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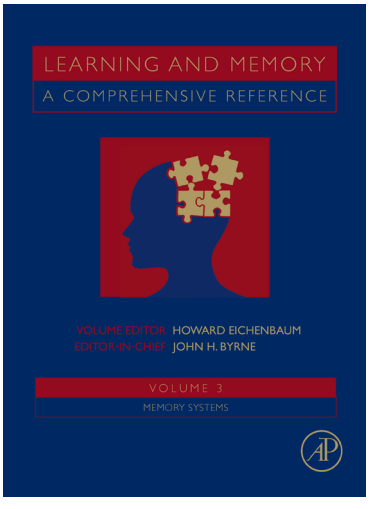

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3.07 Structural Basis of Semantic Memory

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3.07.1 Introduction

Semantic memory refers to a major division of long-term memory that includes knowledge of facts, events, ideas, and concepts. Thus, semantic memory covers a vast cognitive terrain, ranging from information about historical and scientific facts, to details of public events and mathematical equations, to the information that allows us to identify objects and understand the meaning of words. This chapter focuses on our current understanding of how semantic memories, especially object concepts, are represented in the brain. As we discuss later, ideas about the neural systems underpinning conceptual knowledge have a long history in behavioral neurology and neuropsychology dating back at least to the late nineteenth century. In recent times, however, the idea of semantic memory as a distinct memory system began in 1972 with Endel Tulving's distinction between semantic and episodic memory (Tulving, 1972). Although the notion of episodic memory has undergone considerable evolution since that original formulation (for a brief history see Tulving, 2002), it remains helpful to describe the properties of semantic memory in relation to episodic memory. In current formulations, episodic memory can be thought of as synonymous with autobiographical memory. Episodic memory is the system that allows us to remember (consciously recollect) past experiences (Tulving, 2002) and perhaps may also be critical for imagining and/or simulating future events (Hassabis et al., 2007; Schacter and Addis, 2007). Semantic memories, in contrast, are devoid of information about personal experience. Unlike episodic memories, semantic memories lack information about the context of

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learning, including situational properties like time and place, and personal dimensions like how we felt at the time the event was experienced. Remembering that you had cereal and toast for breakfast, that you read the newspaper, and that you had a slight headache is dependent on episodic memory. Knowing and, indeed, being able to visually recognize objects like cereal, toast, and newspaper, as well as understanding the words you are now reading, is dependent on semantic memory. In relation to episodic memory, semantic memory is considered to be both a phylogenically and an ontologically older system. In fact, rather than arising as an independent evolutionary development, it is commonly assumed that episodic memory emerged as an add-on or embellishment to semantic memory (Tulving, 2002). Although many animals, especially mammals and birds, acquire information about the world, they are assumed to lack the neural machinery to consciously recollect detailed episodes of their past. Finally, although retrieval of semantic memory often requires explicit, conscious mediation, the organization of semantic memory can also be revealed via implicit tasks such as semantic priming (e.g., Neely, 1991).

The idea that our semantic and episodic memories were dependent on a distinct neural substrate was perhaps first proposed by the American neurologist J.M. Nielsen (1958). As Nielsen noted, amnesia came in two types. One type, which he termed temporal amnesia, was defined by a loss of memory for personal experiences. The other type, which he termed categorical amnesia, was defined by a loss of acquired facts. Nielsen further noted that there were different varieties of categorical amnesias, including amnesias for animate objects and amnesias for inanimate objects (Nielsen, 1946, 1958), presaging a distinction that is prominently highlighted later in this chapter. Nielsen also maintained that the temporal (episodic) and categorical (semantic) amnesias could occur in isolation, thereby noting that their respective neural substrates might be at least partially independent (Nielsen, 1958). Indeed, studies of patients with conceptual deficits have provided some support for Nielsen's claim (Hodges and Graham, 2001; Simons et al., 2002). However, before discussing those patients, we first discuss studies of semantic memory in patients with profound amnesias resulting from damage to the medial temporal lobes. These studies have provided evidence that medial temporal lobe structures play a critical role in acquiring and retrieving both semantic and episodic memories.

3.07.2 Semantic Memory and the Medial Temporal Lobe Memory System

Studies of patients with impaired episodic memory resulting from damage to the medial temporal lobes have established three broadly agreed-on facts about the functional neuroanatomy of semantic memory. First, like episodic memory, acquisition of semantic memories is dependent on medial temporal lobe structures, including the hippocampal region (CA fields, dentate gyrus, and subiculum) and surrounding neocortex (parahippocampal, entorhinal, and perirhinal cortices). Damage to these structures results in deficient acquisition of new information about vocabulary and famous individuals (e.g., Gabrieli et al., 1988; Hamann and Squire, 1995; Verfaellie et al., 2000, patient SS) and public events (Manns et al., 2003), and the extent of this deficit is roughly equivalent to the deficit for acquiring personal information about day-to-day occurrences.

However, despite broad agreement that acquiring semantic memories requires medial temporal lobe structures, there is disagreement concerning the role of the hippocampal region. One position holds that the hippocampus is necessary for acquiring semantic information (for discussion, see Squire and Zola, 1998). In contrast, others have argued that acquisition of semantic memories can be accomplished by the surrounding neocortical structures alone; participation of the hippocampus is not necessary (for discussion, see Mishkin et al., 1998). Recent studies seem to favor the hippocampal position by showing that carefully selected patients with damage limited to the hippocampus are impaired in learning semantic information about public events (Manns et al., 2003). One potentially important caveat to this claim comes from studies of individuals who have sustained damage to the hippocampus at birth or during early childhood (Vargha-Khadem et al., 1997). These cases of developmental amnesia have disproportionately better semantic than episodic memories, suggesting that the hippocampus may not be necessary for acquiring semantic information. For example, cases of developmental delay resulting from hippocampal damage, although failing to provide accurate descriptions of their daily activities (episodic memory), were able to acquire normal language and social skills, keep up with their schoolwork, and perform in the average range on standard measures of vocabulary and general knowledge (Vargha-Khadem et al., 1997). These findings

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pose a clear challenge to the standard hippocampal model of declarative memory. Although discussion of this important issue is outside the purview of this chapter, it is certain that a reconciliation of this issue will depend on detailed and direct comparison of adult onset and developmental amnesias with regard to the extent of medial temporal lobe damage and its behavioral consequences.

The second major finding established by studies of amnesic patients is that the medial temporal lobe structures have a time-limited role in the retrieval of semantic memories, which is, in turn, presumably related to a prolonged consolidation process (Squire and Alvarez,1995; but see Moscovitch et al., 2005, for a critique of prolonged consolidation and a reappraisal of the role of the hippocampus in memory retrieval). Evidence in favor of the claim of a time-limited role for the hippocampal region in retrieving semantic memories comes from studies assessing the status of information acquired prior versus after the amnesia onset. Such studies have revealed that, for example, public event knowledge is temporally graded, with increasing accuracy for events further in time from the onset of the amnesia (Kapur and Brooks, 1999; Manns et al., 2003). The length of this temporally graded amnesia, however, can be surprisingly long and probably varies as a function of type of information tested and testing method. For example, in the Manns et al. study, the temporal gradient for news events lasted from 10 to 15 years when evaluated by a test of recall but less than 5 years when evaluated by a recognition test (Manns et al., 2003).

Studies of object and word knowledge are also consistent with the claim that the hippocampus has a time-limited role in retrieving semantic memories. Conceptual information about the meaning of objects and words known to be acquired decades prior to amnesia onset remains intact as assessed by both explicit and implicit tasks. Patients with damage to the hippocampal region are unimpaired on tests of object naming, object property verification, and object category sorting (e.g., Schmolck et al., 2002) and show normal semantic priming (Cave and Squire, 1992).

The third major finding established by studies of amnesic patients is that semantic memories of all types are stored in the cerebral cortex. Most importantly for our present concerns, impaired knowledge about objects and their associated properties acquired prior to amnesia onset is not related to medial temporal lobe damage but rather to the extent of damage to cortex outside this region (e.g., Levy et al., 2004).

3.07.3 Cortical Lesions and the Breakdown of Semantic Memory

Studies of semantic memory in amnesia have concentrated largely on measures of public event knowledge. The reason for this is that these tasks allow memory performance to be assessed for events known to have occurred either prior to or after amnesia onset. These measures also allow performance to be evaluated for events that occurred at different times prior to amnesia onset to determine whether the memory impairment shows a temporal gradient – a critical issue for evaluating theories of memory consolidation (Moscovitch et al., 2005). However, because these patients have either no or, more commonly, limited damage to regions outside the medial temporal lobes, they are not informative about how semantic information is organized in the cerebral cortex. To address this issue, investigators have turned to patients with relatively focal lesions compromising different cortical areas. In contrast to the studies of amnesic patients, these studies have focused predominantly on measures designed to probe knowledge of object concepts.

3.07.3.1 Object Concepts

An object concept refers to the representation (i.e., information stored in memory) of an object category (a class of objects in the external world) (Murphy, 2002). The primary function of a concept 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 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).

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 (Rosch, 1978). 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 et al., 1976; Rosch, 1978). It is the level used nearly

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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 that it is an animal or a poodle). It is also the level at which subordinate category members share 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 imagine an elephant but not an animal). As discussed next, studies of patients with cortical damage have documented the neurobiological reality of this hierarchical scheme and the central role of the basic level for representing objects in the human brain.

3.07.3.2 Semantic Dementia and the General Disorders of Semantic Memory

Several neurological conditions can result in a relatively global or general disorder of conceptual knowledge. These disorders are considered general in the sense that they cut across multiple category boundaries; they are not category specific. Many of these patients suffer from a progressive neurological disorder of unknown etiology referred to as semantic dementia (SD) (Snowden et al., 1989; Hodges et al., 1992). General disorders of semantic memory are also prominent in patients with Alzheimer's disease (who typically have a greater episodic memory impairment than SD patients) (Martin and Fedio, 1983) and can also occur following left hemisphere stroke, prominently involving the left temporal lobe (e.g., Hart and Gordon, 1990).

The defining characteristics of semantic dementia, initially described by Elizabeth Warrington in the mid-1970s, are relatively isolated deficits on measures designed to probe knowledge of objects and their associated properties (Warrington, 1975). These deficits include impaired object naming (with errors typically consisting of semantic errors – retrieving the name of another basic level object from the same category, or retrieving a superordinate category name), impaired generation of the names of objects within a superordinate category (i.e., semantic category fluency), and an inability to retrieve information about object properties – including sensory-based information (shape, color) and functional information (motor-based properties related to the object's customary use – but may include other kinds of information not directly related to sensory or motor properties) (Warrington, 1975; Martin and Fedio, 1983; Patterson and Hodges, 1995). In contrast to modality-specific agnosias, the impairment is not limited to stimuli presented in a single modality like vision but, rather, extends to all tasks probing object knowledge regardless of stimulus presentation modality (visual, auditory, tactile) or format (words, pictures). In agreement with studies of the psychological nature of concepts, the semantic deficit reveals a hierarchical structure. Broad levels of knowledge are often preserved, whereas specific information is impaired. Thus, these patients can sort objects into superordinate categories, having, for example, no difficulty indicating which are animals, which are tools, which are foods, and the like (Warrington, 1975; Martin and Fedio, 1983). Their primary difficulty manifests as a problem distinguishing among the basic level objects as revealed by impaired performance on measures of naming and object property knowledge. For example, when confronted with a picture of a specific basic level object like 'camel,' these patients often produce the name of another object from the same conceptual category (e.g., 'goat') or a superordinate term ('animal') (Warrington, 1975; Martin and Fedio, 1983).

Recent studies have expanded our understanding of SD in two important ways: one related to location of neuropathology, the other to functional characteristics of the disorder. The initial neuropathological and imaging studies of SD indicated prominent atrophy of the temporal lobes, especially to the anterolateral sector of the left temporal lobe, including the temporal polar cortex, the inferior and middle temporal gyri, and the most anterior extent of the fusiform gyrus (Hodges and Patterson, 1996). However, recent advances in neuroimaging that allow for direct and detailed comparison of brain morphology in SD patients relative to healthy control subjects have shown that the atrophy extends more posteriorally along the temporal lobe than previously appreciated (Mummery et al., 2000; Gorno-Tempini et al., 2004; Williams et al., 2005). In fact, the amount of atrophy in ventral occipitotemporal cortex, including the posterior portion of the fusiform gyrus, has been reported to be as strongly related to the semantic impairment in SD as is atrophy in the most anterior regions of the temporal lobes (Williams et al., 2005).

The other major advance in our understanding of SD is that it is not as global a conceptual disorder as initially thought. Rather, certain domains of knowledge may be preserved, and the pattern of impaired and preserved knowledge appears to be related to the locus of pathology. Specifically, left-sided atrophy seems to impair information about all object categories except person-specific knowledge

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(i.e., information about famous people), which in turn is associated with involvement of the right anterior temporal lobes (Thompson et al., 2004). Also relatively spared is knowledge of number and mathematical concepts (Cappelletti et al., 2005), a domain strongly associated with left posterior parietal cortex (Dehaene et al., 2003).

3.07.3.3 Category-Specific Disorders of Semantic Memory

Although case reports of relatively circumscribed knowledge disorders date back over 100 years, the modern era of the study of category-specific disorders began in the early 1980s with the seminal reports of Warrington and colleagues (Warrington and Shallice, 1984; Warrington and McCarthy, 1987). Category-specific disorders have the same functional characteristics as SD, except that the impairment is largely limited to members of a single superordinate object category. For example, a patient with a category-specific disorder for 'animals' will have greater difficulty naming and retrieving information about members of this superordinate category relative to members of other superordinate categories (e.g., tools, furniture, flowers). Similar to patients with SD, patients with category-specific disorders have difficulty distinguishing among basic level objects (e.g., between dog, cat, horse), thereby suggesting a loss or degradation of information that uniquely distinguishes members of the superordinate category (e.g., four-legged animals) (for recent collection of papers on these patients see Martin and Caramazza, 2003).

A variety of category-specific disorders have been reported such as relatively circumscribed deficits for knowing about fruits and vegetables (Hart et al., 1985; Crutch and Warrington, 2003). However, consistent with Nielsen's clinical observations (Nielsen 1946, 1958), most common have been reports of patients with relatively greater knowledge deficits for animate entities – especially animals, than for a variety of inanimate object categories. Although less common, other patients show the opposite dissociation: a greater impairment for inanimate manmade objects – including common tools – than for animals and other living things (for extensive review of the clinical literature, see Capitani et al., 2003).

3.07.3.3.1 Models of category-specific disorders

Two major theoretical positions have been advanced to explain these disorders. Following the explanation posited by Warrington for her initial cases, most current investigators assume that category-specific deficits are a direct consequence of an object property-based organization of conceptual knowledge, an idea that was prominent in the writings of Karl Wernicke, Sigmund Freud, and other behavioral neurologists during the late nineteenth and early twentieth centuries. The central idea is that object knowledge is organized in the brain by sensory (e.g., form, motion, color, smell, taste) and motor properties associated with the object's use (Martin et al., 2000), and in some models other functional/verbally mediated properties such as where an object is typically found (for discussion of sensory/functional models, see Forde and Humphreys, 1999). In this property-based view, category-specific semantic disorders occur when a lesion disrupts information about a particular property or set of properties critical for defining and for distinguishing among category members. Thus, damage to regions that store information about object form, and form-related properties like color and texture, will produce a disorder for animals. This is because visual appearance is assumed to be a critical property for defining animals and because the distinction between different animals is assumed to be heavily dependent on knowing about subtle differences in their visual forms. A critical prediction of sensory-/motor-based models is that the lesion should affect knowledge of all object categories with this characteristic, not only animals. In a similar fashion, damage to regions that store information about how an object is used should produce a category-specific disorder for tools and all other categories of objects defined by how they are manipulated. Cognitive studies with normal individuals on the relationship between and among object features and attributes show broad consistency with the known patterns of category-specific disorders, thus providing additional evidence in support of property-based models (Cree and McRae, 2003).

The alternative to these property-based theories is the domain-specific view championed most recently by Alfonso Caramazza and colleagues (Caramazza and Shelton, 1998; Caramazza and Mahon, 2003). On this account, our evolutionary history provides the major constraint on the organization of conceptual knowledge in the brain. Specifically, the theory proposes that selection pressures have resulted in dedicated neural machinery for solving, quickly and efficiently, computationally complex survival problems. Likely candidate domains offered are animals, conspecifics, plant life, and possibly tools (for a detailed discussion

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of these models, see Caramazza, 1998). Property-based and category-based accounts are not mutually exclusive. For example, it is certainly possible that concepts are organized by domains of knowledge, implemented in the brain by large-scale property-based systems (Mahon and Caramazza, 2003). Much of the functional neuroimaging evidence to be discussed later is consistent with this view.

3.07.3.3.2 Functional neuroanatomy of category-specific disorders

There is considerable variability in the location of lesions associated with category-specific disorders for animate and inanimate entities. Nevertheless, some general tendencies can be observed. In particular, category-specific knowledge disorders for animals are disproportionately associated with damage to the temporal lobes (Gainotti, 2000). The most common etiology is herpes simplex encephalitis, a viral condition with a predilection for attacking anteromedial and inferior (ventral) temporal cortices (Adams et al., 1997). Category-specific knowledge disorders for animals also have been reported following focal, ischemic lesions to the more posterior regions of ventral temporal cortex, including the fusiform gyrus (Vandenbulcke et al., 2006). In contrast, category-specific knowledge disorders for tools and their associated actions have been most commonly associated with focal damage to lateral frontal and parietal cortices of the left hemisphere (Tranel et al., 1997; Gainotti, 2000). However, it is important to stress that the lesions in patients presenting with category-specific knowledge disorders are often large and show considerable variability in their location from one patient to another (Capitani et al., 2003). As a result, these cases have been relatively uninformative for questions concerning the organization of object memories in cerebral cortex. In contrast, recent functional neuroimaging studies of the intact human brain have begun to shed some light on this thorny issue.

3.07.4 The Organization of Conceptual Knowledge: Neuroimaging Evidence

3.07.4.1 Neuroimaging of Semantic Memory

For nearly two decades cognitive neuroscientists have used positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) to explore the functional neuroanatomy of semantic memory. Although the particular methods, experimental paradigms, and stimuli vary widely, the general tack taken in most studies has been to compare brain activity when subjects engage in tasks requiring the encoding or retrieval of conceptual information (e.g., Is this object a man-made artifact?) versus the activity associated with equally difficult nonconceptual processing (e.g., Does this object's name contain the letter b?), using the same stimuli. The neuroanatomical claims made by these studies are further strengthened when subsequent research observes activity in the same brain regions using stimuli that are conceptually related (e.g., judging whether objects are artifacts) but physically different (e.g., seeing photographs vs. hearing sounds vs. reading names of artifacts). Such findings demonstrate that the regions are responding to the stimuli's conceptual content rather than their physical characteristics. As we will see, however, this does not mean that objects' physical properties are unimportant to their neural representations. On the contrary, using a variety of concepts and object categories, it has been well documented that object concepts are represented in the brain as distributed property circuits, whereby the information most relevant to real-world interactions with an object is stored in the same sensorimotor regions active when that information was acquired.

Studies comparing conceptual to nonconceptual processing consistently identify three brain regions – the left ventrolateral prefrontal cortex (VLPFC) and the ventral and lateral regions of the temporal lobes. A large functional neuroimaging literature demonstrates that the VLPFC serves as a control center for semantic memory, guiding retrieval and postretrieval selection of concept property information stored in other brain regions (Bookheimer, 2002; Martin, 2001; Thompson-Schill, 2003). These functional neuroimaging findings are consistent with neuropsychological findings with patients who, subsequent to left inferior frontal lesions, exhibit word retrieval difficulties while retaining conceptual knowledge for those same words (Baldo and Shimamura, 1998; Thompson-Schill et al., 1998). Information about this region's role in semantic memory has been augmented by recent functional neuroimaging studies that find distinct mechanisms within the VLPFC for information retrieval and selection among competing alternatives (Badre et al., 2005). Although claims for dissociable retrieval and selection subregions in VLPFC remain controversial, there is wide agreement that this region's primary role is to control and manipulate information stored elsewhere (Gold et al., 2005, 2006).

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3.07.4.2 Object Concepts as Sensorimotor Property Circuits

In addition to the VLPFC, a significant body of research demonstrates that various property regions located in or near perceptual cortex store information about object concepts. In particular, these studies find that the posterior ventral and lateral temporal lobes are particularly important for storing information about object concepts (Martin and Chao, 2001; Thompson-Schill, 2003; Martin, 2007). We will see that important clues about how knowledge is represented in the human brain come from how information is organized within these regions.

As described earlier, cases of category-specific deficits point toward a central role for property information in the organization of semantic memory. Early functional neuroimaging research using PET imaging supported these lesion study findings. Using a property production task in which subjects were required to generate a word describing a specific property of a visually presented object, Martin and colleagues (Martin et al., 1995; also see Chao and Martin, 1999; Wiggs et al., 1999) demonstrated that producing color-associate words (e.g., saying 'yellow' in response to an achromatic picture of a pencil or to its written name) elicited activity in the fusiform gyrus just anterior to regions activated when subjects passively viewed color stimuli. In contrast, producing action word associates (e.g., saying 'write' in response to a pencil) elicited activity in premotor cortex as well as a region of the left posterior middle temporal gyrus (pMTG) just anterior to primary visual motion-selective cortex MT/V5. Similar effects have now been observed for other property modalities as well, with sound, touch, and taste properties activating the corresponding auditory, somatosensory, and gustatory cortical regions (Kellenbach et al., 2001; Goldberg et al., 2006).

Functional neuroimaging findings demonstrating that retrieving object property information activated regions near perceptual and motor cortex are highly suggestive of the sensorimotor hypotheses generated in the literature on category-specific disorders. More recently, however, strong evidence for these accounts has come from fMRI studies demonstrating direct overlaps in the neural bases of knowledge, perception, and action. For example, Simmons et al. (in press) demonstrated a direct overlap in the neural bases of color perception and color knowledge retrieval. Using an attention-demanding task requiring fine-grain discriminations among color hues, they first mapped the brain regions underlying color perception. Next, in separate scanning runs, they presented subjects with a verbal property verification task in which they indicated whether color or motor property words could be true of a concept word. Using the color perception task as a functional localizer, they observed that the most color-responsive region in the perception task, located in the left fusiform gyrus, was also activated for color knowledge retrieval relative to retrieving motor knowledge (**Figure 1**). Evidence for direct overlaps between knowledge retrieval and sensorimotor

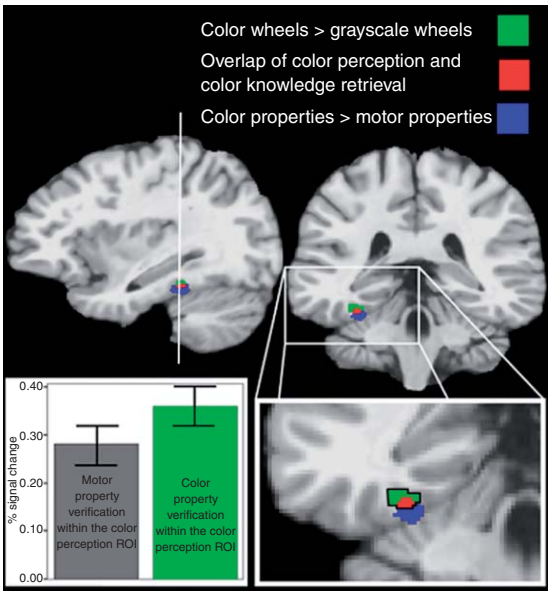

Figure 1 Overlap in perceptual and conceptual color processing. On top, the figure depicts sagittal and coronal sections from the N27 template brain warped to Talairach space (template available in AFNI). The functional overlays represent Talairach-normalized group data from the random effects analysis. Green patches indicate regions where activity was greater for processing color than grayscale wheels in the color perception task ($p < 0.0001$). Blue patches indicate regions where activity was greater for verifying color properties than motor properties in the knowledge retrieval task ($p < 0.01$ with a cluster size of at least 108 mm^3). The red patch in the left fusiform gyrus indicates the region of overlap between the two tasks. The inset bar graph demonstrates that within the left fusiform ROI, where color perception produced a greater response than grayscale perception (in other words, within the combined green and red patches), the average BOLD response to color property words in the property verification task was greater than the response for motor property words ($p = 0.006$). The *y*-axis indicates percent signal change relative to signal baseline, with error bars representing $\pm$ 1 standard error of the subject means. Adapted from Simmons WK, Ramjee V, Beauchamp MS, McRae K, Martin K, Martin A, and Barsalou LW (in press) A common neural substrate for perceiving and knowing about color. *Neuropsycholgia*.

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property systems are not limited to color properties. For example, Pulvermuller and colleagues have demonstrated that simply reading words referring to actions performed with a particular body part (e.g., lick, kick, pick) activated the corresponding motor cortex (e.g., face, foot, and hand representations, respectively) (Hauk et al., 2004).

Together, these findings support claims that knowledge about a particular object property, such as its color or the actions associated with it, resides in the same sensorimotor regions that are active when that information is experienced in the external world. If this is correct, then object categories should have predictable neural representations based on their multimodal property profiles. This appears to be the case. For example, the most salient properties of appetizing foods are how they look, how they taste, and how rewarding they are to eat. Using fMRI, Simmons et al. (2005) demonstrated that viewing images of appetizing foods (e.g., cookies, pizza) while performing a low-level picture repetition detection task was enough to elicit bilateral activity in ventral occipito-temporal regions tuned to represent object form information (e.g., how objects look). Consistent with the sensorimotor account of knowledge representation, the researchers also observed activity in regions of the right insula/operculum (primary gustatory cortex) and left orbitofrontal cortex (OFC) (secondary gustatory cortex) activated in prior fMRI studies when subjects received tastants orally in the scanner (**Figure 2**).

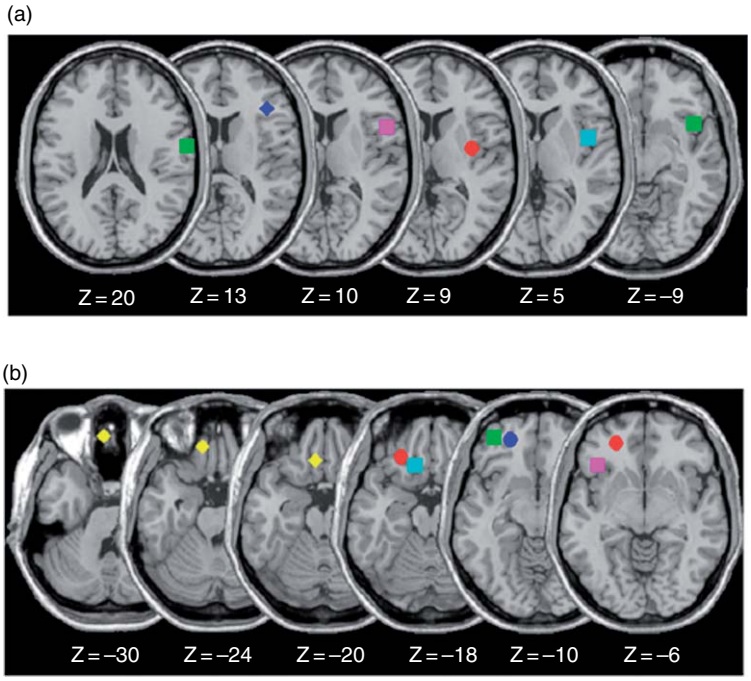

Figure 2 (a) Locations of peak right hemisphere insula/operculum activations reported in taste perception studies. (b) Locations of peak left orbitofrontal cortex (OFC) activations across various tasks. The green squares in the insula/operculum at $Z = 20$ and $Z = -9$ represent peak activations observed when participants taste sucrose, whereas the green square in the lateral OFC at $Z = -10$ is the peak activation in the area observed to respond to the combination of gustatory and olfactory stimuli, and thus it is a likely candidate for being the center of flavor representation (de Araujo et al., 2003b). The blue diamond in the insula/operculum at $Z = 13$ indicates an area of common activation when participants tasted either glucose or salt (O'Doherty et al., 2001b). The pink squares in the insula/operculum at $Z = 10$ and in the OFC at $Z = -6$ indicate the peak activations observed when participants taste umami (de Araujo et al., 2003a). The aqua squares in the insula/operculum at $Z = 5$ and in the OFC at $Z = -18$ represent peak activations when participants tasted glucose (Francis et al., 1999). Yellow diamonds in the inferior medial OFC represent peak activations observed when participants receive abstract rewards (O'Doherty et al., 2001a). The blue circle in the OFC at $Z = -10$ represents peak activation observed when participants verify the taste properties of concepts using strictly linguistic stimuli (Simmons, Pecher, Hamann, Zeelenberg, and Barsalou, Poster presented at the Annual Meeting of the Cognitive Neuroscience Society, New York, NY, April 2003). Finally, the red circles in the insula/operculum at $Z = 9$ and in the OFC at $Z = -18$ and $Z = -6$ indicate the activation peaks observed in the present study when participants viewed food pictures. When necessary, coordinates reported in other studies were converted from Talairach to MNI space. Adapted from Simmons WK, Martin A, and Barsalou LW (2005) Pictures of appetizing foods activate gustatory cortices for taste and reward. *Cereb. Cortex* 15: 1602–1608.

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These findings demonstrate that information about object-associated properties is stored and represented across numerous property regions in the brain, rather than in a single unitary semantic memory storehouse. In addition, the property regions that compose a concept's neural representation overlap with the brain regions mediating that property's perception. Findings to this effect provide strong evidence that at least some aspect of object knowledge is maintained in a modality-specific, perceptual format (Barsalou, 1999). This stands in stark contrast to accounts describing human knowledge solely in terms of amodal, propositional, and linguistic formats that bear arbitrary relationships to the perceptual experiences through which the information was acquired (Fodor, 1975; Pylyshyn, 1984; Kintsch, 1998).

3.07.4.3 Object Categories in the Brain

The vast majority of studies examining the neural bases of object concept knowledge have presented subjects with photographs of exemplars from various object classes. Given that a large body of monkey neurophysiology and human neuroimaging evidence indicates that the occipitotemporal cortex plays a central role in object perception (Grill-Spector, 2003; Grill-Spector and Malach, 2004), it is unsurprising that in these studies the different object categories invariably activate this region. This does not imply, however, that the ventral occipitotemporal cortex is an undifferentiated object-processing system. Rather, comparisons between classes of objects demonstrate that local regions within the ventral occipitotemporal cortex are particularly responsive to some categories relative to others. Perhaps the most well-known category-responsive brain region is the fusiform face area (FFA), which responds reliably and selectively to face stimuli (Kanwisher et al., 1997; see Kanwisher and Yovel, 2006, for review). Other frequently studied object categories include environmental scenes (places), which reliably activate a region in parahippocampal cortex (Aguirre et al., 1998; Epstein and Kanwisher, 1998), as well as animals and tools, each activating lateral and medial fusiform cortex, respectively (Chao et al., 1999; see Martin and Chao, 2001, and Martin, 2007 for reviews).

The topographic relations among these category-responsive ventral temporal regions are a topic of much research interest. Clearly, distinct categories are associated with activation peaks in particular regions. fMRI pattern analysis techniques, however, have demonstrated that they are also associated with distinct neural signatures across large swaths of ventral occipitotemporal cortex (Haxby et al., 2001; Spiridon and Kanwisher, 2002; Cox and Savoy, 2003). For now, it remains an open question as to how central these nonpeak areas are in the cognitive representation of concepts from any particular category (Haxby et al., 2001; Spiridon and Kanwisher, 2002; Reddy and Kanwisher, 2006). In contrast, however, to this debate about the distributedness of concept representation within a single brain region, human functional neuroimaging evidence leaves little room for debate as to whether conceptual information is distributed across brain regions. Conceptual knowledge is unequivocally distributed throughout the brain, and some of the best evidence to this effect comes from the study of two broad classes of knowledge: animate entities and tools.

3.07.4.4 Two Case Studies in Category Representation: Animate Entities and Tools

Motivated by category-specific deficits for animals and tools reported in the neuropsychological literature, many functional neuroimaging studies have focused on defining the neural substrate underlying knowledge of animate entities and small, manipulable artifacts such as tools. As we will see, these studies have shown that tasks involving animate objects (i.e., people and animals) are associated with activity in the distributed neural circuit engaged while perceiving animate entities' most salient properties, namely, what they look like and how they move. For example, Chao et al. (1999) demonstrated that naming pictures or reading words denoting animal concepts activated lateral regions in the fusiform gyrus (located along the ventral surface of the temporal lobes and including the FFA), as well as the posterior extent of the superior temporal sulcus (pSTS), located laterally along the temporal lobe (**Figure 3**). In contrast, these authors demonstrated that performing these tasks with manipulable artifacts (e.g., tools) activates a distributed neural circuit underlying not only what these objects look like and how they move but also their function-associated motor properties, including medial regions in the fusiform gyrus, the pMTG, and in a later study, posterior parietal and ventral premotor regions (Chao and Martin, 2000).

The fusiform region activated by animal and tool stimuli is part of a larger object-form processing stream stretching along the ventral surfaces of the

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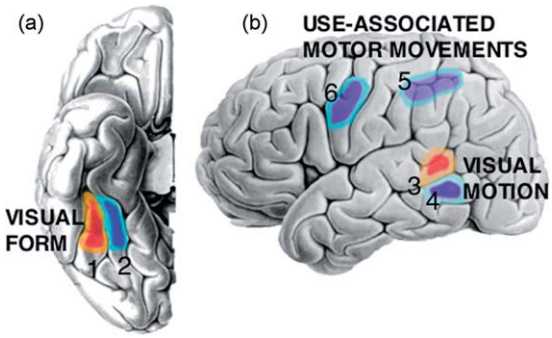

Figure 3 Schematic illustration of regions exhibiting category-related activity for animate entities such as animals and people (red) and manipulable artifacts such as tools (blue). (a) Ventral view of the right hemisphere showing relative location of regions assumed to represent visual form and form-related properties like color and texture of animate entities (1. lateral region of the fusiform gyrus, including, but not limited to, the fusiform face area) and tools; (2. medial region of the fusiform gyrus). (b) Lateral view of the left hemisphere showing relative location of regions assumed to represent biological motion typical of animate entities (3. pSTS) and rigid motion vectors typical of tools (4. pMTG). Also shown are the relative locations of the posterior parietal (5. typically centered on the intraparietal sulcus) and ventral premotor (6.) regions of the left hemisphere assumed to represent information about the motor movements associated with using tools.

occipital and temporal lobes (Ungerleider and Mishkin, 1982). Within this so-called ventral visual stream the form features of visual inputs are processed in a hierarchically organized manner, with more anterior regions representing higher-order information about what objects look like (Riesenhuber and Poggio, 1999; Grill-Spector and Malach, 2004). In contrast, the lateral temporal regions activated by animal and tool stimuli are located immediately anterior to the much-studied visual motion area V5/MT (Watson et al., 1993).

Although the location of these category-responsive regions relative to form and motion processing areas was suggestive as to their functional significance, the clearest evidence for the specific functions played by these two regions in conceptual processing *per se* comes from the work of Beauchamp and colleagues. In a series of studies, subjects were shown static and moving stimuli of humans (photographs and video clips of people performing actions such as jumping, walking, and sitting) and manipulable objects (e.g., photographs and video clips of tools such as hammers, saws, and scissors, moving in characteristic ways) (Beauchamp et al., 2002, 2003). As expected, the two classes of stimuli activated distinct regions in the ventral and lateral temporal lobes (**Figure 4**). Beauchamp et al. (2002) observed that in the fusiform gyrus, lateral regions responded more strongly to depictions of humans, and medial regions responded more to manipulable objects. Importantly, however, both regions responded equally to their preferred stimuli, regardless of whether those stimuli were static or dynamic. In a subsequent study, Beauchamp et al. (2003) observed that the lateral and medial fusiform responded much more to videos of humans and tools, respectively, than they did to point-light displays of humans and tools that lacked the form and color features of the video stimuli, but which maintained their motion vectors. Taking these two sets of findings together, we can infer that the lateral and medial fusiform regions are not modulated by motion but, rather, respond to the form features characterizing object concepts from their preferred categories – form features that are present in both static and dynamic depictions of an object.

Unlike the ventral temporal cortex, lateral temporal regions were more responsive to dynamic than static stimuli, with the pSTS and pMTG exhibiting strong category selectivity. The pSTS responded more strongly to dynamic depictions of human actions than to tool motion. This finding is consistent with monkey neurophysiology and human fMRI studies demonstrating that this region is particularly tuned to flexible, fully articulated motion vectors that characterize biological motion (Oram and Perrett, 1994; Puce et al., 1998; Grossman and Blake, 2001; Pelphrey et al., 2005). In contrast, relative to human actions, the pMTG responded more strongly to the rigid, unarticulated motion vectors characterizing dynamic depictions of tool motions. Thus, in the same way that activity in ventral temporal cortex differentiates along category boundaries, presumably due to different visual form characteristics for animate objects and manipulable artifacts, so activity in lateral temporal cortex similarly differentiates the distinctive motion properties of the two categories.

As reviewed earlier, behavioral (Cree and McRae, 2003) and imaging (see Martin, 2007) evidence demonstrate that an object concept's property profile (e.g., its form, motion, taste, sound) predicts the conglomeration of sensorimotor regions underlying that object concept's storage and representation in the brain. In light of this, it should come as no surprise that in addition to the temporal regions representing their form and motion properties, tasks involving manipulable artifacts also recruit posterior parietal and ventral premotor regions supporting the representation of

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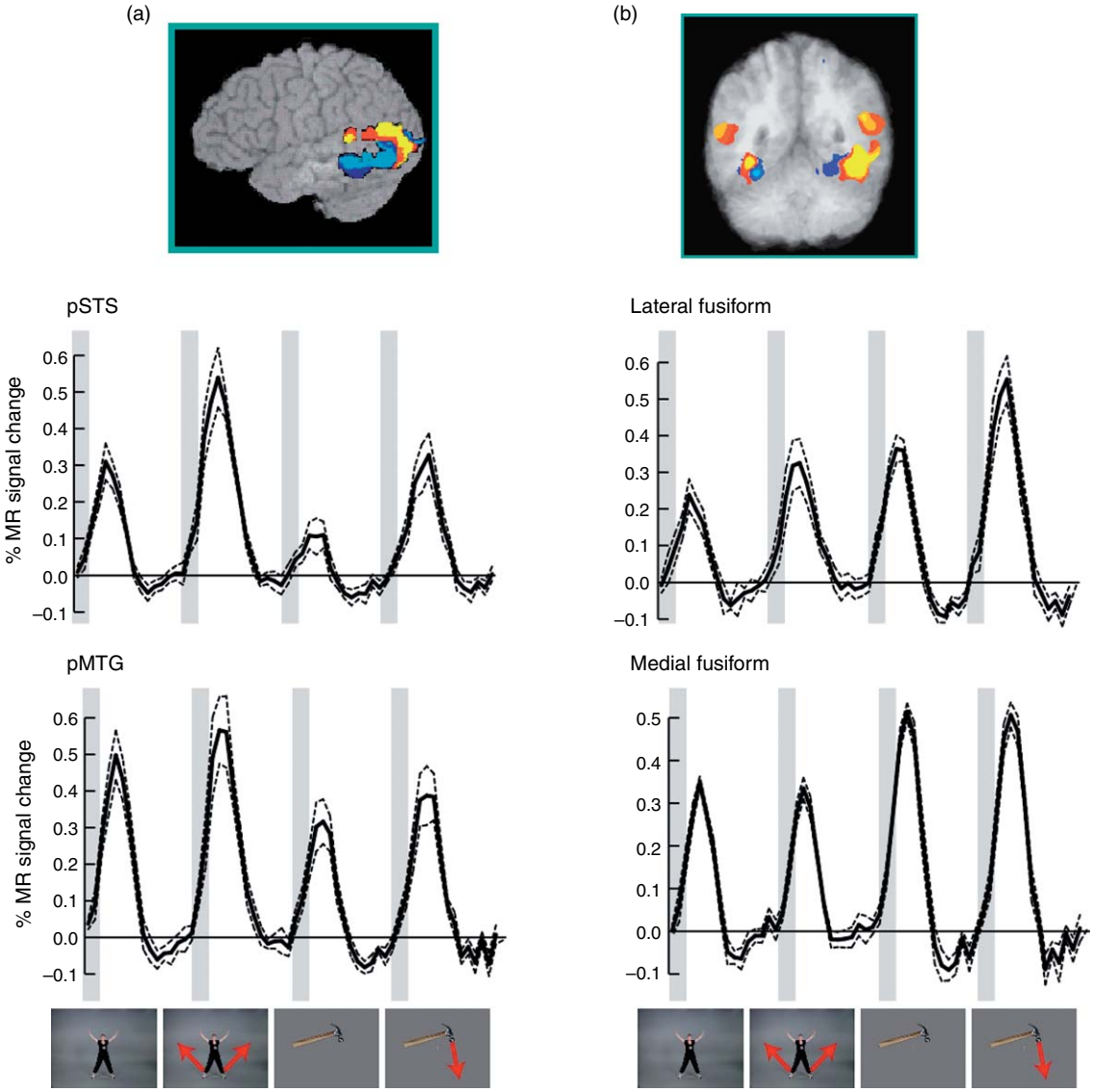

Figure 4 (a) Lateral view of the left hemisphere showing MTG regions that are more responsive when subjects identify static and moving images of tools than people (blue), and pSTS regions that are more responsive for identifying people than tools (yellow). (b) Coronal section illustrating medial fusiform regions that are more responsive when subjects identify static and moving images of tools than people (blue), and the lateral fusiform region that is more active for identifying people (yellow). Below each brain are group-averaged bold response functions depicting activity for static and moving images in each region shown in (a) and (b). The lateral cortical areas in (a) exhibit category and motion effects, where as ventral areas depicted in (b) exhibit only category effects. Vertical gray bars indicate stimulus presentation periods. Dashed lines indicate ±1 SEM. Adapted from Beauchamp MS, Lee KE, Haxby JV, and Martin A (2002) Parallel visual motion processing streams for manipulable objects and human movements. *Neuron* 34: 149–159.

object-associated actions (Chao and Martin, 2000). This finding is consistent with monkey neurophysiology evidence demonstrating that neurons in the ventral premotor and parietal cortices respond when monkeys grasp objects, as well as when they merely see objects they have previously manipulated (Jeannerod et al., 1995; Rizzolatti and Fadiga, 1998).

3.07.4.5 Category-Related Activations in Property Regions Are the Bases of Conceptual Representations of Objects

Processing various object categories elicits activity in sensorimotor property regions. But how do we know that the activity in property regions represents

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conceptual information? Three findings in particular from the literature on animate and manipulable artifact object concepts strengthen the case that property regions are involved in conceptual-level processing.

3.07.4.5.1 Reason #1 to think that property regions are involved in conceptual-level processing: Activity in category regions transcends stimulus features

For both animate and manipulable artifact categories, substantial evidence demonstrates that activity in the categories' property regions is not stimulus specific. For example, differential responses are observed in the lateral fusiform to animate entities in response to pictures and written names of animals (Chao et al., 1999; Okada et al., 2000; Price et al., 2003; Devlin et al., 2005; Rogers et al., 2005; Wheatley et al., 2005; Mechelli et al., 2006), human voices (von Kriegstein et al., 2005), and when simply imagining faces (O'Craven and Kanwisher, 2000). In addition, lateral fusiform activity is also observed in response to stimuli depicting point-light displays of human bodies in motion (Grossman and Blake, 2001, 2002; Beauchamp et al., 2003; Peelen et al., 2006) and degraded and abstract visual stimuli such as human-like stick figures (Peelen and Downing, 2005). These findings are important because they demonstrate that this region is responsive to representations of animate entities, even after most form and color information has been stripped from the stimuli.

Perhaps most significantly, lateral fusiform activity has even been observed when participants view abstract representations of social situations depicted in interactions among simple geometric shapes (Heider and 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 et al., 2000, 2002), and sharing (Martin and Weisberg, 2003).

Similarly, differential responses in the medial fusiform to manipulable objects are observed in response to both pictures and written names of tools (Chao et al., 1999, 2002; Whatmough et al., 2002; Devlin et al., 2005; Mechelli et al., 2006), the spoken names of tools (Noppeney et al., 2006), and point-light displays depicting tools in motion (Beauchamp et al., 2003). Medial fusiform activity has even been observed when participants view simple geometric shapes that move and interact in ways that suggest mechanical interactions such as a bowling ball knocking down pins or billiards (Martin and Weisberg, 2003). Clearly, activation in these category-related property areas is not due to particular stimulus features but, rather, appears to be related to high-level conceptual representations.

3.07.4.5.2 Reason #2 to think that property regions are involved in conceptual-level processing: Activations in property areas occur as property inferences

Further evidence that property regions for animate and manipulable objects are involved in conceptual processing comes from studies in which property inferences manifest as activations in property areas; in other words, when a response occurs within a property area even though that particular property is not, in fact, present in the stimulus. For example, perceiving pictures of animals or people or reading animal names activates the region of the pSTS sensitive to biological motion, even when the stimuli presented are static photographs (Chao and Martin, 1999; Beauchamp et al., 2002). Similarly, perceiving static pictures of tools or reading tool names activates the region of the pMTG known to represent nonbiological motion (Chao and Martin, 1999; Beauchamp et al., 2002; Chao et al., 2002; Phillips et al., 2002; Kellenbach et al., 2003; Creem-Regehr and Lee, 2005; Devlin et al., 2005; Kable et al., 2005; Tranel et al., 2005a, b; Mechelli et al., 2006; Noppeney et al., 2006). In addition to the motion property inferences, however, motor property inferences are also observed in response to tool photographs, with subjects exhibiting activations in premotor cortex, even though they are not physically manipulating the tools (Chao and Martin, 2000; Chao et al., 2002; Creem-Regehr and Lee, 2005; Kan et al., 2006).

These findings are in the same vein as the observations described earlier when subjects viewed appetizing foods. Upon viewing pictures of appetizing foods, activations were observed in insula/operculum and OFC regions known to represent the tastes and taste rewards of foods, even though subjects were not receiving any gustatory stimulation (Simmons et al., 2005).

The ability to make inferences about an entity's properties is at the very core of what most cognitive scientists call conceptual knowledge. Across various categories, human subjects frequently exhibit activations in property regions that correspond to salient object concept information, often when that information is not present in the immediate stimulus. Given

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its great utility, and likely survival value, we might expect that the ability to infer properties would be preserved across primate species, and recent evidence demonstrates that it is.

In a study demonstrating evolutionary continuity in the neural mechanisms for representing conceptual information, Gil-da-Costa et al. (2004) presented both species-specific calls and nonbiological sounds to awake rhesus macaques undergoing PET imaging. Although both the species-specific calls and nonbiological sounds were attended by activity in auditory cortex, the conspecific calls also elicited activation in area TE/TEO, the presumed monkey homologue of human fusiform gyrus, and in the STS (**Figure 5**). Note that these ventral and lateral temporal activations in visual form and motion property regions occurred to auditory stimuli. As with humans, when monkeys process information about animate entities, in this case other monkeys, activation occurs across a distributed network of property regions to represent those entities' salient features, namely, what they look like and how they move, even when those properties are not immediately present in the stimulus.

3.07.4.5.3 Reason #3 to think that property regions are involved in conceptual-level processing: Retrieving information from memory depends on reactivating property regions engaged while learning that information

A recent finding using fMRI brain state classification provides yet more evidence that property regions are involved in conceptual processing *per se*, rather than simply responding to features present in experimental stimuli. Polyn et al. (2005) demonstrated that

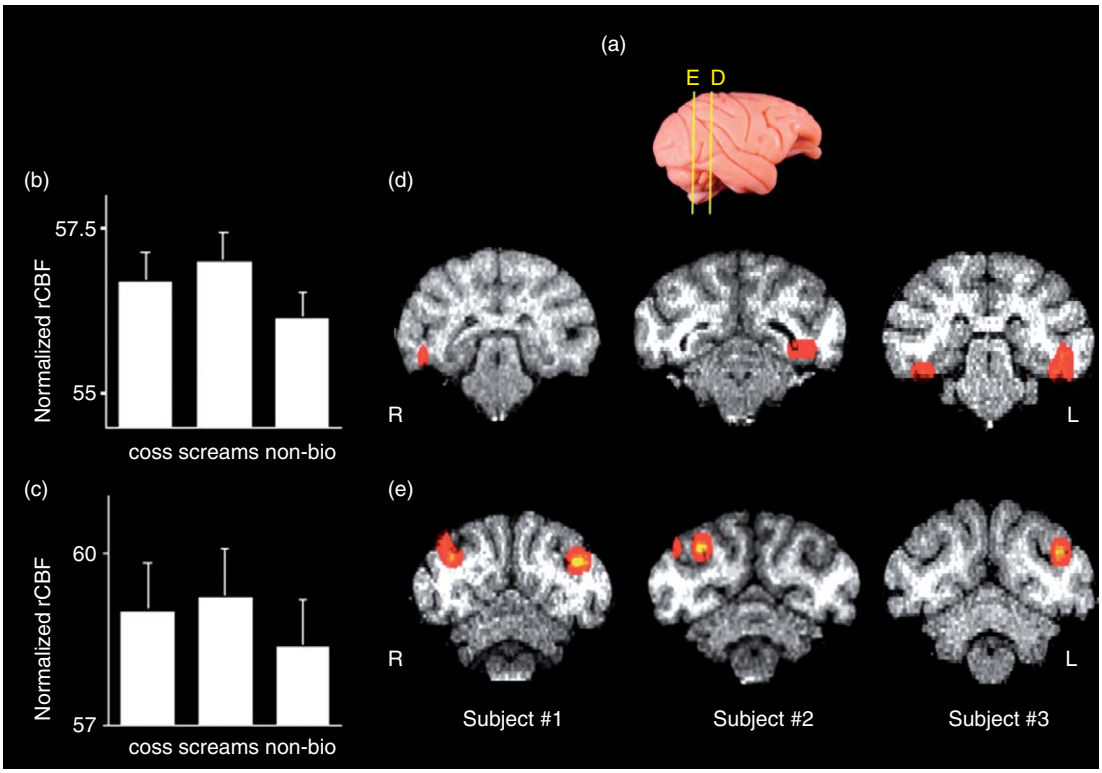

Figure 5 Activation of visual cortical areas in response to species-specific vocalizations in the rhesus macaque. (a) Lateral view of a rhesus monkey brain demonstrating the approximate locations of the coronal sections in (d) and (e). Both (b) and (c) show the mean (± SEM) normalized rCBF for the activations in TE/TEO and MT/MST/STS, respectively. In both regions, coos and screams exhibited reliably greater activation than nonbiological sounds. The coronal slices in (d) and (e) illustrate regions in each monkey that were more responsive to conspecific vocalizations (coos and screams) than to nonbiological sounds. Adapted from Gil-da-Costa R, Braun A, Lopes M, et al. (2004) Toward an evolutionary perspective on conceptual representation: Species-specific calls activate visual and affective processing systems in the macaque. *Proc. Natl. Acad. Sci. USA* 101: 17516–17521.

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machine-learning algorithms are capable of detecting activity across the property regions underlying faces, places, and manipulable objects immediately prior to the free recall of information about each of these categories. During the classifier training phase of the study, subjects learned associations between labels and photographs of famous people, places, and common manipulable objects while undergoing fMRI. Later, while still undergoing fMRI, subjects were instructed to recall the items they had learned during the training phase. Brain state classifiers that were trained on data collected during encoding were able to detect distinct patterns of category-related activity that occurred several seconds prior to recall. Importantly, lateral fusiform activity served as the best predictor of famous face recall, left pMTG and parietal cortex activity best predicted manipulable object recall, and parahippocampal activity best predicted recall of places. By demonstrating that retrieving an item from memory depends on reactivating the pattern of activity in property regions that occurred during learning, this finding further establishes the centrality of property-specific information systems in the memory encoding, storage, and retrieval of conceptual information.

3.07.4.6 Learning about Objects by Building Property Circuits

The close correspondence between brain regions underlying perception and action with an object, and its representation in memory, suggests that conceptual property circuits develop out of experience with objects. A small but growing body of literature demonstrates that this is indeed the case. For example, Weisberg et al. (2007) asked subjects to perform a simple visual matching task on photographs of novel objects while undergoing fMRI. After scanning, the subjects were then given extensive training interacting with the objects, each of which was designed to perform a specific tool-like function. After training, the subjects were once again scanned while performing the visual matching task. Comparing the data from the two imaging sessions revealed that physical experience using the objects in a tool-like manner led to significant changes in the objects' neural representation. Whereas the novel objects elicited only diffuse ventral temporal activation in the first scan session, ventral temporal activity after training was largely restricted to the medial aspect of the fusiform gyrus, the same region previously implicated in representing the visual shape or form of tools. Similarly, new activations emerged after training in other regions observed in studies of tool knowledge, namely, the left pMTG (nonbiological motion) and left intraparietal sulcus and premotor cortex (physical manipulation).

Learning effects have also been observed for animate entities. As described earlier, viewing point-light displays of human forms in motion elicits activity in lateral fusiform and pSTS. Grossman et al. (2004) trained subjects to perceive human forms in point-light displays embedded within visual noise. After training, the subjects were not only 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. Interestingly, the amount of activity in both regions was positively correlated with a subject's behavioral performance.

Yet further evidence for the development of property circuits with learning comes from James and Gauthier (2003), who demonstrated that property circuits can develop even through verbal learning. Prior to scanning, subjects learned verbally presented facts about families of novel animate-like entities called 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 the learned associations. James and Gauthier found 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).

James and Gauthier's findings are important for at least two reasons. First, along with the findings of Weisberg et al. (2007), they illustrate how experience with category exemplars leads to the development of property circuits, which can later activate as property inferences. In both studies, simply seeing a particular object from the training set elicited activation in either premotor (for tools) or auditory and motion-sensitive cortex (for greebles), even though that information was unnecessary for successfully performing the task and not present in the stimuli. Second, it illustrates that this process can occur even when experience is verbally mediated. This finding is important precisely because so much of

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our knowledge is acquired verbally, rather than through direct sensorimotor experience with objects and their properties.

3.07.5 Summary

The neuropsychological and functional neuroimaging findings presented here tell us much about the organization of conceptual knowledge in the brain. Surveying these studies, it appears that information about any particular object concept is distributed across a discrete network of cortical regions, rather than being represented in a single brain region. In addition, the particular neural circuit for a given object concept includes property regions that are most commonly engaged during perceptual experience with, or functional use of, the object, as demonstrated by training studies that documented the development of property circuits as subjects gained experience with an object.

One reason for suspecting that these property regions are not strictly perceptual but, rather, support conceptual representations is that some property regions activate automatically when an object is identified, regardless of whether their respective properties are immediately present in the stimulus. As such, these activations constitute property inferences about the object. At present, the extant findings suggest that for any given object, properties such as form, motion, and function-associated motor actions are particularly likely to be retrieved automatically. As such, these three property types may form a core set of information that is necessary and sufficient for representing object concepts in memory. There is good reason to believe, however, that future research using a wider array of object categories will reveal important roles for other property types as well (e.g., taste properties may be particularly important for food concepts). Finally, a close physical proximity exists between the neural systems underlying perception and knowledge representation for objects. Indeed, for color and motor properties, the neural bases underlying perceptual and conceptual property representation may partially overlap. Taken together, these findings strongly support so-called embodied cognition accounts of knowledge representation, which claim that conceptual property information is stored in the perceptual and motor systems active when that property information is learned.

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