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71 Circuits in Mind: The Neural Foundations for Object Concepts

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ABSTRACT Functional neuroimaging studies have provided convincing evidence to support three main conclusions about the neural circuitry that underpins our understanding of objects in the world. First, our conceptual system contains property-based neural circuits *grounded* in the systems that support perceiving, acting, and feeling. Second, our conceptual system prominently includes relatively distinct neural circuits for processing and storing *domain-specific* information. Third, these circuits reflect the *interpretation* or meaning assigned to an object, not its physical features. Outstanding questions and problems with an embodied, domain-specific view of conceptual representation, as well as the role of the anterior regions of the temporal lobes in conceptual processing and semantic memory, are discussed.

Every day we encounter new exemplars of objects that we have never seen before. Yet we identify each as belonging to a particular category—as a chair, a dog, a tree—instantly and effortlessly. In fact, it has been shown that as soon as we *see* it we *know* what it is (Grill-Spector & Kanwisher, 2005). This mundane phenomenon underscores the fact that object recognition must be—in part—an act of memory. Perceiving, as William James recognized 120 years ago, is largely dependent on stuff that "comes out of our own heads." Indeed, for James, this idea was important enough to be considered "the general law of perception" (W. James, 1890). This chapter will focus largely on what we have learned about the stuff in our heads that allows us not only to perceive, but also to imagine and think about objects in the world.

What is an object concept?

For our purposes, *object concept* will be used to refer to the representation (i.e., the information stored in memory) of an object category (a class of objects in the external world) (Murphy, 2002). In this view, concepts are in our heads, categories are in the world. This distinction in no way undermines the fact that any object category (hammers, dogs) can be *categorized* in a nearly infinite variety of ways. For example, both hammers and dogs belong to the category of things that are smaller than a house. The neural basis for creating flexible ad hoc categories (Barsalou, 1989) will not be discussed here other than to note that the available neurophysiological evidence suggests that this ability rests heavily on activity in the prefrontal cortex, in interaction with the temporal lobes (see Miller, Nieder, Freedman, & Wallis, 2003, for review). Here I focus on the neural underpinnings for basic-level categories as defined in the following paragraphs.

The primary function of concepts is to allow us to quickly draw inferences about an object's properties. That is, identifying an object as, for example, a "hammer" means that we know that this is an object that is used to pound nails, so that we do not have to rediscover this property each time the object is encountered (see Murphy, 2002, for an extensive review of cognitive studies of concepts). In this sense, object perception involves not only making contact with stored information about the features present in the stimulus (e.g., what hammers typically look like), but also inferred information about other features or properties (e.g., those related to its function).

A major feature of object concepts is that they are hierarchically organized, with the broadest knowledge represented at the superordinate level, more specific knowledge at an intermediary level commonly referred to as the basic level, and the most specific information at the subordinate level. For example, "dog" is a basic-level category that belongs to the superordinate categories "animal" and "living things," and has subordinate categories such as "poodle" and "collie." As established by Eleanor Rosch and colleagues in the 1970s, the basic level has a privileged status (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976; Rosch, 1978). It is the level used nearly exclusively to name objects (e.g., "dog" rather than "poodle"). It is also the level at which we are fastest to verify category membership (i.e., we are faster to verify that a picture is a "dog" than an "animal" or a "poodle"). It is also the level at which subordinate category members share

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the most properties (e.g., collies and poodles have similar shapes and patterns of movement). Finally, the basic level is the easiest level at which to form a mental image (you can easily form an image of an elephant but not of an "animal"). This hierarchical organization has played a prominent role in the neuropsychology and computational modeling of semantic memory (e.g., McClelland & Rogers, 2003; and see chapter 72 in this volume by McClelland, Rogers, Patterson, Dilkina, & Lambon Ralph). Nevertheless, the great majority of neuropsychological and neuroimaging studies have concentrated on understanding how basic-level concepts are represented in the brain.

Neural foundations for conceptual representations

Before describing what we know about the circuitry underpinning the representation of basic object concepts, it is important to draw a distinction between explicit and implicit levels of knowledge representation and expression. There is no need for any organism to acquire information unless that information can be expressed. Organisms learn, and the evidence for that learning is demonstrated by a change in behavior. What is represented (stored) in the brain is information. What is expressed is knowledge. How this knowledge is expressed is of fundamental importance for understanding how information is represented. For humans, a primary, and arguably *the* primary mode of expression, is the language system. Questions designed to probe knowledge about a specific entity are posed orally or in written form, and subjects respond verbally. Occasionally, a manual response may be required (e.g., show me how you would use a hammer) either by actually manipulating the object or by pantomime. However, regardless of whether the response is verbal or manual, knowledge is expressed explicitly. This explicit knowledge is typically referred to as associative knowledge or encyclopedic knowledge, and it is this level that is typically probed in both normal and brain-damaged individuals. Associative or encyclopedic knowledge has three main characteristics. First, as noted earlier, retrieval is explicit. Second, there is no intrinsic limitation on the amount of information that can be stored and retrieved. For a specific category of objects, (e.g., *dogs*), we may know lots of things. We know they are living things, have four legs, are smaller than a car, like to take walks, like to play fetch, and so on, and so on. Moreover, it does not matter whether the information is true. If you believe that dogs can fly, then that information is part of your semantic knowledge about dogs and is represented somewhere in your brain. Finally, this level of knowledge is idiosyncratic. Some people know lots about dogs, whereas others know very little.

This explicitly expressed knowledge about objects can be contrasted with a different level of object concept representation referred to as core properties or "semantic primitives" (Martin, 1998). In contrast to encyclopedic knowledge, semantic primitives are accessed implicitly and automatically in the service of comprehension, are highly constrained in number, and are universal. This level of representation allows us to quickly and efficiently identify objects and understand words, and forms the foundation for our vast stores of encyclopedic knowledge about objects.

While the model to be described here does not address the organization of encyclopedic knowledge, it makes strong claims about the organization of semantic primitives with regard to both their representational content and organization in the brain. For example, the semantic primitives associated with common tools include stored representations of what they look like, how they move when used, and how they are manipulated. They are stored within the same neural systems active when we learned about those properties. Specifically, they are stored within visual processing systems for perceiving object form and object motion, as well as action systems responsible for visuomotor transformations and for grasping and manipulating objects. These primitives are assumed to underpin object meaning in perception—regardless of the stimulus modality (visual, auditory, tactile) or format (pictures, words)—and in thought and imagination.

The distinction between an implicit level and an explicit level of representation underscores the fact that the embodied view of conceptual representation to be discussed in this chapter is not meant to provide an exhaustive description of a concept. It is undoubtedly true that a great deal of what we know about any concept is mediated by, and stored in, the language system. As will be described, some of this information is directly grounded in perceiving, acting, and feeling (e.g., verbal information about sensory- and motor-system-based properties). Other types of information may be truly abstract (nonembodied) and verbally mediated only (although see Barsalou, 1999, for a different view of the relationship between abstract concepts and perceptual systems).

Object concepts are grounded in the neural systems that support perceiving, acting, and feeling

Embodied cognition, including the notion that object concepts are grounded in perception and action systems, has become an increasingly popular view in modern cognitive science (e.g., Barsalou, 1999, 2008; Lakoff & Johnson, 1999; Wilson, 2002; Zwaan & Taylor, 2006). Although it is new to cognitive science, this idea has, in fact, a long history in behavioral neurology. For example, in an article published in the first volume of the journal *Brain*, the neurologist W. H. Broadbent wrote, "The formation of an idea of any external object is the combination of the evidence respecting it received through all the senses" (Broadbent, 1878). This claim was echoed a number of years later by a young

Sigmund Freud in his classic monograph *On Aphasia*: "The idea of the object is a complex of associations composed of the most varied visual, auditory, tactile, and kinesthetic and other impressions" (Freud, 1891) (see figure 71.1). Of course, the idea of an object must include information obtained through the senses. Where else would the information come from? What made these claims nontrivial, however, was that for both authors the information they spoke of was located or stored in the sensory processing systems themselves. In their view, our concepts were not abstract, verbal information stored in a place (association cortex?), but rather concepts were directly grounded in our sensory systems (see also Lissauer, 1890/1988). This very modern view of embodiment stands in marked contrast to the view that dominated cognitive psychology since the downfall of behaviorism in the 1950s whereby concepts were considered to be abstract, propositional, and amodal (e.g., Anderson, 1983; for discussion see Barsalou, 1999). Strictly amodal formulations now have largely disappeared, largely because of neuropsychological and especially neuroimaging evidence. Thus, as recently stated by a prominent group of neuropsychologists specializing in the study of semantics, "Essentially all current theoretical positions about semantic memory share the view that much of the content of our semantic memory relates to perception and action, and is represented in brain regions that overlap with, or possibly even correspond to, the regions that are responsible for perceiving and acting" (Patterson, Nestor, & Rogers, 2007).

Most of the direct evidence to support this type of embodiment claim comes from neuroimaging studies. In one of the earliest attempts to explore this issue, we used positron emission tomography (PET) to measure brain changes when subjects verbally generate different types of object-associated properties. Subjects provided words denoting object-associated colors in one condition (e.g., "yellow" in response to an achromatic picture of a pencil), and the names of associated actions in another condition ("write" in response to that same object). In line with an embodied view, direct comparison of these conditions showed that generating color associates activated regions in the ventral temporal cortex, downstream from regions known to respond to low-level visual processing of object form and form-related properties like color, whereas verb generation produced activity in the lateral part of the temporal lobe just anterior to, and thus assumed to be downstream from, the region responsible for low-level visual motion processing (other regions were also selectively active, especially during verb generation; for details see Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). The findings and conclusions were strengthened by the fact that the same results were found regardless of whether the stimuli were object pictures or their written names (Martin et al., 1995).

Nevertheless, there was a bit of hand waving here. The brain regions engaged during color perception and motion perception were not mapped, so the claim of embodiment—the correspondence between knowing and

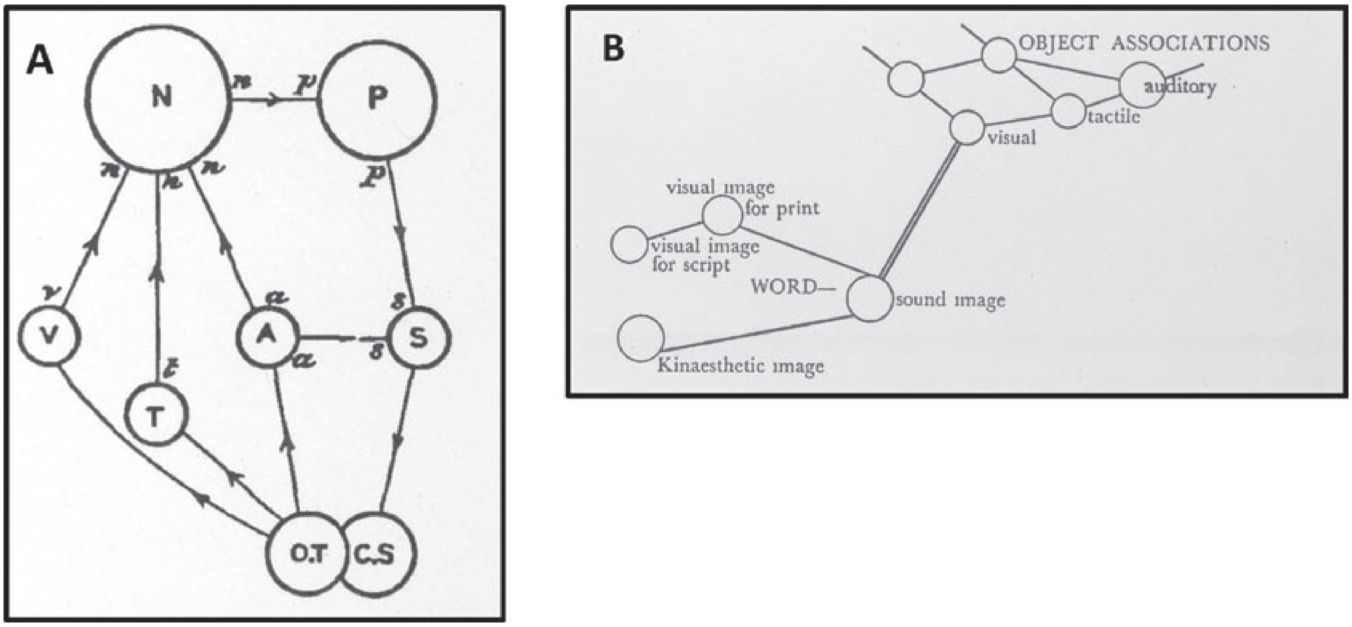

Figure 71.1 (*A*) Example of an embodied view of conceptual representation as depicted by W. H. Broadbent in 1878. *N* refers to the "Idea Centre" or "Naming Centre"; *V*, visual; *A*, auditory; *T*, tactile. *P* refers to "the propositional centre in which the phase was formed" (Broadbent, 1878). (*B*) Freud's diagram. He referred to this as "Psychological schema of the word concept" (Freud, 1891).

perceiving—was based on the presumed close spatial relationship between the activations elicited by the property-production tasks and the previously reported locations of the activity associated with color and motion processing. The embodied cognition view requires that the brain regions engaged when retrieving information about a sensory-based property like color overlap with the regions engaged when perceiving that property. In these initial studies overlap could not be determined. Moreover, subsequent attempts to directly evaluate this possibility failed to provide support. Rather, those data supported the initial conclusion that, although there was a close correspondence between the neural systems supporting perceiving and knowing (based on the location of their respective activations), they did not directly overlap (Chao & Martin, 1999). Consistent with previous reports (e.g., Zeki et al., 1991), viewing colors activated the lingual gyrus in occipital cortex, whereas retrieving information about color activated a more anterior region located in the fusiform gyrus in the posterior temporal lobes (Chao & Martin, 1999).

The finding that the neural substrates for perceiving and knowing were close but not overlapping could be used to undermine claims of embodiment (e.g., Mahon & Caramazza, 2008). After all, "close" is a relative term, and there is certainly no guarantee that there is any processing relationship between regions located a centimeter or more apart on the cortical surface (Chao & Martin, 1999). More recent evidence, however, has resolved this apparent problem by showing a direct overlap in the neural bases of perceiving and knowing. This result was accomplished by using a more demanding perceptual task than the passive viewing tasks previously employed to map sensory processing systems.

In a study on color perception, Beauchamp, Haxby, Jennings, and DeYoe (1999) reported activation in the lingual gyrus of the occipital cortex using a passive viewing task. This finding replicated previous neuroimaging studies, as noted previously. However, when the task was made more demanding by requiring subjects to judge subtle differences in hue, activity associated with perceiving color now extended downstream from the occipital cortex into the fusiform gyrus on the ventral surface of the temporal lobe. Thus the full extent of the color-processing system was revealed when the task was made more demanding, even though the same stimuli were used in both the passive-viewing and attention-demanding contexts (Beauchamp et al., 1999). Simmons, Ramjee, McRae, Martin, and Barsalou (2007) took advantage of this procedure to once again address the question of whether there was neural overlap between the systems underpinning perceiving and knowing about a specific object property. Using the attention-demanding hue-judgment task to evaluate color perception, and a verbal property-verification task to assess property knowledge, Simmons and colleagues found that retrieving information about object color—but not object motion—did, in fact, activate the same region in the fusiform gyrus active when color is perceived (Simmons et al., 2007) (figure 71.2). Thus, in support of the embodied concept view, these data provide strong evidence that information about a particular object property, like its typical color, is stored in the same neural system active when that property is perceived.[1]

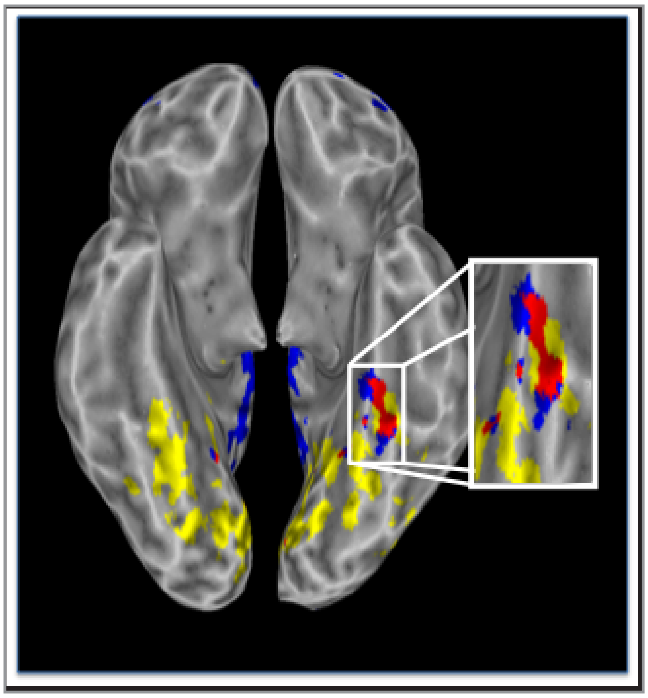

Figure 71.2 Overlap between the neural circuitry for perceiving and knowing about color. Shown is an inflated map of the ventral surface of the brain. Regions shown in yellow were more active when subjects performed a difficult color-perception task, relative to performing that same task with gray-scale stimuli. Regions in blue were more active when answering written questions about object color, relative to answering questions about object motor and motion properties. Red shows region of overlap in the left fusiform gyrus for the color-perception and color-knowledge tasks. (Adapted from Simmons, Ramjee, McRae, Martin, & Barsalou, 2007.) (See color plate 84.)

There are now many examples to support this claim (for extensive recent reviews and discussion see Barsalou, 2008; Gallese & Lakoff, 2005; Martin, 2007; Thompson-Schill, Kan, & Oliver, 2006). Examples include studies showing that retrieving information about different object-associated sensory properties (how they look, sound, feel, and taste) activated regions associated with sensory processing in each of these modalities (Goldberg, Perfetti, & Schneider, 2006), that making semantic judgments about words referring to body movements activated a region involved in perceiving biological motion (posterior region of the STS; Noppeney, Josephs, Kiebel, Friston, & Price, 2005), that reading emotionally charged words activated regions involved in perceiving emotions (amygdala, Kensinger &

Corkin, 2004), and that viewing pictures of appetizing foods activated gustatory processing and taste-specific reward areas (insula and orbitofrontal cortex, Simmons, Martin, & Barsalou, 2005). (It should be noted, however, that the majority of these studies did not independently localize the target sensory processing system, but rather relied on previously published localization studies.)

Similar findings have also been reported for the motor system. In perhaps the best known example, Pulvermuller and colleagues reported that simply reading words referring to actions performed with a particular body part (e.g., *lick*, *kick*, *pick*) activated corresponding regions in premotor and motor cortex (e.g., face, foot, and hand representations, respectively, as directly mapped by a movement study; Hauk, Johnsrude, & Pulvermuller, 2004). However, the correspondence between the primary motor representation for a specific body part (leg) and a concept associated with moving that same body part (*kick*) may be problematic, as will be discussed later (and see Mahon & Caramazza 2005, 2008, for insightful and penetrating critiques of the problems with some strong versions of the embodied viewpoint).

These findings underscore two important and related points. The first point concerns the need to distinguish between the neural bases for *sensation* and *perception* (Mesulam, 1998). As supported by the findings described previously, color *sensation* (color detection), as assessed by passive viewing, seems to be mediated by regions of occipital cortex located early in the visual processing stream, whereas color *perception* seems to require more extensive neural activity extending downstream into the fusiform gyrus. This distinction, in turn, fits nicely with the clinical literature that has documented a double dissociation between acquired color blindness (achromatopsia)—most commonly caused by a lesion of the lingual gyrus in the occipital lobes (Zeki, 1990)—and color agnosia—most commonly associated with lesions of posterior, ventral temporal cortex (Shuren, Brott, Schefft, & Houston, 1996). In this view, the posterior region in the lingual gyrus would be necessary for color sensation—detecting color and delivering this information to the rest of the processing system—whereas full perception of color—the experience of color bound to objects in the world—would require participation of more anterior regions. This anterior site may also provide the neural substrate for acquiring new object-color associations and representing those associations in memory.

The second important point concerns the fact that the overlap between perceiving and knowing is limited to only part, and in this case the most anterior part, of the sensory processing system. The claim then is not that conceptual information is stored throughout the entire sensory or motor processing system. Rather, the claim is that there is overlap between portions of these systems. This is an important point. Strong versions of embodied concept representation that can be construed as maintaining that concepts are grounded in the early stages of perception (V1) or motor processing system (M1) are vulnerable to a charge of reductio ad absurdum. (For example, with regard to the representation of action concepts, why not include the spinal cord? Why not include the muscles? See Mahon & Caramazza, 2005.) Formulations of embodiment that include primary sensory and motor cortices as part of the conceptual system must also account for why we do not move when we read the word "kick." They also need to explain how we are able to tell the difference between our visual perception of objects in the world and our visual imagery. In the current formulation, the overlap between the systems underpinning perceiving, acting, and knowing is limited. The overlap is partial, not complete. Information about a specific object property is stored in the anterior aspects of systems that are also active when objects are perceived and manipulated. This feature accounts for clinical dissociations and guards against a reductio ad absurdum argument while maintaining an embodied view. By so doing, however, the format and nature of the stored representations remain an open question. I will return to this issue at the end of the chapter.

Property information is organized in domain-specific neural circuitry

The most important point to come out of the studies that I have discussed, as well as from a wealth of neuropsychological investigations dating back well over 100 years, is that conceptual knowledge is not stored in a single location. The information that underpins our ability to know about our world is distributed throughout the brain. There is no single semantic memory store. Moreover, much of the available evidence suggests that this information is organized into relatively distinct, but broadly defined, domain-specific systems (e.g., Caramazza & Shelton, 1998). For our present purposes, a domain-specific system will refer to an information processing and storage system defined by the *type* or category of information it processes. These systems are composed of discrete cortical regions wired together to form relatively stable neural circuits. It is further assumed that the connections between the nodes or regions in these circuits are, in part, genetically predetermined. Different brain regions are predisposed to form connections with one another.

Motivated by the clinical literature on category-specific knowledge deficits, perhaps the most investigated domain-specific neural systems have been those concerned with representing animate entities, defined as living things that move on their own (people and other animals; Chao, Haxby, & Martin, 1999), and manipulable, manmade objects like common "tools," defined as objects with a systematic relationship between their visual form and function/manipulation (Mahon et al., 2007). The neural substrate for representing animate things includes two regions of posterior temporal cortex; one of these lies on the ventral surface and is located in the more lateral portion of the fusiform gyrus (including, but not limited to, the fusiform face area, FFA, and its adjacent region for body representation; Schwarzlose, Baker, & Kanwisher, 2005); the other is on the lateral surface located in the posterior region of the superior temporal sulcus (pSTS). There is a substantial body of literature linking these regions to the representation of biological form (lateral portion of the fusiform gyrus) and biological motion (pSTS) (for reviews see Adolphs, 2001; Bookheimer, 2002; Haxby, Hoffman, & Gobbini, 2000; Martin, 2001, 2007; Martin & Chao, 2001; Thompson-Schill, 2003). This circuitry also includes the amygdala. The amygdala is a highly differentiated structure and plays multiple roles in emotion processing and behavior, including being critical for acquiring, storing, and expressing conditioned fear responses (Phelps & LeDoux, 2005; Phelps, 2006). In addition, there is growing evidence that the amygdala is predisposed to respond automatically to animate things. This is especially so for faces expressing fear, but the amygdala also responds more to neutrally posed faces relative to other objects (e.g., Pessoa, McKenna, Gutierrez, & Ungerleider, 2002), suggesting a predisposition for certain categories of objects over others (Ohman & Mineka, 2001). Indeed, recent studies from our laboratory suggest that the amygdala responds more to animate entities (faces and animals) than to other objects. Moreover, this response is especially strong for animate objects rated as being highly threatening and arousing (i.e., faces with expressions of fear, spiders, snakes), even when compared to equally threatening and arousing inanimate things (e.g., weapons, dental drills) (Yang, Bellgowan, & Martin, 2008). These data and others (e.g., Vuilleumier, Armony, Driver, & Dolan, 2003; G. Williams, Nestor, & Hodges, 2005) provide support for the inclusion of the amygdala in the circuitry for animate entities, both for assessing affective valence and arousal value, and for the fast, early detection of stimuli that have, from an evolutionary standpoint, posed the greatest threat—animals and other people.

The three regions listed—the lateral portion of the fusiform, pSTS, and the amygdala—respond strongly to both people and animals relative to other object categories. The available evidence further suggests that these regions code for different properties of animate things such as form, motion, and affective valence, respectively. Nevertheless, it should go without saying that the substrate for representing a property like visual form must distinguish between people and animals. All objects must have a distinct neural substrate, or how else would we distinguish among them? This distinction is clear in the clinical literature (Caramazza & Shelton, 1998). Thus, although a number of prosopagnosia patients also have difficulty identifying animals—for example, one of the most carefully studied prosopagnosic patients also was unable to identify animals from their shapes (patient LH; Etcoff, Freeman, & Cave, 1991)—convincing cases of pure prosopagnosia have been well documented (e.g., Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008). Thus these regions should be seen as part of the circuitry underpinning perceiving and knowing about animate entities, broadly defined, but with finer distinctions made between the representation of conspecifics and heterospecifics. Although how this distinction is represented in this circuitry has not been well defined, two hints are available. One hint comes from the neuroimaging literature that suggests that faces are more focally represented (Chao, Haxby, & Martin, 1999). This is not an unreasonable expectation given that different faces are highly homogeneous in shape and movement relative to animals, and they denote a single basic-level category, whereas animals are composed of stimuli with large variation in shape, and consist of multiple basic-level categories each with a unique name. The other hint comes from the clinical literature suggesting that they may be hemispheric difference, with a right-sided bias for lesions yielding face-processing deficits (Riddoch et al.) and a left-sided bias for lesions resulting in knowledge deficits for animals (Capitani, Laiacona, Mahon, & Caramazza, 2003).

In addition to the posterior, lateral region of the fusiform gyrus, pSTS, and the amygdala, other likely nodes in the animacy circuit include the medial portions of anterior and posterior cortex (ventral prefrontal and posterior cingulate/precuneus cortices, e.g., Mitchell, Macrae, & Banaji, 2006; Mitchell, 2008) and temporal polar cortices (Olson, Ploaker, & Ezzyat, 2007). Each of these nodes, along with a region located in posterior lateral cortex at the junction of the temporal and parietal lobes (Saxe, 2006), has been linked to rather abstract, higher-order aspects of social cognition, including the ability to make inferences about the mental state of others (with finer dissociations observed as well—for example, between different regions of medial prefrontal cortex when thinking about the mental states of similar versus dissimilar others; Mitchell et al.). Although some evidence exists that suggests that these regions may be involved in knowing about animacy in general (e.g., medial prefrontal cortex was found to be active when making judgments about mental states regardless of whether the target was another person or a dog; Mitchell, Banaji, & Macrae, 2005), most evidence suggests that these regions may be particularly important for thinking about conspecifics.

Each of the regions or nodes of this circuit has a specific function, and a major goal of cognitive neuroscience is to specify the functional properties of these regions in the service of social cognition. Clearly this issue is far from settled, and debate about the functional characteristics of each node is likely to continue for some time. Nevertheless, the critical point to be stressed here is that regardless of their function, each of the regions discussed so far is engaged

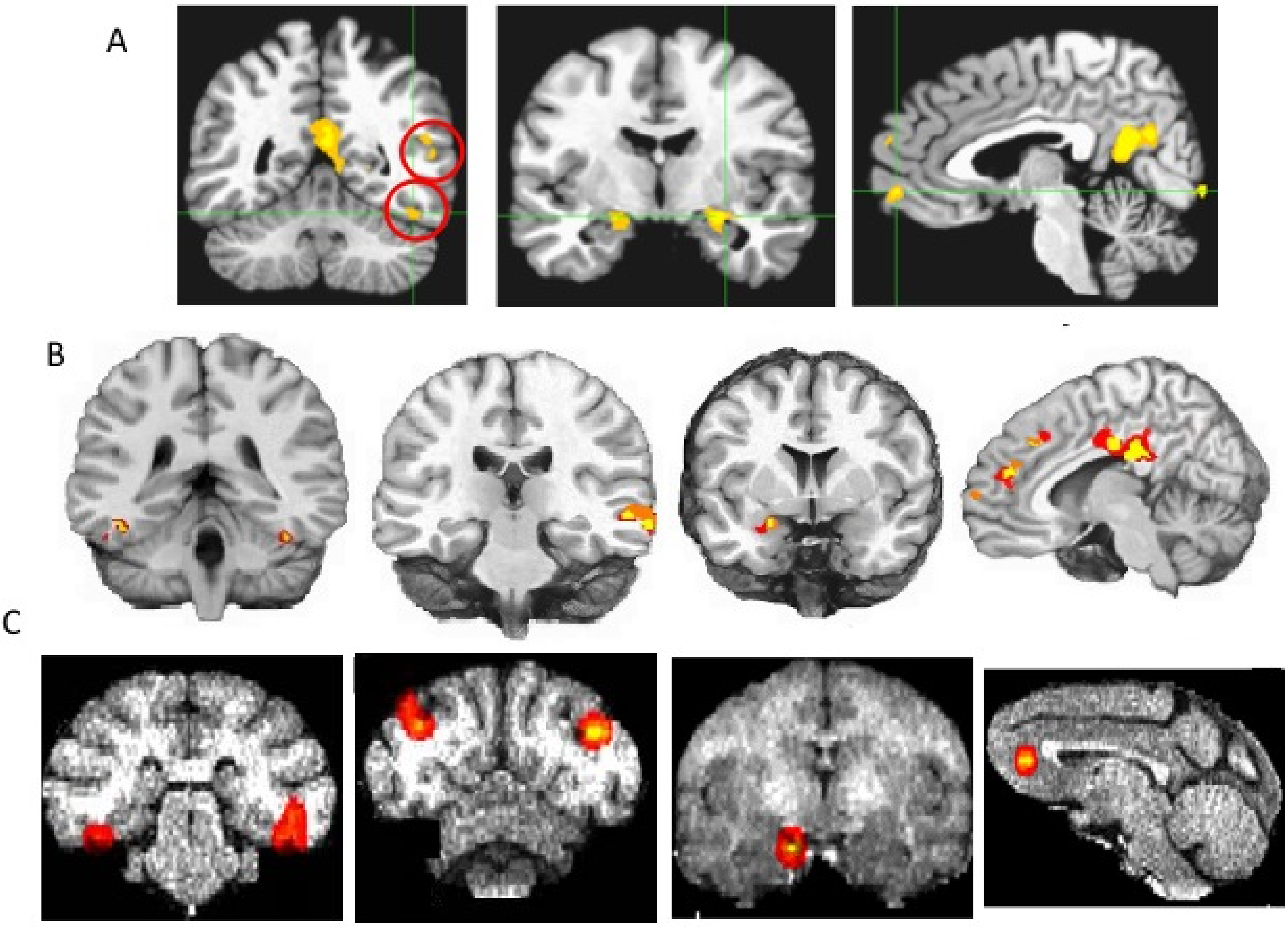

FIGURE 71.3 Correspondence across tasks and species in the location of the neural circuitry for perceiving and knowing about animate entities. (*A*) Regions shown in yellow were more active when subjects viewed photographs of faces relative to viewing photographs of common tools. Going from left to right, the first image shows a coronal slice through posterior cortex indicating the location of activity in the lateral portion of the right fusiform gyrus (lower red circle) and in the right pSTS (upper red circle). The next coronal image depicts bilateral activity in the amygdalae. The third image shows a sagittal section revealing activity in the medial prefrontal cortex and in the posterior cingulate/precuneus. (Unpublished data from our laboratory.) (*B*) Brain slices depicting conjunction of regions more active when subjects perceived simple shapes in motion as animate, relative to when they were judged to be inanimate, and when they imagined these stimuli as animate versus inanimate. Going from left to right, the first image is a coronal slice showing bilateral activity in the lateral fusiform gyrus. The next coronal slice shows the location of activity in the STS, the third depicts activity in the left amygdala, and the last shows activations located in the medial prefrontal and posterior cingulate cortices. (Adapted from Wheatley, Milleville, & Martin, 2007.) (*C*) Activity in the macaque brain when listening to species-specific calls. Shown are PET scans obtained from a single animal. Going from left to right, the first image shows a coronal slice through ventral regions TEO/TE, the next coronal slice shows activity in the STS, the third slice shows activation in the amygdala, and the fourth slice shows an activation located in Area 32 on the medial surface of the brain. (Adapted from Gil-da-Costa et al., 2004.) (See color plate 85.)

whenever an animate object is attended to. For example, as illustrated in figure 71.3*A*, simply viewing a face will produce activity throughout the entire circuit.

This characteristic of being activated whenever an object is viewed also holds for the nodes of the circuits underpinning perceiving and knowing about "tools." The current evidence suggests that the circuitry underpinning processing in this domain includes two regions in the posterior temporal lobe, one situated in the more medial extent of the posterior fusiform gyrus, the other located in the left posterior portion of the middle temporal gyrus. These regions have been linked to representing the visual form and visual motion associated with these objects (e.g., Beauchamp, Lee, Haxby, & Martin, 2002, 2003). The other two nodes in this circuit, both strongly lateralized to the left hemisphere, are in posterior parietal cortex (in the intraparietal sulcus and often also including a more anterior region in the inferior parietal lobule) and in ventral premotor cortices. These regions have been linked to the representation of goal-directed action associated with an object's function (for recent reviews and discussion see Beauchamp & Martin, 2007; Frey, 2007; Lewis, 2006). As with the animacy circuitry discussed earlier, the circuitry underpinning perceiving and knowing about "tools" is engaged whenever these objects are viewed (e.g., Chao et al., 1999; Chao & Martin, 2000; Handy, Grafton, Sheroff, Ketay, & Gazzaniga, 2003) (see Mahon et al., 2007, for neuroimaging and neuropsychological evidence supporting the specificity of this circuitry for "tools" relative to other manmade, manipulable objects).

Activity in domain-specific neural circuitry transcends stimulus features

These findings suggest that the brain contains property-based, domain-specific neural circuits for perceiving and knowing about specific object categories. A case was made that one of these circuits developed for representing animate things, another for "tools." It was also suggested that these circuits are active whenever objects from these broad categories are perceived. However, this fact alone says nothing about the relationship between these circuits and conceptual processes. To make that link requires showing that activity in these circuits is associated with the *interpretation* of a stimulus, rather than its physical characteristics. There is now considerable evidence to support this claim. For example, the lateral region of the fusiform gyrus that has been linked to representing the visual form of animate entities responds to animate entities as represented by pictures and written names of animals (Chao et al., 1999; Devlin, Rushworth, & Mathews, 2005; Mechelli, Sartori, Orlandi, & Price, 2006; Okada et al., 2000; Price, Noppeney, Phillips, & Devlin, 2003; Rogers, Hocking, Mechelli, Patterson, & Price, 2005; Wheatley, Weisberg, Beauchamp, & Martin, 2005), human voices (von Kriegstein, Kleinschmidt, Sterzer, & Giraud, 2005), point-light displays of human bodies in motion (Beauchamp et al., 2003; Grossman & Blake, 2001, 2002; Peelen, Wiggett, & Downing, 2006), and humanlike stick figures (Peelen & Downing, 2005). In contrast, the more medial aspect of the fusiform associated with representing the visual form of "tools" has been reported in response to pictures and written names of tools (Chao et al.; Chao, Weisberg, & Martin, 2002; Devlin et al.; Mechelli et al.; Whatmough, Chertkow, Murtha, & Hanratty, 2002), the spoken names of tools (Noppeney, Price, Penny, & Friston, 2006), and point-light displays depicting tools in motion (Beauchamp et al.).

Perhaps even more convincingly, activity throughout the animacy circuit has even been observed when participants view abstract representations of social situations as illustrated by the interactions among simple geometric shapes in motion (Heider & Simmel, 1944). For example, the lateral fusiform gyrus responds to animations suggesting social interactions such as hide-and-seek (Schultz et al., 2003), mocking and bluffing (Castelli, Happe, Frith, & Frith, 2000; Castelli, Frith, Happe, & Frith, 2002), and sharing (Martin & Weisberg, 2003). These studies also reported activity in other nodes of the animacy circuit including pSTS, the amygdala, and ventromedial prefrontal cortices. In contrast, activity in the temporal lobe regions associated with the visual form and motion of "tools" (medial fusiform and left middle temporal gyrus, respectively) has been observed when animations composed of simple geometric shapes were interpreted as depicting mechanical interactions (Martin & Weisberg, 2003).

Wheatley and colleagues have recently provided even more compelling evidence that activity in these circuits is linked to the interpretation of a stimulus rather than its physical features (Wheatley, Milleville, & Martin, 2007). In that study, different background settings were used to bias the interpretation of a simple geometric shape in motion as depicting either an animate entity or an inanimate object. All the previously mentioned regions in the animacy circuit (lateral portion of the fusiform gyrus, STS, medial prefrontal cortex, posterior cingulate, amygdala) were active when the objects were interpreted as animate, relative to when that same form and motion were interpreted as depicting an inanimate object. Moreover, these regions were also active when subjects were asked to imagine the object they had previously seen based on viewing the backgrounds alone (figure 71.3*B*; see Wheatley et al., 2007, for details). Thus activation in this domain-specific, property-related circuit was not due to particular stimulus features, but rather appeared to be directly related to conceptual representation.

Several other studies have provided data to support this claim. Each of these studies used a learning paradigm to show that acquiring new information about novel objects changes the brain's response to those objects. Moreover, the locations of these responses were directly related to the type of information acquired. For example, Weisberg, van Turennout, and Martin (2007) asked subjects to perform a simple visual matching task on photographs of novel objects. After scanning, the subjects were given extensive training manually manipulating the objects to perform specific tool-like functional tasks. After training, the subjects were again scanned while performing the visual matching task. Comparison of the data collected prior to training with those collected after training revealed that experience using the objects as tools led to predictable changes in how these objects were now represented in the brain. Whereas prior to training visual matching of the novel objects elicited only broad activity in ventral occipitotemporal cortex, after training ventral temporal activity was largely restricted to the medial aspect of the fusiform gyrus, the same region previously implicated in representing the visual shape or form of

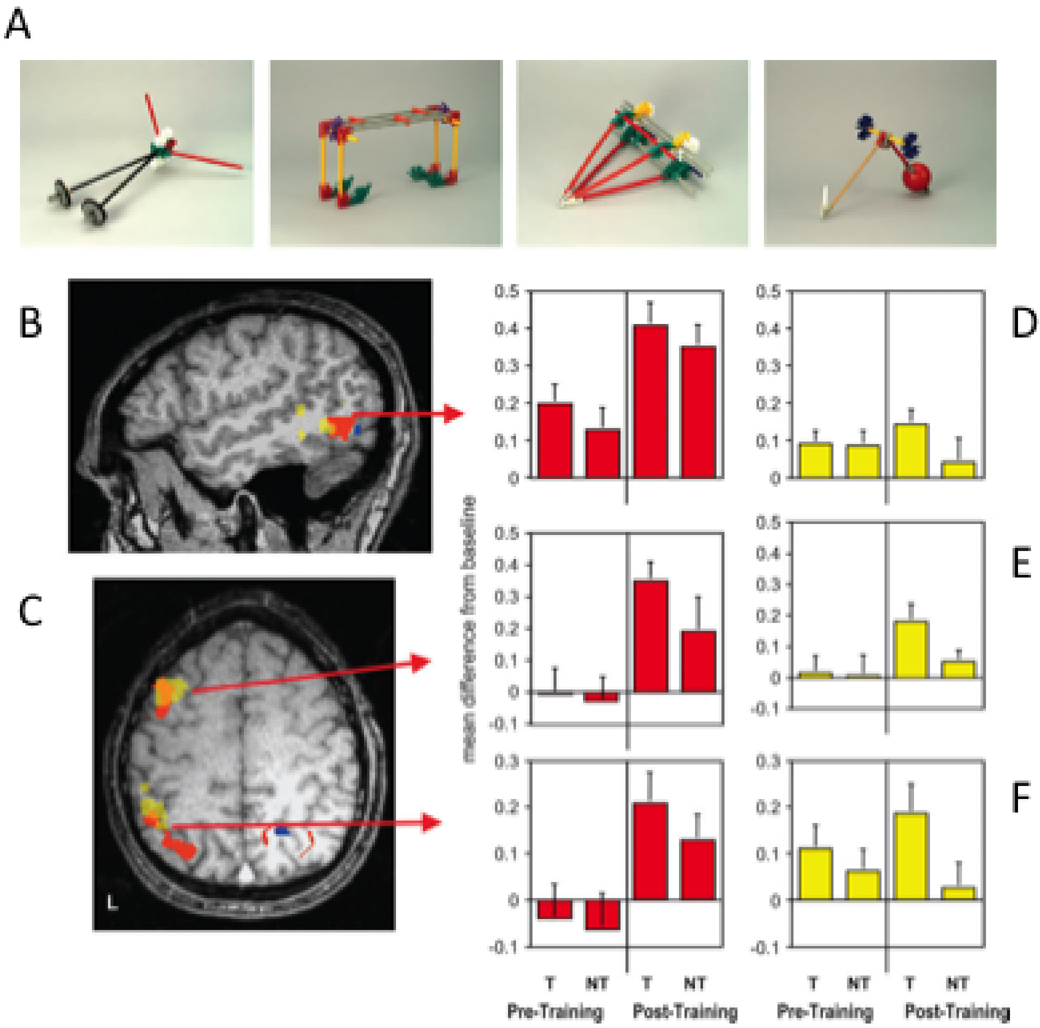

FIGURE 71.4 (*A*) Examples of novel objects designed to perform specific toollike functions. (*B*) Sagittal section showing the location of learning-related activity in the left middle temporal gyrus. Regions in red were more active after training than before training. Regions in yellow, which overlap with regions in red, were more active for trained (*T*) objects than for not-trained (*NT*) objects. (*C*) Axial section showing the location of learning-related activity in the left premotor/prefrontal cortex and intraparietal cortices. (*D*, *E*, *F*) Histograms showing the difference between novel-object-matching and scrambled-image-matching baseline task in the middle temporal gyrus, left premotor, and intraparietal regions, respectively. Red bars represent brain regions that showed increased activity for object matching after but not prior to training; yellow bars represent regions that demonstrated greater activity for trained objects than not-trained objects after but not prior to training. (Adapted from Weisberg, van Turennout, & Martin, 2007.) (See color plate 86.)

"tools." Similarly, new activations emerged after training in other regions of the circuitry associated with perceiving and knowing about "tools," including the left posterior region of the middle temporal gyrus (linked to nonbiological motion perception; Beauchamp et al., 2002, 2003), left intraparietal sulcus, and left premotor cortex (goal-directed manipulation related to object function) (figure 71.4).

Learning effects have also been observed for animate entities. It has been well documented that viewing point-light displays of human forms in motion elicits activity in lateral fusiform and pSTS (Beauchamp et al., 2003; Grossman & Blake, 2001, 2002). Grossman, Blake, and Kim (2004) trained subjects to perceive human forms in point-light displays that were embedded within visual noise. After training, not only were the subjects better at indicating when a human form was present in a noisy visual display, but they also exhibited greater fusiform and pSTS activity in response to detecting those forms, and the amount of activity in both regions was positively correlated with a subject's behavioral performance.

Finally, in addition to visual learning paradigms, it has been demonstrated that a verbal learning procedure can be used to demonstrate the development of property-based circuitry (T. James & Gauthier, 2003). Prior to scanning, subjects learned verbally presented information about the auditory and motor-related properties of different families of novel animate-like entities ("greebles"). For example, subjects were trained that a particular family of greebles were associated with an auditory property (e.g., roars or squeaks), whereas other types of greebles had action properties (e.g., hops or jumps). After training, subjects underwent fMRI while performing a visual matching task that did not require retrieval of these learned associations. The results showed that viewing greebles associated with auditory properties produced activity in auditory cortex (as defined by an auditory functional localizer) and viewing greebles associated with action properties produced activity in the biological-motion-sensitive region of the pSTS (as localized by moving point-light displays). These findings, along with the findings of Weisberg et al. (2007), demonstrate that experience with novel objects leads to the development of activity in domain-specific property circuits. Simply seeing an object from the training set elicited activity in specific regions of the previously described circuits, even though that information was not necessary for successfully performing the task and not present in the stimuli. Subjects learned that, for example, a particular object was associated with a particular type of movement (e.g., hopping). Having acquired that knowledge, a region in pSTS that is active when viewing biological motion became active when that object was viewed, even though the subject's task did not require retrieving that information. The posterior region of the STS was activated automatically when the object was seen again.

A mechanism that allows us to quickly and effortlessly form inferences about objects in the world has obvious survival value. As a result we would expect that the ability to infer properties would be preserved across primate species. Recent evidence suggests that this may be the case with regard to the circuitry supporting perception of animate entities. Using PET to study perception of species-specific calls in the macaque, Gil-da-Costa and colleagues (2004) showed that the calls elicited activity in area TE/TEO, a presumed monkey homologue of human fusiform gyrus, and in the pSTS, relative to acoustically similar controls (figure 71.3*C*). In addition, calls known to carry emotional connotations activated the amygdala and medial prefrontal cortices over and above calls presumed to connote more neutral associations (see Gil-da-Costa et al. for details). While strong claims cannot be made about the meaning of these calls for the macaques, it should be safe to conclude, at the very least, that the calls were interpreted as indicating the presence of another monkey. Thus, as with humans, when monkeys process information about animate entities, activation occurs across a distributed circuit. The nodes of this circuitry are presumed to represent the salient properties of those entities, including what they look like and how they move, even when those properties are not present in the stimulus, and therefore must be inferred.

Additional architectural considerations: The role of the anterior regions of the temporal lobes

Clearly, these circuits do not operate in isolation. For one thing, information must be selected and retrieved, and much work has established that the left inferior prefrontal cortex plays a prominent role in performing these functions (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; for review see Thompson-Schill, Bedny, & Goldberg, 2005). Object-property information must also be integrated, and this requirement raises a form of the binding problem on the level of conceptual representation. One potential mechanism for achieving an integration of information stored in different locations is through their interaction. In that scenario, each node would represent the information it was specialized for, as well as reflecting or re-representing other types of information stored elsewhere (see Konen & Kastner, 2008, and Schwarzlose, Swisher, Dang, & Kanwisher, 2008, for neuroimaging data consistent with this view). Another possibility is that information from all circuits is integrated in a specific region. Several candidates have been proposed for this "hub" architecture, including posterior regions of left lateral temporal cortex (Hickok & Poeppel, 2000), left prefrontal cortex (reviewed in Thompson-Schill et al.), and thalamus (Kraut et al., 2002).

More recently, a highly influential version of a hub architecture has been proposed that locates this mechanism in the most anterior portion of the temporal lobes (Lambon Ralph, Lowe, & Rogers, 2007; McClelland & Rogers, 2003; Patterson et al., 2007; also see McClelland et al., chapter 72 in this volume). As argued by Patterson and colleagues (2007) in order to operate in the service of semantic cognition, property-based circuits require that all stored information about objects be integrated at a single location (Patterson et al.). Under this view, a central hub is needed because a distributed architecture alone cannot account for one of the central defining characteristics of a conceptual system; the ability to generalize across exemplars belonging to the same category (e.g., telephone) when the specific exemplars in this category can have very different physical features (desk phones, cellular phones) (see Patterson et al. for details of this argument). Moreover, according to this view, the ability to generalize requires amodal conceptual representations, as opposed to the modality-based representations described here. Amodal representations require a central hub (Patterson et al.; also see McClelland & Rogers, 2003).

A hub of this type may in fact be necessary on computational grounds, and that possibility will not be disputed here. It should be stressed, however, that arguments about the need for a conceptual hub and the physical location of that hub in the brain are independent. It is this later claim, specifically the claim that the hub is located in the most anterior part of the temporal lobes, that I will address here.

The anterior temporal lobes include a number of distinct anatomical divisions, including the temporal pole, amygdala, and entorhinal and perirhinal cortices, as well as the anterior extents of the fusiform, inferior, middle, and superior temporal gyri. Therefore it should not be surprising that there are currently several different but non-mutually-exclusive views of anterior temporal lobe function. One view, and one that has the most support from neuroimaging and neuropsychological investigation, is that the anterior regions of the temporal lobe are involved in social and emotional processing (see Olson et al., 2007, for a recent review). Another view, also supported by neuroimaging (Gorno-Tempini & Price, 2001; Grabowski et al., 2001) and neuropsychological investigation (e.g., Tranel, Damasio, & Damasio, 1997; Damasio 1989), is that the anterior temporal lobes are involved in representing unique entities (i.e., famous people and places). A third view is that anterior temporal regions play a role in modulating access to distributed modality-specific information stored elsewhere, but are not involved in integrating this information (Martin & Chao, 2001). Finally, a fourth position is that the anterior temporal lobes are the location of the conceptual hub. Support for this claim comes primarily from study of patients with semantic dementia, a progressive disorder that is associated with pathology with a proclivity for attacking the temporal lobes, especially the more anterior portion where the damage often appears to originate (McClelland & Rogers, 2003; Patterson et al., 2007).

Several points are in order. First, studies using voxel-based morphometry to measure the extent of atrophy associated with semantic dementia indicate that pathology in these patients is not limited to the anterior temporal lobes. Rather, these studies uniformly show that the pathology often extends to the more posterior regions of the temporal lobes engaged in many of the neuroimaging studies reviewed previously. Moreover, the semantic deficits in these patients are nearly as strongly related to atrophy in posterior temporal cortex as with atrophy in anterior temporal cortex (G. Williams, Nestor, & Hodges, 2005). Semantic dementia is a progressive disorder. As symptoms increase in severity, pathology gets more widespread throughout the temporal lobes. Thus the discrepancy between the findings with semantic dementia patients and the neuroimaging literature may not be nearly as strong as some have suggested (Patterson et al., 2007). It is probably also noteworthy that these patients often have pathology outside the temporal lobes, most prominently in frontal cortex. Thus it is not at all clear that the devastating impairments in semantic cognition that characterize these patients can be attributed solely to anterior temporal lobe pathology (Lambon Ralph et al., 2007). The available evidence suggests that the anterior regions of the temporal lobes likely support multiple functions. It is more than likely that one of these functions involves conceptual and semantic processing. The exact nature of this role, however, and, in particular, whether the anterior temporal lobes are necessary for creating amodal representations, remains to be determined.

Summary and concluding comments

The evidence discussed in this chapter indicates that the information about salient object properties—such as how they look, move, and are used, along with our affective associations to them—is stored in the neural systems that support perceiving, acting, and feeling. It is in this sense that conceptual knowledge is argued to be grounded and embodied. The evidence further suggests that this information is not stored in every part of our sensory and motor systems. The circuits for sensing, perceiving, and knowing are partially, not fully, overlapping.

These architectural constraints, however, say nothing about the nature or format of this information. It has been assumed that information stored in discrete regions of the fusiform gyrus represents the visual form of objects. This assumption has been made because this region is part of the ventral visual object-processing stream known to underpin object identification. Yet it appears that these same regions respond in a categorical manner in the blind when palpating objects (Pietrini et al., 2004). This finding is consistent with the idea that this region codes from object shape or form, but it also suggests that the way shape is represented may be quite abstract. Information about object shape may be stored in the ventral stream, even when that shape information was obtained through a different modality, in this case touch rather than vision. This finding, in turn, challenges us to specify the sense in which the information grounded in perceptual and action systems should be considered modality specific or sensory or motor in nature.

The evidence reviewed here also suggests that object-property-based information is organized into broadly defined domain-specific circuits. These circuits appear to be remarkably stable in the sense that the spatial arrangement among their defining nodes seem to be consistent from one individual to another. This stability is most apparent when considering the spatial arrangement of regions in ventral temporal cortex purported to support identification of words (McCandliss, Cohen, & Dehaene, 2003), faces (Yovel & Kanwisher, 2004), animals (Chao et al., 1999), tools (Chao et al., 2002), and environmental scenes (Epstein, 2008). Although discussion of this important issue is outside the scope of this chapter, several suggestions have been offered to explain this fact (Op de Beeck, Haushoffer, & Kanwisher, 2008; Martin, 2006; Mahon et al., 2007).

The evidence also suggests that activation of these circuits is dependent on how a stimulus or event is interpreted, not on the physical features of the stimuli impinging on our senses. These findings indicated that while different regions of the cortex are specialized for processing and storing information about specific properties (e.g., biological motion), these same regions can be reactivated in top-down fashion based the interpretation applied to a stimulus, even when that critical property is not physically present (Wheatley et al., 2007).

This type of finding raises important questions about the function played by these activated regions. In the Wheatley and colleagues (2007) study, the task was simply to indicate whether the depicted object represented an animate thing. Nevertheless, animacy identification led to activation of a suite of regions that, based on other data, support a range of complex higher-order social processes (e.g., theory of mind, making self-other similarity judgments; Mitchell, 2008). In fact, as illustrated in figure 71.3*A*, this entire circuit becomes active when simply viewing photographs of the human face. Clearly, activation in ventromedial prefrontal cortex or in the amygdala is not necessary to perceive faces. Thus a major challenge for future studies is to specify what role these activations play in these tasks. One possibility, and I believe the most likely explanation, is that these activations reflect the automatic generation of inferences that are a central part of what we mean by a conceptual representation. In this sense, these activations may serve to prime the conceptual system for future action. That is, they are predictive of future events. Seeing a hammer activates the dorsal stream because hammers are objects likely to be grasped and used to perform some function. Seeing other individuals activates a broad circuit of regions so we are prepared to interpret their state of mind and actions. Our ability to sort out the role played by these regions in the context of different tasks will require investigations that combine functional neuroimaging and lesion approaches. Investigations of this type have just begun, but they have already yielded tantalizing clues (Calder, Keane, Manes, Antoun, & Young, 2000; Mahon et al., 2007).

NOTE

1. It should be stressed that the overlap observed in this and in other studies of this type does not necessarily mean that the *same neurons* are involved in both perceiving and knowing. Support for that claim would require single-unit recordings from the human brain. Functional neuroimaging evidence consistent with this claim could be obtained by showing that the amplitude of the BOLD signal in a region of cortex was reduced when verbally retrieving information about a property, for example, color, following activity produced by viewing that color (i.e., by showing an across-task repetition suppression effect. For a discussion of the logic behind this approach see Grill-Spector & Malach, 2001; Henson, 2003). Nevertheless, the embodiment view proposed here does not require that perceiving and knowing be coded in the same neurons. It does, however, require that these processes be carried out in the same brain region, strictly defined. For example, the embodied view would hold if the neurons involved in visual perception and those involved in information storage were found to be interdigitated in the same tightly constrained space.

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