the subjects named the objects to themselves, as instructed. In addition, naming animals and naming tools both produced strong, bilateral activity in the posterior region of the fusiform gyrus of the temporal lobe, greater on the left than on the right. This failure to find category-related differences in the ventral temporal lobe was somewhat problematic, and we will revisit this issue.

In addition to these regions that were active during both animal and tool naming, other brain regions were differentially activated by animal and tool naming. First, naming tools was associated with activity in the left middle temporal gyrus, in the same region that was active in the previously discussed action verb generation studies. Tool naming was also associated with activity in the left premotor cortex, in the same region active when subjects imagined grasping objects with their dominant hand (Decety et al., 1994). Taken together, these findings were consistent with the idea that identifying individual tools was dependent on accessing information about object-associated patterns of visual motion, stored in the posterior region of the left middle temporal gyrus, and accessing information about object-associated patterns of motor movements stored in left premotor cortex (Martin et al., 1996).

In contrast, relative to naming tools, naming animals was associated with activation of medial occipital cortex. This activation was bilateral, but stronger on the left than the right. We suggested that this occipital activity reflected top-down activation, which would occur whenever information about visual features is needed to distinguish between category members. Thus, there were two parts to this argument. First, that animals are defined by their physical form, and that in order to name them we need to gain access to this stored-form information. Second, when the differences between members of a category are determined by relatively subtle differences in form (as in the previously mentioned animal examples), the occipital cortex is brought into play to help to visualize (image) these differences. Thus, the second part of the argument was the same as the idea proposed by Kosslyn (e.g., Kosslyn, Thompson, and Alpert, 1995; Kosslyn et al., 1995) with regard to involvement of occipital cortex in visual imagery tasks that require imaging fine details of an object or scene. But while in Kosslyn’s tasks subjects are explicitly asked to create and manipulate an image, in this formulation the image would be generated automatically, and often outside of awareness (and see Shulman et al., 1997, for additional evidence for top-down modulation of medial occipital cortex associated with other types of visual processing tasks).

Replication and converging evidence

RECOGNITION OF ANIMALS AND THE MEDIAL OCCIPITAL CORTEX Of course, the alternative, and more straightforward interpretation of the medial occipital activation when naming animals is that it reflects differences in the visual complexity of the stimuli. Under this view, pictures of animals produce greater activity in medial occipital cortex because the line drawings depicting these objects were more visually complex than the line drawings depicting tools. Similarly, a patient could have greater difficulty naming animals than tools because the pictures are more visually complex, and less familiar, than pictures of tools and other manipulable objects, such as kitchen utensils (see Gaffan and Heywood, 1993; Stewart, Parkin, and Hunkin, 1992, for supportive data; Farah, Meyer, and McMullen, 1996, for counter-evidence). Therefore, we attempted to rule out stimulus differences in visual complexity by transforming each of the object pictures to a silhouette, thereby eliminating differences between animal and tool pictures with regard to internal visual detail. This transformation produced a modest slowing of naming speed and increased errors, but importantly, eliminated the speed and accuracy advantage for tool naming relative to animal naming found in the study using line drawn stimuli.

Silent naming of the object silhouettes produced the same differential patterns of activation for animal and tool naming found in the first study, including greater activation of the left medial occipital region when naming animals than when naming tools (Martin et al., 1996). Greater medial occipital activation for animal than tool stimuli was also reported by Perani and colleagues (1995) using a semantic, exemplar match paradigm, and by Damasio and colleagues (1996) using an object naming task. Thus, these findings were more consistent with a top-down explanation than with a bottom-up explanation for the association of medial occipital activation and naming pictures of animals.

Additional, and more direct, evidence for the differential patterns of activation associated with identifying and naming animals and tools comes from a recent study of patients with category-specific knowledge disorders. Tranel, Damasio, and Damasio (1997) identified 28 individuals with focal brain lesions that had impaired recognition and naming of animal pictures. Unlike the patients in their previous report (Damasio et al., 1996) of category-specific naming, but not knowledge, disorders, the patients included in the 1997 study failed to provide evidence of intact knowledge about the stimuli they could not name. For example, they were unable to provide accurate, detailed descriptions of the items, thus suggesting that they had a semantic, category-specific deficit. Each of the 28 patients had a lesion that included the medial aspect of the occipital lobe. In 14 of the cases, the lesion was lateralized to the left hemisphere; in the remaining cases, the lesion was lateralized to the right. These were not the first cases with unilateral occipital lesions and category-specific disorders. For example, Nielsen (1958) described six patients with what he termed a selective agnosia for animate objects, all of whom had unilateral occipital lesions, mostly on the left. Thus the functional brain imaging studies of normal subjects and studies of patients with focal brain lesions provide converging evidence that the medial occipital cortex is more involved in recognizing and naming animals than tools (figure 71.3A,B; see also color plate 46), and that its role in mediating this ability is not easily attributed to bottom-up processing of stimulus characteristics.

RECOGNITION OF TOOLS AND THE LEFT MIDDLE TEMPORAL GYRUS The Tranel, Damasio, and Damasio (1997) study also identified eight patients with impaired recognition and naming of tools. The lesions in those patients all included the posterior region of the left middle temporal gyrus, in nearly the same region active during tool naming, and action word generation (figure 71.3C,D). Thus, these patients provided converging evi-

dence that the left posterior middle temporal gyrus is necessary for naming tools, but not animal pictures. In addition, in a PET study of verbal fluency to orally presented category cues, Mummery and colleagues (1996) found activation of this same region of the left middle temporal gyrus when normal subjects simply generated the names of tools and other manipulable objects, such as weapons and toys, relative to generating the names of animals, vegetables, and fruits. Therefore, these studies provide additional evidence consistent with the idea that this region of the left temporal lobe may be where information about object associated motion is stored.

RECOGNITION OF TOOLS AND LEFT PREMOTOR CORTEX Although the Tranel, Damasio, and Damasio (1997) study did not identify patients with anterior lesions, there are reports of at least five patients with lesions that included the left frontal lobe who were more impaired with man-made objects than animals (reviewed in Gainotti et al., 1995). However, as is common with patients with category-specific disorders, the lesions were large, and included the left parietal lobe (all five cases), as well as the left temporal lobe (three of five cases). Therefore, although consistent with the idea that the left premotor region may be involved in naming and knowing about tools, these cases do not provide evidence for the specific involvement of left premotor cortex.

Supportive evidence, however, has been provided by other functional brain imaging studies. Activation of the left premotor site associated with naming tools, but not animals, was found when subjects imagined grasping objects with their right hand (Decety et al., 1994; Grafton et al., 1996), imagined performing a sequence of joystick movements with their right hand (Stephan et al., 1995; activation of the left middle temporal gyrus was also reported in this study), and silently generated action words to pictures of tools (Grafton et al., 1997) (figure 71.4).

Interestingly, studies by 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. 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 (Rizzolatti et al., 1996a). 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 information about the patterns of motor movements associated with the use of an object. If so, the fact that naming tools, but not animals, activates this region further

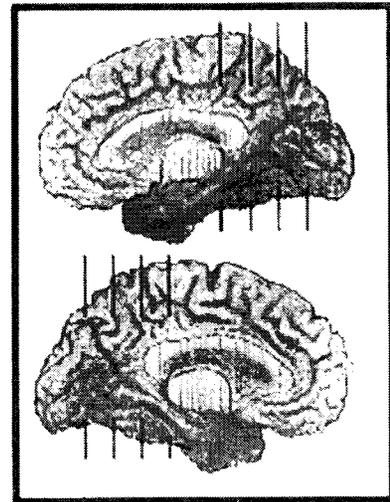
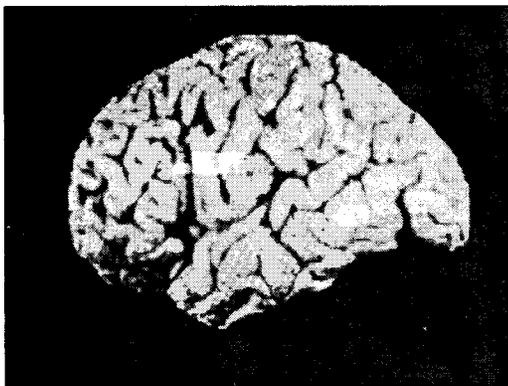
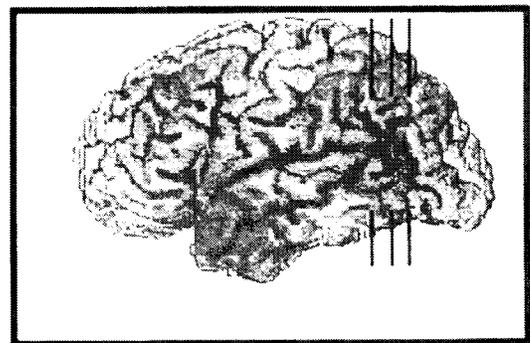
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FIGURE 71.3 (A) View of the medial surface of the left hemisphere showing the region of activation in the medial occipital lobe when subjects silently named drawings of animals relative to naming drawings of tools (adapted from Martin et al., 1996). (B) View of the medial surface of the left and right hemispheres showing the location of lesions in 28 subjects that had impaired recognition and naming of drawings of animals (adapted from Tranel, Damasio, and Damasio, 1997). (C) View

of the lateral surface of the left hemisphere showing regions active in the premotor cortex and middle temporal gyrus when subjects silently named drawings of tools relative to naming drawings of animals (adapted from Martin et al., 1996). (D) View of the lateral surface of the left hemisphere showing the location of lesions in 8 subjects that had impaired recognition and naming of drawings of tools (adapted from Tranel, Damasio, and Damasio, 1997).

suggests that this information is automatically accessed when manipulable objects are identified. Indeed, while some neurons in monkey F5 responded when movements were observed, other neurons responded as soon as a graspable object was visually presented (see Jeannerod et al., 1995 for review).

Posterior temporal cortex revisited: The representation of object form and motion

As noted previously, in the study by Martin and colleagues (1996), the ventral region of the posterior temporal lobe was activated bilaterally, and to an equal extent by animal and tool naming. Perani and associates (1995) also reported activity in the ventral temporal region for both animals and tools; but again, this region

was not differentially involved in processing objects from one category or the other. These findings were problematic for two reasons. First, if greater activation of the medial occipital lobe when naming animals than tools results from top-down modulation, there should be differentiation more anteriorly in the ventral object-processing stream to drive this process. If there is no anterior site that responds more during animal than tool naming, then where is the top-down influence originating from? Second, although, as reviewed above, there have been reports of patients with unilateral occipital lesions that had category-specific impairment for animals and other animate or living objects, many other cases have had lesions confined to the temporal lobes, often as a result of herpes encephalitis (see Ferreira, Giusiano, and Poncet, 1997, for recent cases; and see Gainotti et

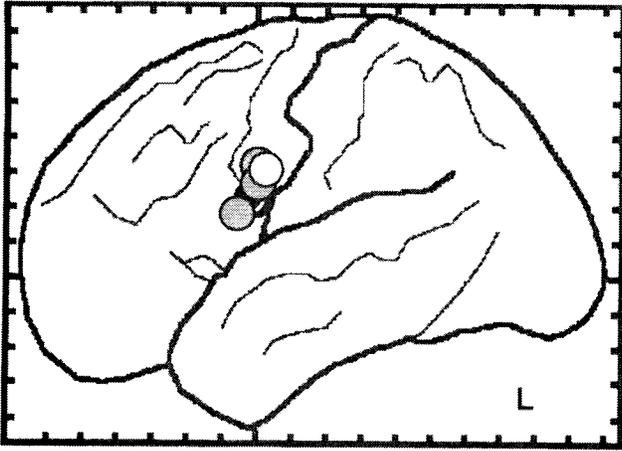


FIGURE 71.4 Summary of findings suggesting that information about patterns of motor movements associated with the use of objects is stored in left premotor cortex. Black circles show the location of regions active when subjects silently named line drawings and silhouettes of tools relative to naming animals (Martin et al., 1996). The white circle shows the location of the region active when subjects silently generated action words in response to pictures of tools (Grafton et al., 1997). Gray circles show locations active when subjects imagined grasping objects with their right hand (Decety et al., 1994; Grafton et al., 1997), and imagined a sequence of joystick movements (Stephan et al., 1995).

al., 1995, for review). The functional brain imaging data indicated that the posterior region of the middle temporal gyrus was selectively involved in recognizing and naming tools, and the human lesion data showed that a lesion in this region could produce a category-specific deficit for tools (Tranel, Damasio, and Damasio, 1997). However, the functional brain imaging data have not identified a region of the temporal lobe selectively involved in processing and knowing about animals, even though the human lesion data suggest that such a region, or regions, should be found.

One possibility is that this discrepancy between the functional brain imaging and lesion data is a result of the limited spatial resolution of PET. Perhaps there is a consistent category-related topology in the ventral region of the temporal lobe, but the sites are situated too close to one another to be visualized by PET. Evidence in support of this idea has been provided by studies of epileptic patients with chronically implanted electrodes, and fMRI studies of normal subjects. These studies have identified relatively small regions in the ventral temporal lobe that selectively respond to the presentation of different types of stimuli, such as human faces (e.g., Allison et al., 1994; Haxby et al., 1997; Kanwisher, McDermott, and Chun, 1997; McCarthy et al., 1997; Puce et al., 1995), letters (Allison et al., 1994; Puce et al., 1995; Polk and Farah, 1998), houses (Haxby et al.,

1997), chairs (Ishai et al., 1997), and representations of the local visual environment (Epstein and Kanwisher, 1998).

The most consistent finding has been the selective activation of the more lateral aspect of the fusiform gyrus, usually stronger on the right than on the left, in response to human faces. In addition, using fMRI, Haxby and colleagues have found that whereas the lateral fusiform is more responsive to faces, the more medial aspect of the fusiform gyrus is more responsive to pictures of houses (Haxby et al., 1997; Ishai et al., 1997). This topological arrangement was highly consistent across subjects, variation in stimuli (i.e., photographs and line drawings), and task (passive viewing, delayed match to sample). Moreover, a similar, highly consistent topology in the fusiform gyrus has also been revealed for the processing of animals and tools across several different paradigms (passive viewing, delayed match to sample, and naming) (Chao et al., 1998a,b).

First, pictures of animals produced a robust response in essentially the same region activated by human faces (i.e., lateral fusiform gyrus, bilaterally), regardless of whether the animal's face was visible or not (Chao et al., 1998b). Second, in contrast to human faces, animal pictures also elicited weaker, yet significant, bilateral activity in the more medial aspect of the fusiform gyrus that responded most strongly to houses; faces, in contrast, produced essentially no activity in this region.² Third, relative to animals, tools were associated with greater activation of the more medial aspect of the fusiform gyrus that overlapped with, but was not identical to, the medial fusiform region most responsive to houses (Chao et al., 1998a).

Therefore, in contrast to the PET data, fMRI revealed distinct and consistent patterns of activity for animals and tools in the ventral region of the temporal lobe, bilaterally. Viewing, matching, and naming pictures of animals were associated with stronger activation of the lateral aspect of the fusiform gyrus than was performing these tasks with pictures of tools, whereas tools produced greater activity in the more medial aspect of the fusiform gyrus than did animals.

It is important to note, however, that in these studies no area was identified that responded exclusively to one class of objects and not others. Rather, each object type activated a relatively broad region of the fusiform gyrus (albeit more narrowly for faces), but the peaks of these activations were centered on different parts of the fusiform gyrus. Therefore, rather than being organized by object category, per se, this pattern of results was more consistent with the idea that this cortex is tuned to different object features that members of a category have in common. The nature of these features remain to be

determined. However, because the fusiform gyrus is part of the ventral, object-processing stream, a likely possibility is that this region may be tuned to features of object form. Thus, information about object form may be stored in the fusiform gyrus and other regions of ventral temporal cortex, downstream from the regions of occipital cortex that mediate form perception. Moreover, this cortex may have a consistent topological arrangement based on stored features of form shared by objects in the same category (i.e., faces, houses, animals, tools).

Animals and tools were also associated with activations of neighboring regions. Consistent with the PET data, tools were associated with activity in the middle temporal gyrus in most subjects, stronger on the left than on the right (i.e., the same region active when subjects retrieve action verbs). Animals and faces, however, were associated with activation in the superior temporal sulcus (STS) in about half the subjects, usually stronger on the right than on the left (also reported by Kanwisher, McDermott, and Chun, 1997).

Single-cell recording studies in awake monkeys have shown activity in STS when the monkeys were viewing faces and face components, and when the monkeys observed 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 (Kanwisher, McDermott, and Chun, 1997), viewing mouth and eye movements (Puce et al., 1998), and when observing human movements (Bonda et al., 1996; Rizzolatti et al., 1996b). Thus it may be that the STS is involved not only in the perception of biological motion, but also in storing information about biological motion, perhaps in different parts of this region. If so, the fact that viewing animals and faces activates a portion of STS suggests that this information may be necessary, or at least available, to support processing of these stimuli. Similarly, the consistent finding of left middle temporal gyrus activity in response to pictures of tools suggests that information about motion properties of nonbiological objects may be stored in this region of the temporal lobe.

Finally, as was the case for the ventral temporal lobe, the lateral temporal cortex may not be organized by object category, per se, but rather may be tuned to different object features that members of a category have in common. Again, although the nature of these features remain to be determined, the proximity of these activations to the more posterior motion processing areas suggests that this region may be tuned to features of object motion. Yet-to-be-determined properties associated with biological motion produce activity centered around the STS, whereas properties of man-made object-associated

motion produce activity centered around the middle temporal gyrus and inferior temporal sulcus (figure 71.5).

Summary: Multiple, distinct regions for processing and storing information about object attributes

Studies of patients with focal cortical lesions and the findings from functional brain imaging of the intact human brain provide converging evidence for the idea that recognition and naming of 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 were associated with activation of the more medial aspect of the fusiform gyrus, left middle temporal gyrus, and left premotor cortex; and these sites may be related to the automatic activation of stored information about object form, nonbiological motion, and object use-associated motor movements, respectively.

The important point here is that regardless of the functions or computations ultimately attributed to these regions, these data suggest that the proper level of analysis for understanding semantic object representations is at the level of features, not at the level of whole-object concepts like animals and tools (for an alternative view, see Caramazza and Shelton, 1998, and Caramazza, this volume).

Finally, although much of the evidence reviewed here concerns processing of pictures of objects, it is assumed that these networks will be active regardless of the physical characteristics of the stimulus (picture or word) or modality of presentation (visual or auditory).

Conclusion: Semantic primitives

If there is one aspect of a semantic system that invites consensus, it is that the system must be productive. And, in order to be productive, it must be compositional (e.g., Fodor and Lepore, 1996). In this chapter we have reviewed evidence that suggests what some of those components may be. These components can be thought of as prelexical, semantic primitives for processing and storing information about form, color, motion, and movement (Martin, 1998). This list is not meant to be exhaustive. A good case could be made for other semantic primitives concerned with space, time, number, and

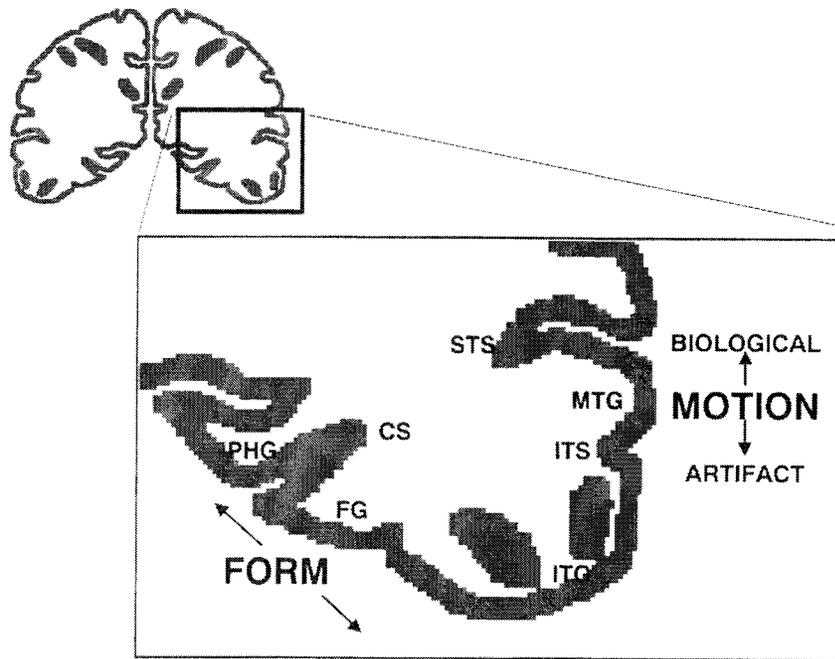


FIGURE 71.5 Schematic representation of posterior temporal cortex proposed to be tuned to features of object form (ventral surface) and motion (lateral surface) shared by members of a category. It is assumed that information is stored in this region according to some as-yet undetermined, but probably innate, properties. It is further assumed that this region would be ac-

ffective valence. These should be thought of as innately determined, neurobiologically plausible mechanisms that function in the service of meaning. Such a scheme, on the level of features and attributes, provides us with combinatorial power out of which different, and finer shades of meaning can be created.

NOTES

1. Re-analysis of the initial study by Petersen and colleagues (1988) indicated that the posterior region of the left middle temporal gyrus was active during their verb generation condition. This activation was not reported because it was below the threshold for statistical significance. Subsequent studies of verb generation by these investigators showed robust activation of the left middle temporal region when the rate of stimulus presentation was slowed from 1 per second (used in Petersen et al., 1988) to 1 per 1.5 seconds, thus giving subjects more time to retrieve each verb (see Raichle et al., 1994, and Fiez et al., 1996).
2. The differential patterns of activity in the lateral and medial fusiform gyrus in response to pictures of animals and human faces may provide a clue to why patients can present with a selective deficit for faces, and not other types of objects such as animals. It is not because the lateral region of the fusiform gyrus processes only faces; rather, it is because faces, as stimuli, are more focally represented than other classes of objects. Thus, when the lateral fusiform is damaged, face processing suffers to a greater extent than the processing of other object types.

tive in support of object identification, regardless of stimulus format (object or word) or modality of input. PHG, parahippocampal gyrus; CS, collateral sulcus; FG, fusiform gyrus; ITG, inferior temporal gyrus; ITS, inferior temporal sulcus; MTG, middle temporal gyrus; STS, superior temporal sulcus.

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