

The Representation of Object Concepts in the Brain

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Abstract

Evidence from functional neuroimaging of the human brain indicates that information about salient properties of an object—such as what it looks like, how it moves, and how it is used—is stored in sensory and motor systems active when that information was acquired. As a result, object concepts belonging to different categories like animals and tools are represented in partially distinct, sensory- and motor property-based neural networks. This suggests that object concepts are not explicitly represented, but rather emerge from weighted activity within property-based brain regions. However, some property-based regions seem to show a categorical organization, thus providing evidence consistent with category-based, domain-specific formulations as well.

Contents

INTRODUCTION.....	26
CONCEPTUAL PROCESSING AND POSTERIOR TEMPORAL CORTEX.....	27
Dissociating Conceptual Processing from Explicit Visual Image Generation.....	29
Strengthening the Link Between Posterior Temporal Cortex and Conceptual Processing.....	29
RETRIEVING INFORMATION ABOUT OBJECT PROPERTIES.....	31
REPRESENTING OBJECT CATEGORIES.....	33
Linking Category-Related Representations to Form and Motion Perception.....	35
Beyond Form and Motion: Representing Higher-Order Concepts.....	36
Linking the Representation of Tools to Motor Systems.....	36
Learning About Object Properties.....	37
CONCLUSION.....	38

INTRODUCTION

Semantic memory refers to a major division of declarative memory that includes knowledge of the meaning of objects and words. This review focuses on one aspect of the functional neuroanatomy of semantic memory: the representation of the meaning of concrete objects and their properties. The motivation for many of the studies to be discussed comes from reports of patients with category-specific knowledge disorders—specifically, patients with relatively selective knowledge impairments for animals and other animate objects, and those with relatively selective impairments for manmade, inanimate objects such as tools (for review, see Capitani et al. 2003). The studies to be re-

viewed here were motivated by an appreciation of the importance of these clinical cases for understanding the organization of conceptual knowledge, object recognition, and storage of long-term memories.

For well over one hundred years, thinking about the representation of object concepts in the brain has been dominated by sensory-motor property models (dating from Lissauer 1890 and Freud 1891 to recent accounts by many investigators; for review, see Humphrey & Forde 2001). The central idea is that object knowledge is organized by sensory features (e.g., form, motion, color) and motor properties associated with the object's use (and in some models, other functional/verbally mediated properties such as where an object is typically found, its social significance, etc.). In this view, category-specific knowledge disorders occur when a lesion disrupts information about a particular property or set of properties critical for defining that object category and for distinguishing among its members. Thus, damage to regions that store information about object form will produce a disorder for animals 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 form. 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 other objects defined by how they are manipulated (see, e.g., Warrington & McCarthy 1987 and Warrington & Shallice 1984). Information is organized in the brain by property, not by conceptual category.

The alternative to property-based models is domain-specific models (Caramazza & Shelton 1998). On this account, evolutionary history, not sensory and motor systems, provides the major constraint on the organization of conceptual knowledge. Specifically, the theory proposes that selection pressures have resulted in dedicated neural machinery for solving, quickly and efficiently,

Semantic memory:
a large division of long-term memory containing knowledge about the world including facts, ideas, beliefs, and concepts

computationally complex survival problems. Likely candidate domains offered are animals, conspecifics, plant life, and possibly tools. These systems, in turn, could be organized by property (Mahon & Caramazza 2003) (see Caramazza 1998 for detailed discussion of models proposed to explain category-selective knowledge deficits). The neuroimaging findings reviewed here provide strong support for sensory-motor property-based models by revealing considerable overlap in the neural circuitry supporting perceiving, acting on, and knowing about objects. Thus, consistent with the idea of embodied cognition, these findings suggest that object concepts are grounded in perception and action (e.g., Allport 1985, Barsalou 1999, Gallese & Lakoff 2005, Martin 1998). However, consistent with domain-specific accounts, these studies also reveal that some of the regions for representing object properties may be organized by category.

The review concentrates on two broad domains of knowledge: animate agents—living things that move on their own, and tools—manmade manipulable objects for which there is a direct relationship between how an object is manipulated and its function. The review is divided into three major sections. First, I discuss functional brain imaging studies of normal subjects that indicate that the posterior regions of the temporal lobes play a prominent role in conceptual processing. This is followed by a review of studies showing that different regions of posterior temporal cortex, as well as other areas of the brain, are involved in perceiving and knowing about specific properties. In the third section, I review studies suggesting that object concepts are represented in at least partially distinct property-based neural circuits.

CONCEPTUAL PROCESSING AND POSTERIOR TEMPORAL CORTEX

Functional brain imaging studies on conceptual and semantic/lexical processing (i.e., using word stimuli) have consistently isolated

two key brain regions: left ventrolateral prefrontal cortex (VLPFC) and the ventral and lateral regions of posterior temporal cortex—typically stronger in the left than in the right hemisphere (**Figure 1**) (for reviews, see Bookheimer 2002, Martin 2001, Martin & Chao 2001, Thompson-Schill 2003). Activity in VLPFC has been strongly associated with top-down control of semantic memory; specifically, guiding retrieval and postretrieval selection of conceptual information stored in posterior temporal and perhaps other cortical areas. The role of left VLPFC in retrieving and selecting among competing alternatives has been confirmed by studies of patients with left VLPFC damage (e.g., Thompson-Schill et al. 1998) and most recently by applying transcranial magnetic stimulation (TMS) to left inferior frontal cortex to produce a local, transient disruption in processing (Gough et al. 2005). Recent evidence also suggests that there may be two anatomically distinct mechanisms within left VLPFC; one for retrieving, the other for selecting among competing alternatives (Badre et al. 2005). Although the details of the role of left VLPFC in conceptual processing remain a matter of debate, there is agreement that its main function is controlling and modulating access to information stored elsewhere (e.g., Gold et al. 2005; see Thompson-Schill et al. 2005 for a discussion of VLPFC functioning in the context of other frontal lobe mechanisms for cognitive control).

A large body of functional neuroimaging evidence has implicated the temporal lobes, particularly the posterior region of the left temporal lobe, as a critical site for stored representations, especially about concrete objects. Neuropsychological investigations have linked focal damage to left posterior temporal cortex to a loss of conceptual object knowledge (e.g., Hart & Gordon 1990). Early functional neuroimaging studies provided evidence for this link using a wide variety of tasks with object pictures and their written names (see previously cited reviews). Demonstrating that a common neural

Object concept:

memory representations of a class or category of objects. Necessary for numerous cognitive functions including identifying an object as a member of a specific category and drawing inferences about object properties

Category-specific disorder:

a relatively greater impairment in retrieving information about members of one superordinate object category (e.g., animals) as compared with other categories following brain injury or disease

TMS: transcranial magnetic stimulation

Repetition suppression:

decreased neural response associated with repeated presentation of an identical, or a semantically/conceptually related, stimulus

LO: lateral occipital cortex

substrate was active regardless of whether objects were represented by pictures or words provided support for interpretations appealing to conceptual and/or lexical processes rather than visual feature processing per se.

Recent studies have provided additional support for this view by demonstrating that regions of left posterior temporal cortex known to be active during conceptual processing of pictures and words (fusiform gyrus and inferior and middle temporal gyri) (**Figure 1**) were also active during auditory sentence comprehension (e.g., Davis & Johnsrude 2003, Giraud et al. 2004, Rodd et al. 2005). In these studies, activity was modulated by speech intelligibility (Davis & Johnsrude 2003, Giraud et al. 2004) and semantic ambiguity (Rodd et al. 2005). As comprehension increased, so did activity in left posterior temporal regions.

Another recent approach to investigating the functional neuroanatomy of conceptual processing has been to use stimulus repetition tasks. It has been well established that prior experience with a stimulus results in more efficient processing (repetition priming) and a reduced hemodynamic response—typically referred to as repetition suppression, but also as adaptation, neural priming, and repetition attenuation—when that stimulus is encountered at a later time (Henson 2003, Schacter et al. 2004; see Grill-Spector et al. 2006 for a recent review of neural models of repetition suppression). Recent studies have documented the usefulness of using repetition paradigms—also referred to as adaptation paradigms—for evaluating the processing characteristics of select brain regions (Grill-Spector & Malach 2001).

Using object repetition paradigms, van Turennout et al. (2000) and Vuilleumier et al. (2002) reported that although repeating non-meaningful (nonsense) and meaningful (real, nameable) objects produced repetition suppression in occipital cortex, more anterior re-

gions of the visual object processing stream, specifically, the fusiform gyrus on the ventral surface of the temporal lobes, showed repetition suppression only to real objects. This finding was consistent with earlier studies showing that while the lateral region of occipital cortex (area LO; **Figure 1**) responded robustly and with equivalent strength to real and nonsense objects (Kanwisher et al. 1997, Malach et al. 1995, Martin et al. 1996), the fusiform gyrus showed a preferential response to real objects (e.g., Martin et al. 1996).

Schacter and colleagues used an object repetition paradigm to provide a stronger link between the fusiform gyrus and conceptual processing (Koutstaal et al. 2001, Simons et al. 2003). In both studies, repetition suppression in the left fusiform gyrus was found not only for repetition of previously seen objects, but also, to a lesser extent, for different exemplars of previously seen objects (i.e., objects with the same basic level name, but with a different visual form than the object previously presented). In contrast, area LO and the right fusiform gyrus showed repetition suppression to only identical objects. Because different exemplars share conceptual and lexical, but not shape, representations, the finding that repetition suppression in the left fusiform gyrus survived an exemplar change provided additional evidence that neural responses in this region are related to conceptual and/or lexical processes, rather than stimulus features per se. However, it is possible that repetition suppression could have been driven by overlap in features in the pictures of the two exemplars of the same object concept. This possibility has been addressed by priming studies using the written names of objects rather than object pictures. These word-based priming studies also provide evidence against the view that activation of the ventral object-processing stream is solely due to the explicit generation of visual object images after the meaning of the stimulus has been established by neural systems located elsewhere.

Dissociating Conceptual Processing from Explicit Visual Image Generation

An important piece of evidence for the idea that information about visual object form is stored in ventral temporal cortex comes from studies showing that regions active when objects are visually recognized are also active when subjects generate visual images of those objects (e.g., Ishai et al. 2000, O'Craven & Kanwisher 2000). These findings, which support the idea that visual object information is stored in this region of the brain, also offer an alternative to interpretations based on appeals to conceptual processing: specifically, that posterior temporal activity simply reflects the explicit retrieval of visual object imagery that accompanies task performance. Thus, within this view, stimuli denoting concrete objects, either pictures or words, trigger visual imagery, which then recruits posterior ventral temporal cortex indirectly; this area does not do any conceptual work. This view is further strengthened by studies showing that activity in the fusiform gyrus is associated with word imageability and concreteness (Sabsevitz et al. 2005, Wise et al. 2000) and visual property verification (Kan et al. 2003, although Kan et al. directly challenge the idea that their findings were due to explicit visual image generation).

Wheatley et al. (2005) addressed this issue by using an automatic semantic priming paradigm in which word pairs were presented using a short stimulus onset asynchrony (SOA; the time from the onset of the first word in a pair to the onset of the second word). Each word was presented for 150 msec, with a 250-msec SOA. The authors reasoned that modulations of cortical activity associated with automatic semantic priming would occur too quickly to be ascribed to explicit visual image generation. Thus, finding repetition suppression in the fusiform gyrus when reading briefly presented semantically related word pairs, relative to unrelated pairs, would add considerable weight

to the claim that this region is involved in conceptual processing. Repetition-related reductions in hemodynamic responses (repetition suppression) were observed, in fact, in several regions, including the left fusiform gyrus. Activity was greatest for unrelated pairs (e.g., apple-lion), less for semantically related pairs (dog-horse), and least for same word repetitions (table-table), mirroring the pattern of behavioral performance (slowest for unrelated, faster for related, and fastest for reading identical words; Wheatley et al. 2005). Thus, the fusiform gyrus was sensitive to object meaning. Because of the extremely short duration between words, these data seem to rule out the possibility that fusiform activity was due to the explicit generation of visual object images (see Gold et al. 2006 for a replication using a lexical decision task).

These findings do not argue against the association of fusiform activity with retrieval of visual object information. To the contrary, it is likely that fusiform gyrus activity during automatic semantic priming is a direct reflection of accessing this information. However, given the processing time constraints imposed by the automatic semantic priming paradigm, retrieving this information may be best thought of as reflecting the implicit generation of visual images that occurs as an obligatory component of reading for meaning, not a nonobligatory, explicit generation of visual images occurring after the word's meaning had been determined.

Strengthening the Link Between Posterior Temporal Cortex and Conceptual Processing

Three recent neuroimaging studies have provided evidence suggesting that the posterior temporal cortex plays a direct role in conceptual processing. Two of the studies tested patients with semantic deficits due to cortical lesions, and the third used TMS to disrupt conceptual processing in normal individuals. The damaged or disrupted (via TMS) brain

Semantic priming: a short-lasting facilitation in processing a stimulus due to the prior presentation of a semantically related stimulus

SEMANTIC DEMENTIA AND THE ANTERIOR TEMPORAL LOBES

Semantic dementia (SD) is a progressive neurological disorder that produces a profound impairment of semantic memory, including impaired object naming and degraded knowledge of specific object properties (Hodges et al. 1992). Early neuropathological and structural brain-imaging studies showed that SD was associated with severe atrophy of the anterior temporal lobes (Hodges & Patterson 1996). As a result, this brain region has featured prominently in many neuropsychological and computational models of object semantics (e.g., Rogers et al. 2004, Tyler & Moss 2001). However, the specific functions of anterior temporal regions have not been clearly delineated. This has been due, in part, to difficulty obtaining reliable functional imaging data because of artifacts that decrease signal in this area of the brain. Characterizing the role of the anterior temporal lobes is further complicated by the fact that it is not a homogeneous structure, but rather contains numerous anatomically discrete regions, each of which may play a distinct role in the acquisition, storage, and manipulation of conceptual information. In addition, recent advances in structural neuroimaging have further complicated the picture by showing that the cortical atrophy in SD is not limited to anterior temporal regions, but rather extends more posteriorly than previously appreciated (Gorno-Tempini et al. 2004, Mummery et al. 2000, Williams et al. 2005). In fact, the amount of atrophy in ventral occipitotemporal cortex, including the fusiform gyrus, is as strongly related to semantic impairments in SD patients as is atrophy in the most anterior regions of the temporal lobes (Williams et al. 2005). Improved functional neuroimaging of anterior temporal structures resulting from recent technological advances (Bellgowan et al. 2005) should help to clarify the role(s) of this brain region in conceptual and semantic processing.

region was distant from posterior temporal cortex in each study. As a result, the effects on neural responses in posterior temporal cortex from a disturbance in another brain region could be directly evaluated.

The first study evaluated patients with semantic dementia (SD; Mummery et al. 1999). As typically found in SD, the patients performed poorly on object naming and other conceptual and semantic processing tasks.

Voxel-based structural morphometry revealed marked atrophy in left polar and anterolateral, but not posterior, regions of the left temporal lobe. Nevertheless, functional imaging during performance on picture- and word-based semantic association tasks showed that the patients failed to activate posterior temporal regions that were active in normal subjects (while also overactivating left VLPFC and the atrophic anterior temporal cortex; Mummery et al. 1999).

A similar action-at-a-distance effect was observed in patients with impaired auditory processing due to a focal lesion in the left superior temporal gyrus (Sharp et al. 2004). Although sentence comprehension was impaired, performance was normal on the same visually based semantic association task used in the SD study by Mummery et al. (1999), thus indicating that the network needed for conceptual processing of visual stimuli was intact. However, scanning during an auditory version of the semantic association task revealed that, relative to normal subjects, the patients showed markedly reduced activity in the left fusiform gyrus. Moreover, left fusiform activity was also reduced in normal subjects when comprehension was impaired by degrading the auditory speech signal (Sharp et al. 2004). Taken together, these findings provide compelling evidence that posterior temporal cortex, and especially the left fusiform gyrus, is a critical node in a network of regions involved in conceptual and semantic processing. Moreover, involvement of the fusiform gyrus is independent of stimulus modality (visual, auditory) and format (pictures, words).

The data from the SD patients also indicate that posterior temporal regions can be activated top-down by higher-order processing regions (polar and anterior temporal cortices). As reviewed above, VLPFC has been strongly associated with the top-down control of posterior temporal cortices. Neuroimaging evidence for this top-down influence during conceptual processing comes from a study that combined TMS with functional brain

SD: semantic dementia

imaging (Wig et al. 2005). TMS was applied to left VLPFC and to a nearby control site while subjects engaged in a conceptual processing task (making living/nonliving judgments about object pictures). Functional imaging many minutes later showed a normal pattern of repetition suppression in left VLPFC, posterior temporal cortex, and LO for pictures of objects initially encoded during TMS to the control site. However, for pictures initially encoded during VLPFC TMS, repetition suppression was eliminated not only in VLPFC, but also in posterior temporal cortex, while being maintained in the occipital lobe (area LO) (Wig et al. 2005). These data provide direct evidence for a top-down effect of left VLPFC on posterior temporal cortex during conceptual processing and add further evidence to the processing distinction between LO and adjacent, more anterior regions of the ventral object processing stream.

RETRIEVING INFORMATION ABOUT OBJECT PROPERTIES

The underlying logic of the studies reviewed above was to contrast neural activity associated with performing conceptual and non-conceptual processing tasks (typically requiring low-level perceptual processing) using the same stimuli. When tasks are equated for difficulty, this strategy is ideal for revealing brain regions supporting conceptual processing. However, these designs are not informative about the representational content of the brain regions they identify. The studies reviewed below use a different strategy to address this issue. A single processing task—property production or property verification—is used to evaluate knowledge about different kinds of properties. As a result, questions concerning the possibility that different object properties are stored in different brain regions can be addressed.

For example, Martin et al. (1995) used property production to probe knowledge of object-associated colors and actions. Subjects were presented with achromatic object pic-

tures (in one experiment) or the written names of objects (in the other experiment) and were required to generate words denoting an action (e.g., “pull” in response to a child’s wagon) or a color (“red” for the child’s wagon) associate. In both experiments, the type of information retrieved modulated activity in posterior temporal cortex. Relative to color word generation, action words elicited heightened activity in several brain regions, including a posterior region of the left lateral temporal cortex, centered on the middle temporal gyrus (pMTG) just anterior to the primary visual motion processing area, MT (Figure 1). In contrast, relative to action word generation, color word generation activated the fusiform gyrus anterior to regions associated with color perception (e.g., Zeki et al. 1991) and object perception (LO; e.g., Malach et al. 1995).

Activation of ventral temporal cortex when retrieving color information, relative to other properties, has been replicated several times using property production (Wiggs et al. 1999; Chao & Martin 1999) and property verification tasks (Goldberg et al. 2006, Oliver & Thompson-Schill 2003, Simmons et al. 2006). In addition, numerous reports confirm an association between action word generation and activation of the posterior lateral temporal cortex (reviewed in Martin 2001). Most recently, Tranel et al. (2005b) strengthened the association between left pMTG and action concepts by using a noun-verb homonym production task. Subjects produced a single word in response to pictures of objects (saying “saw” to a picture of a saw) and actions (saying “saw” to a picture of a person sawing). Although both tasks activated left pMTG relative to a baseline task, left pMTG was more active when noun-verb homonyms like “hammer” and “comb” were generated to name actions than when used to name objects, thereby also eliminating concerns related to producing different words in different property production conditions (Tranel et al. 2005b).

Left unanswered by these studies is the question of whether the same neural system

pMTG: posterior middle temporal gyrus

active when retrieving a property like color is also active when colors are perceived. Chao & Martin (1999) addressed this question by evaluating both processes in the same experiment. Color word generation activated posterior ventral temporal cortex as previously reported, but not sites in occipital cortex active during passive viewing of colored stimuli (lingual gyrus; **Figure 1**).

This finding was consistent with studies of color imagery in normal subjects (Howard et al. 1998) and in color-word synesthetes who experience vivid color imagery when hearing words (Paulesu et al. 1995). In both of those studies, color imagery was associated with activity in the same ventral temporal sites as found in the color word generation studies discussed above, but not in occipital sites active during color perception (e.g., Zeki et al. 1991). Coupled with neuropsychological reports of a double dissociation between color perception and color imagery (De Vreese 1991, Shuren et al. 1996), these data suggest that information about object color is stored in ventral temporal cortex and that the critical site is close to, but does not include, sites in occipital cortex that selectively respond to the presence of color.

This claim, however, is at odds with the assertion that the same neural systems are involved, at least in part, in perceiving and knowing about specific object properties. However, Chao & Martin (1999) found that naming the color of colored objects (saying “red” in response to a picture of a red wagon), relative to naming colored objects (e.g., say “wagon” in response to the same picture), not only elicited activity in occipital regions active when passively viewing colored displays, but also in the more anterior site in the fusiform gyrus active during color word generation. Thus, this finding suggests that there may be partial overlap in the neural systems supporting perception and storage of specific object properties.

Recent fMRI evidence has provided more direct evidence for this claim. Beauchamp et al. (1999) replicated previous studies show-

ing that neural activity is limited to the occipital lobes when color perception was tested by passive viewing. However, when the task was made more demanding by requiring subjects to judge subtle differences in hue, activity associated with perceiving color now extended from occipital cortex into the fusiform gyrus in ventral temporal cortex. Using this attention-demanding 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. 2006). Thus, 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. Therefore, although detection of color (color sensation) may be mediated by occipital cortical regions located early in the visual processing stream, active color perception seems to require more extensive neural activity extending anteriorly into the fusiform gyrus. One function of this region may be to provide a neural substrate for acquiring new object-color associations and representing those associations in the service of conceptual processing.

These studies suggest that retrieving other sensory- and motor-based properties should elicit activity in the corresponding sensory and motor processing systems. Goldberg et al. (2006) addressed this possibility using property verification tasks. Answering written questions concerning object-associated visual, sound, touch, and taste properties activated regions involved in sensory processing in each of these modalities (Goldberg et al. 2006; see also Kellenbach et al. 2001). Overlap between the neural systems for representing motor action concepts and action production has also been observed. In perhaps the most impressive demonstration in support of this claim, Pulvermüller and colleagues showed that simply reading words denoting specific

tongue (lick), finger (pick), and leg (kick) actions activated regions in premotor cortex that were also active when subjects actually made tongue, finger, and leg movements, respectively (Hauk et al. 2004).

REPRESENTING OBJECT CATEGORIES

The studies reviewed above suggest that information about different types of object properties are stored in different brain regions. Moreover, evidence suggests that sensory and motor-based object properties are stored within sensory and motor systems, respectively. I now turn to studies that forge a closer link between these property-based networks, perceptual and motor processes, and object concepts. These studies show that the regions associated with representing object properties are differentially engaged as a function of object category membership.

Converging evidence from monkey neurophysiology, neuropsychology, and functional brain imaging has established that object recognition is critically dependent on the ventral occipitotemporal processing stream (see Grill-Spector & Malach 2004 for review). In addition, functional brain imaging studies of object recognition have provided compelling evidence that occipitotemporal cortex is not a homogeneous object-processing system, but rather has a fine-grained structure that appears to be related to object category. The most studied categories have been human faces, houses, animals, and tools (see reviews by Kanwisher et al. 2001, Martin 2001). Direct comparison of one object category with another has revealed distinct clusters of activity (e.g., the fusiform face area, FFA; parahippocampal place area, PPA) (**Figure 1**). In addition, pattern analysis techniques have identified distinct object category-related patterns of activity that discriminate between relatively large numbers of object categories (Cox & Savoy 2003, Haxby et al. 2001, Spiridon & Kanwisher 2002). These object category-related patterns extend over a large expanse

of occipitotemporal cortex, are stable both within and between subjects, and can be identified even when subjects freely view complex scenes (i.e., while watching a movie; Bartels & Zeki 2004, Hasson et al. 2004).¹

Chao et al. (1999) provided evidence that category-related clusters of activity in occipitotemporal cortices associated with viewing object pictures are also seen when subjects engage in a verbal conceptual processing task. Perceptual processing was evaluated using passive viewing and delayed match-to-sample with pictures of animals, tools, faces, and houses; conceptual processing was evaluated using silent picture naming and a property verification task probing knowledge of animals and tools denoted by their written names. The main findings were that perceiving animals (as well as faces) showed heightened, bilateral activity in the more lateral region of the fusiform gyrus (see Grill-Spector 2003 for additional evidence that faces and animals selectively activate the lateral region of the fusiform gyrus including the FFA, and Grill-Spector et al. 2004 for evidence that this activity is significantly correlated with identifying faces and birds but not other objects). In contrast, tools showed heightened bilateral activity in the medial region of the fusiform gyrus (**Figure 2**). Importantly, the same lateral/medial fusiform gyrus distinction between animals and tools was observed for the property verification task. For example, a region in the lateral portion of the fusiform gyrus that was more active when verifying properties of animals than tools was also more active when viewing pictures of animals than tools (Chao et al. 1999). Thus, consistent with the property production data reviewed above,

¹The significance of this widespread activity has been the subject of considerable debate. In one view, information about a single category like faces or houses is restricted to relatively discrete areas. In the other view, information about faces, houses, and all other objects is distributed throughout the ventral occipitotemporal object-processing stream. Discussion of this important topic is outside the scope of this review (see Haxby et al. 2001, Spiridon & Kanwisher 2002).

pSTS: posterior superior temporal sulcus

these data provide support for an overlap between perceptual and conceptual neural processing systems.

Direct comparison of animals and faces revealed fine-grained differences between them, as well (see Chao et al. 1999 for details). For example, viewing pictures of animals produced more widespread activity than did viewing pictures of faces. This is not surprising given that different human faces are much more homogeneous in visual form than animals. Moreover, faces denote a single basic-level concept, whereas stimuli used to denote animals contain multiple exemplars, each with a specific basic-level name. Nevertheless, relative to manmade objects, activity was focused on the lateral region of the fusiform gyrus for both faces and animals (Chao et al. 1999). Thus, although every object concept must have a distinct neural representation, there appears a broad distinction between animate agents and manmade manipulable objects in the lateral and medial portions of the fusiform gyrus, respectively. The recent demonstration that human bodies are represented adjacent to the representation of faces in the lateral portion of the fusiform gyrus is consistent with this view (Peelen & Downing 2005, Schwarzlose et al. 2005; see also Cox et al. 2004).

Chao et al. (1999) also reported category-related differences in lateral temporal cortex associated with retrieving action properties as reviewed above. Specifically, viewing and naming pictures, and word reading during property verification, elicited enhanced activity in left pMTG for tools and in the posterior region of superior temporal sulcus (pSTS) for animals, stronger in the right than left hemisphere (**Figure 2**).

Similar patterns of object category-related activity in ventral and lateral regions of posterior temporal cortex have now been observed using a range of stimuli (pictures, written names, object-associated sounds, heard names). In ventral temporal cortex, enhanced activity in the lateral region of the fusiform gyrus (including the FFA) has been found

using naming, basic level categorization, or semantic decision tasks with animal pictures and/or their written names by Chao et al. (2002), Devlin et al. (2005), Mechelli et al. (2006), Okada et al. (2000), Price et al. (2003), Rogers et al. (2005), and Wheatley et al. (2005). Enhanced activity in the medial fusiform gyrus using tool pictures and/or their written names has been reported by Chao et al. (2002), Devlin et al. (2005), Mechelli et al. (2006), Noppeney et al. (2006; also in response to spoken names), and Whatmough et al. (2002).

In posterior lateral temporal cortex, enhanced activity in pMTG in response to pictures and/or the written names of tools was reported by Chao et al. (2002), Creem-Regehr & Lee (2005; also when imagining tools), Devlin et al. (2005), Kable et al. (2005), Kellenbach et al. (2003), Mechelli et al. (2006), Noppeney et al. (2005, 2006; also in response to spoken names), Phillips et al. (2002), and Tranel et al. (2005a,b). Finally, Lewis et al. (2004, 2005) and Tranel et al. (2005a) have reported increased activity in left pMTG for naming tool sounds relative to naming sounds associated with specific animals, and Noppeney et al. (2005) reported increased activity in right pSTS for making semantic judgments about spoken words referring to whole body movements (e.g., swimming, climbing) versus answering questions probing knowledge of hand movements.

Compelling evidence that these patterns of neural activity reflect retrieval of object information comes from a recent study of object learning and free recall (Polyn et al. 2005). Subjects learned lists composed of labeled photographs of famous people, places, and common manipulable objects. Pattern classifier techniques based on neural activity during learning revealed distinct patterns of category-related activity that occurred several seconds prior to recall. Moreover, and in agreement with the studies reviewed above, activity in the lateral fusiform (as well as right pSTS) best predicted recall of famous people, activity in left pMTG and left posterior

parietal cortex (see below) best predicted recall of manipulable objects, and activity in the PPA best predicted recall of famous places. These findings suggest that accessing a particular item from memory depends on reactivating the pattern of neural activity that occurred during learning. In posterior temporal cortex, the pattern of activity is dependent on, or at least is a reflection of, the item's category membership.

The locations of the category-related activations reported in these studies show a remarkable degree of intersubject consistency despite marked differences in processing task, stimulus format (verbal, nonverbal), and modality of presentation (visual, auditory). However, these factors are clearly relevant. Indeed, studies by Price and colleagues show that category-related neural activity in posterior temporal cortex can be modulated by a host of stimulus and task-related variables (Mechelli et al. 2006; Noppeney et al. 2005, 2006; Price et al. 2003; Rogers et al. 2005). Nevertheless, although neural activity is modulated by these contextual factors, the spatial arrangement of the category-related regions does not change. It is, however, important to note that the organization principles that determine the between-subject consistency of this spatial arrangement remain to be determined (Martin 2006).

Linking Category-Related Representations to Form and Motion Perception

One interpretation of these findings is that differential activity in the fusiform gyrus and other regions of ventral temporal cortex reflects category-related differences in stored representations of form (and form-related properties like color), while differential activity in lateral temporal areas reflect category-related differences in the representation of motion properties (Chao et al. 1999; Kable et al. 2005; Martin et al. 1995, 1996).

Evidence for these claims was provided by Beauchamp and associates in a series of studies

using static and moving depictions of biological motion (people performing identifiable movements such as sitting, jumping, walking) and manipulable objects (typical tools like a hammer, saw, or scissors, moving in their characteristic way when being used) (Beauchamp et al. 2002, 2003). As in the studies reviewed above, different patterns of category-related activity were noted in the fusiform gyrus, with the lateral portion more responsive to images of people and the medial portion more responsive to tools. However, these regions of ventral temporal cortex responded similarly to moving and static objects. Thus, ventral temporal cortex showed strong category effects, but these effects were not modulated by motion (**Figure 3**).

In contrast, lateral temporal areas responded more strongly to moving than to static images, supporting the hypothesis that lateral temporal cortex is the cortical locus of complex motion processing. Moreover, category-related differences were also observed. pSTS showed a stronger response to people in motion compared with tools in motion, consistent with a large number of monkey neurophysiological (e.g., Oram & Perrett 1994) and human functional brain imaging studies of biological motion (e.g., Grossman & Blake 2001, Pelphrey et al. 2005, Puce et al. 1998). In contrast, pMTG showed a stronger response to tool than to human motion, thus suggesting that these motion-sensitive regions of lateral temporal cortex may have a category-based organization (**Figure 3**).

Category-related activity in ventral (fusiform gyrus) and lateral temporal cortex was also found using more abstract motion stimuli of people and tool motion (point-light displays) (Beauchamp et al. 2003). pSTS and the lateral fusiform gyrus responded more to point-light depictions of people than tools (see also Grossman & Blake 2001, 2002), whereas pMTG and the medial portion of the fusiform gyrus (as well as left parietal and ventral premotor cortices) responded more to tools than to people. Importantly, responses in lateral temporal regions were nearly

Biological motion: motion of animate agents characterized by highly flexible, fully articulated motion vectors, in contrast to the rigid, unarticulated motion vectors associated with most tools.

IPS: intraparietal sulcus

VPMC: ventral premotor cortex

equivalent to real object and point-light displays, suggesting that visual motion, not color or form, is a key determinant of activity in lateral temporal cortex. In contrast, in ventral temporal cortex, the response to the point-light displays was significantly reduced relative to real object videos (Beauchamp et al. 2003).

Taken together, these studies provide evidence for both category- and property-related differences in ventral and lateral temporal cortices. Adding motion to depictions of tools and people had little effect on the category-related responses in the fusiform gyrus, but markedly increased responses in lateral temporal cortex (Beauchamp et al. 2002). Eliminating form and color from moving stimuli (point-light displays) had little effect on the category-related responses in lateral temporal regions, but markedly reduced the response in ventral temporal cortex (Beauchamp et al. 2003). These findings suggest that category-related effects may reflect, at least in part, differences in object form (ventral temporal cortex) and object motion (lateral temporal cortex). In lateral temporal cortex, pSTS was selectively responsive to the fully articulated, flexible motion associated with animate entities; pMTG was selectively responsive to the rigid, unarticulated motion associated with manmade objects (Beauchamp et al. 2002, Beauchamp & Martin 2006).

Beyond Form and Motion: Representing Higher-Order Concepts

In 1944, Heider and Simmel showed that simple geometric shapes in motion are readily interpreted as depicting causal interactions, goals, intentions, and the like (Heider & Simmel 1944). Several studies (Castelli et al. 2000, Martin & Weisberg 2003, Schultz et al. 2003) have used displays similar to those of Heider and Simmel to show that the category-related neural activity can be elicited depending on how these stimuli are interpreted. Animations

interpreted as depicting social interactions (e.g., hide-and-peek, Schultz et al. 2003; sharing, Martin & Weisberg 2003) or mental states (e.g., persuading, mocking; Castelli et al. 2000) elicited activity in regions linked to perceiving and knowing about the form (lateral fusiform gyrus) and motion (pSTS) of animate agents, and in regions associated with detecting emotional and biologically salient stimuli (the amygdala; see Phelps 2006 for review) and understanding mental states (medial prefrontal cortex; see Frith & Frith 2006 for review). In contrast, animations interpreted as depicting mechanical interaction (e.g., billiard balls, pinball machine) elicited heightened activity in regions linked to representing the form (medial fusiform gyrus) and motion (pMTG) of manipulable objects (Martin & Weisberg 2003) (**Figure 4**). Thus, different patterns of activity were associated with the meaning assigned to the stimuli. Moreover, because the same geometric forms were used in both the social and mechanical animations, these results cannot be due to bottom-up processing of the visual stimuli. They must reflect top-down influences.

Linking the Representation of Tools to Motor Systems

The relationship between activity in the dorsal stream—particularly in left posterior parietal cortex centered on intraparietal sulcus (IPS) and left ventral premotor cortex (VPMC)—and the representation of manmade, manipulable objects has been an active field of investigation (for reviews, see Culham & Valyear 2006, Johnson-Frey 2004). Naming photographs of tools, or even simply viewing these pictures, has been shown to elicit enhanced activity in left VPMC and IPS, relative to viewing animals, houses, and faces, and relative to naming pictures of animals (Chao & Martin 2000). These findings are consistent with data from monkey neurophysiology showing that neurons in ventral premotor and parietal cortices respond both when monkeys grasp objects and when they

see objects that they have had experience manipulating (e.g., Jeannerod et al. 1995). Recent functional brain imaging studies in humans have shown that these dorsal regions, along with pMTG, are active when subjects perform a wide range of tasks probing knowledge about tools and their related actions (see Tranel et al. 1997, 2003 for evidence that damage to either left pMTG, IPS, or VPMC results in impaired knowledge about tools and their action).

Enhanced activity in left IPS has been reported for judging object similarity based on how objects are manipulated (are a keyboard and a piano manipulated in the same way?) versus similarity based on more verbally mediated functional information (do a cigarette lighter and a match serve the same function?) (Boronat et al. 2005; see Buxbaum & Saffran 2002 for patient data, and Kellenbach et al. 2003 for related neuroimaging data). Other reports have shown enhanced activity in left IPS and VPMC for viewing and imagining grasping common tools versus novel, graspable objects (Creem-Regehr & Lee 2005), making semantic decisions about tool-related actions (Noppeney et al. 2005), holding manipulable, but not nonmanipulable, objects in working memory (Mecklinger et al. 2002), naming tools versus animals (Chao et al. 2002; see Kan et al. 2006 for evidence that left VPMC activity when naming tools varies with motor experience using those tools) and for naming tool-associated sounds versus animal sounds (Lewis et al. 2004, 2005). These findings show that retrieving information about object function engages regions of the cortex that are also active when objects are used. Moreover, as with the previously reviewed studies of object categories, this information is automatically accessed when these objects are identified, regardless of stimulus modality (visual, auditory) or format (verbal, nonverbal).

Learning About Object Properties

The findings reviewed above suggest that it should be possible to predict where in the

brain learning-related changes occur when subjects acquire property information about novel objects. Weisberg et al. (2006) addressed this possibility by giving subjects extensive training using novel objects to perform specific, tool-like tasks. Subjects were scanned while performing a simple visual matching task with pictures of these objects. Prior to training, neural activity during object matching was limited to the ventral occipitotemporal object-processing stream, consistent with previous reports on viewing nonmeaningful objects (e.g., van Turennout et al. 2000). However, after training, activations in ventral temporal cortex became more focal. Specifically, whereas activity prior to training was widespread in the fusiform gyrus, after training activity was markedly reduced in the more lateral parts of the fusiform (i.e., regions preferring animate objects like animals and faces), and markedly increased in the medial portion of the fusiform gyrus associated with identifying common tools. In addition, after training, new activations emerged in the network of left hemisphere regions previously linked to naming and retrieving information about tools and their related actions. Specifically, robust activity was now seen in the left pMTG, IPS, and premotor cortices. These changes occurred even though the task during scanning was purely perceptual. Thus, hands-on experience with the objects seemed to have augmented their representations with detailed information about their appearance (supported by changes in the fusiform gyrus), and with information about the motion (pMTG) and motor-related properties (left IPS, premotor cortex) associated with their use.

Grossman et al. (2004) reported a similar type of learning-related change for perceptual learning about animate objects. As noted above, viewing point-light displays of human forms elicits activity in the lateral fusiform gyrus (FFA) and pSTS. Subjects received extensive training that enabled them to accurately perceive point-light displays embedded in visual noise. After training, enhanced activity was observed in the FFA

and pSTS relative to pretraining levels. These activations were seen in response to trained items and novel noise-embedded point-light displays, indicating that learning had generalized to new exemplars (see also Weisberg et al. 2006). Moreover, the amount of activity in these regions was directly related to behavioral performance (Grossman et al. 2004).

Whereas in these studies subjects were trained on visuomotor (Weisberg et al. 2006) and perceptual (Grossman et al. 2004) tasks, James & Gauthier (2003) showed that similar learning-related effects can be achieved through verbal learning. Subjects were trained to associate verbal labels referring to auditory properties (e.g., squeaks, roars) and action properties (hops, jumps) to novel animate-like stimuli (“greebles”). After training, viewing greebles associated with auditory properties elicited enhanced activity in a region involved in the early stages of auditory processing (i.e., in the superior temporal gyrus, as defined by an auditory localizer task), and viewing greebles associated with actions elicited enhanced activity in pSTS (defined by viewing point-light displays) (James & Gauthier 2003).

Taken together, these studies demonstrate that the locus of learning-related cortical plasticity is highly constrained by the nature of the information to be learned. Learning to associate novel objects with specific tool-like functions produced enhanced activity in regions associated with the form, motion, and use of common tools (Weisberg et al. 2006), learning to perceive moving dot patterns as people in motion resulted in enhanced activity in regions associated with the form and motion of animate objects, and learning to associate verbal information denoting auditory and motion properties elicited enhanced activity in auditory and biological motion processing areas. These changes occurred even though the tasks during scanning required only visual matching of static images. There was no requirement to explicitly retrieve information about how novel objects were manipulated (Weisberg et al. 2006) or about the auditory

and motion properties associated with greebles (James & Gauthier 2003), thus indicating that these newly acquired object-property associations were automatically retrieved when the objects were seen again.

CONCLUSION

The evidence reviewed in this chapter indicates that object properties are stored throughout the brain, with specific sensory and motor-based information stored in their corresponding sensory and motor systems. The evidence further suggests the possibility of dedicated neural circuitry for perceiving and knowing about animate objects and common tools. For animate objects, this circuitry includes two regions in posterior temporal cortex: the lateral portion of the fusiform gyrus and pSTS for representing their visual form and motion, respectively. In addition, evidence is mounting that the amygdala also plays a prominent role in this circuitry, perhaps as a means of alerting the organism to a potentially threatening predator or prey (e.g., Whalen 1998). Indeed, recent studies suggest that the human amygdala responds more to stimuli denoting animals than tools, irrespective of stimulus type (pictures, written words, associated sounds, and heard words; Yang et al. 2005). Other regions, such as medial prefrontal cortex, may also be prominently involved, especially when retrieving information about the mental states of others (e.g., Mitchell et al. 2002). For common tools, the neural circuitry includes the medial portion of the fusiform gyrus as well as pMTG, IPS, and VPMC, all within the left hemisphere, assumed to represent their visual form and action properties (motion and manipulation).

In addition to the findings discussed in this chapter, evidence for other object category-related neural circuits has also been reported. In particular, a large number of studies have shown that the PPA is selectively responsive to depictions of places, buildings (see Kanwisher et al. 2001 for review), and on

a more conceptual level, to objects strongly associated with environmental contexts (e.g., traffic light, beach chair; Bar & Aminoff 2003). Other studies have linked number concepts to neural circuitry that includes a discrete region of the left IPS (reviewed in Dehaene et al. 2003, but see Shuman & Kanwisher 2004). Finally, representations of food (especially high-caloric food) have been associated with circuitry that includes areas involved in taste perception (insula), reward (posterior orbital frontal cortex), and affective response (amygdala) (Killgore et al. 2003, Simmons et al. 2005).

Many questions remain to be resolved. These include an understanding of how the

nodes of the neural circuitry described here are bound together (Damasio 1989) and how activity within the network is coordinated in the service of conceptual processing (Kraut et al. 2002). Also needed is a better understanding of how object conceptual and lexical representations are linked (Damasio et al. 2004). Equally important will be to identify the neural systems that house our vast store of nonsensory-motor, verbally mediated, encyclopedic knowledge about objects. Finally, specifying how object property-based circuits interact with prefrontal cortex to create highly flexible and novel categories is an important topic for future investigations (Freedman et al. 2003).

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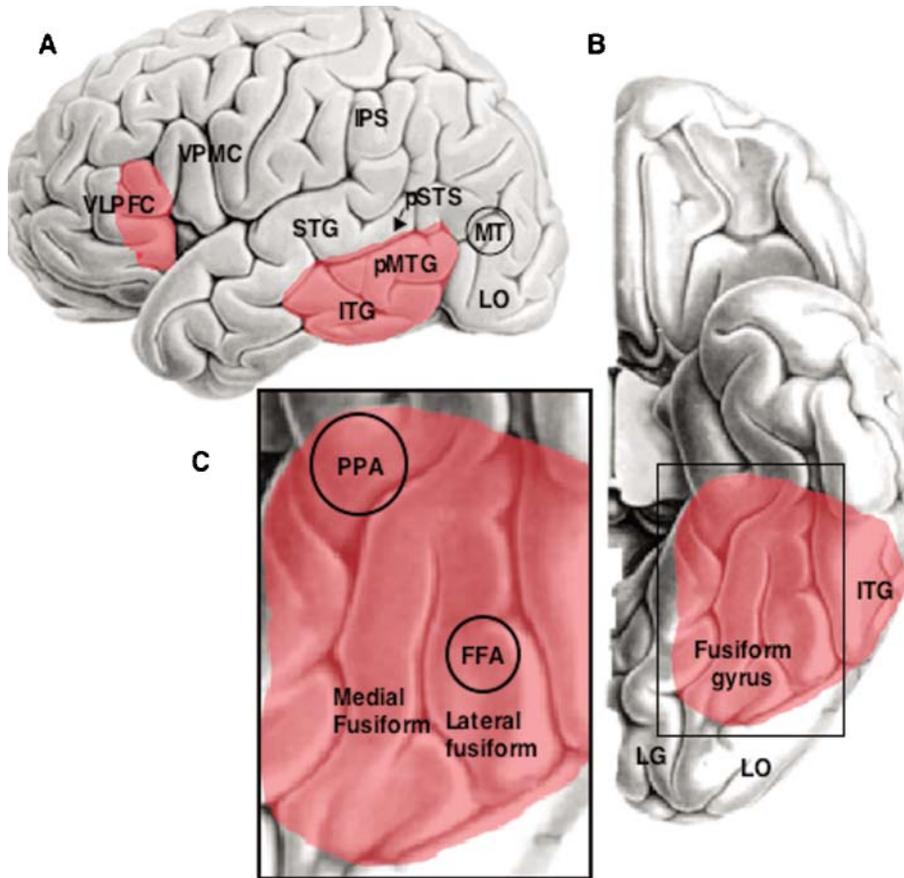


Figure 1

Schematic lateral view of the left hemisphere (*A*) and ventral view of the right temporal and frontal lobes (*B*). The fusiform gyrus is shown in greater detail in (*C*). Regions in red show approximate location of areas typically involved in conceptual processing tasks, especially with concrete objects. ITG, inferior temporal gyrus; LG, lingual gyrus. See text for other abbreviations.

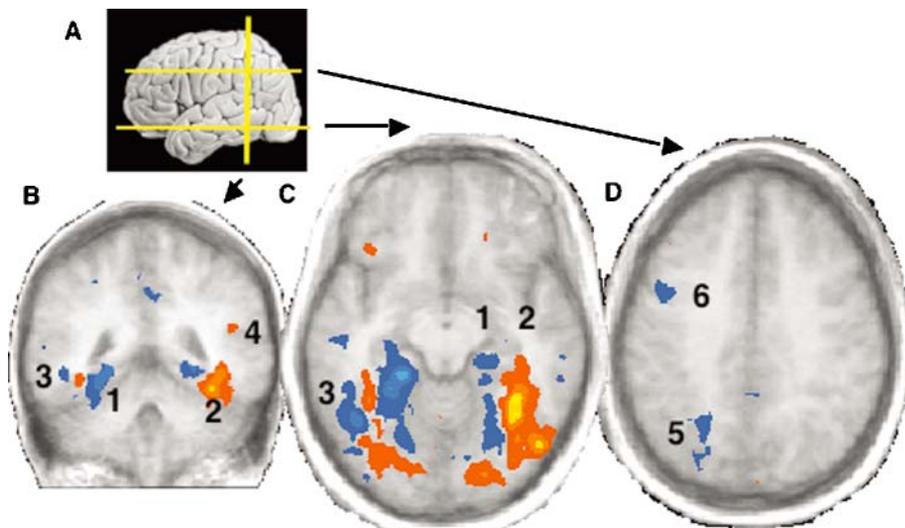


Figure 2

Group fMRI activation map showing the location of hemodynamic activity associated with naming pictures of animals (red-yellow spectrum) and pictures of tools (blue-green spectrum). *Yellow lines* on lateral view of the brain (*A*) indicate location of the coronal (*B*) and axial (*C*, *D*) slices. (*1*) Medial region of the fusiform gyrus; (*2*) lateral region of the fusiform gyrus; (*3*) middle temporal gyrus; (*4*) superior temporal sulcus; (*5*) left intraparietal sulcus; (*6*) left ventral premotor cortex. Adapted from Chao et al. 2002.

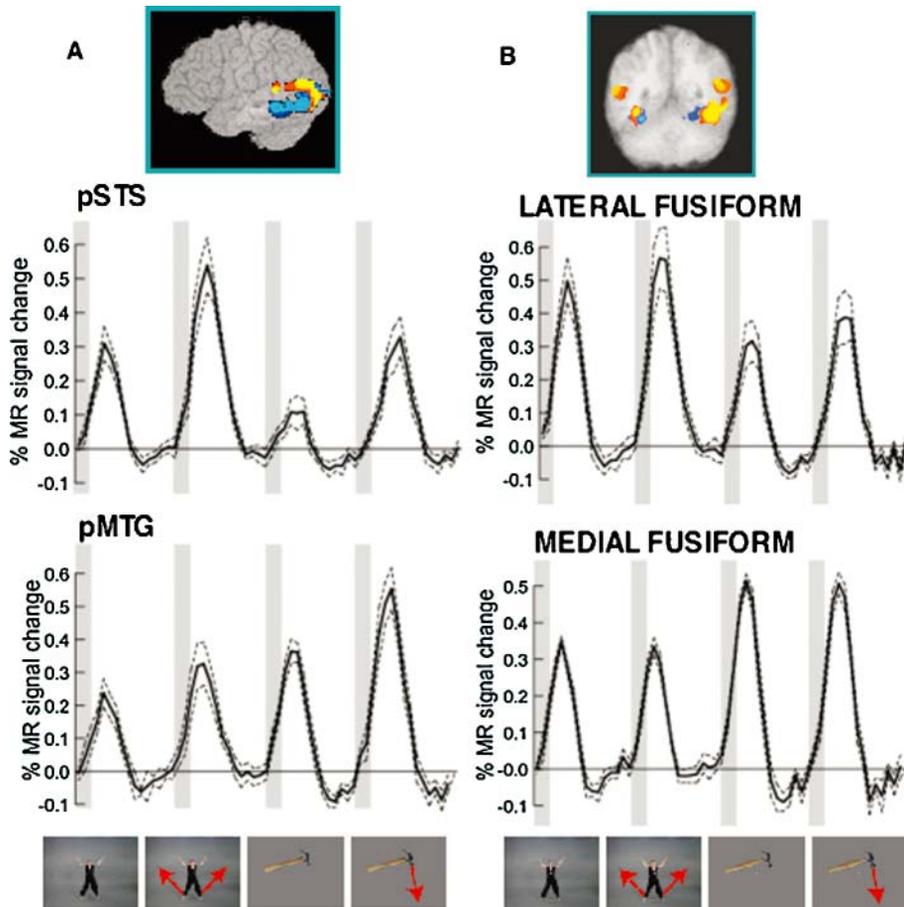


Figure 3

(A) Lateral view of the left hemisphere showing location of enhanced activity for identifying static and moving images of people in superior temporal sulcus (*yellow*) and tools in the middle temporal gyrus (*blue*). (B) Coronal view showing location of enhanced activity for identifying static and moving images of people in lateral portion of the fusiform gyrus (*yellow*), and tools in the medial fusiform gyrus (*blue*). Beneath each brain view are group-averaged hemodynamic responses showing differential activity for static and moving images in each of these regions. Note that lateral cortical areas (A) show category and motion effects. Ventral regions (B) show only category effects. Vertical gray bars indicate stimulus presentation (2 sec). *Dashed lines* indicate ± 1 SEM. Adapted from Beauchamp et al. 2002.

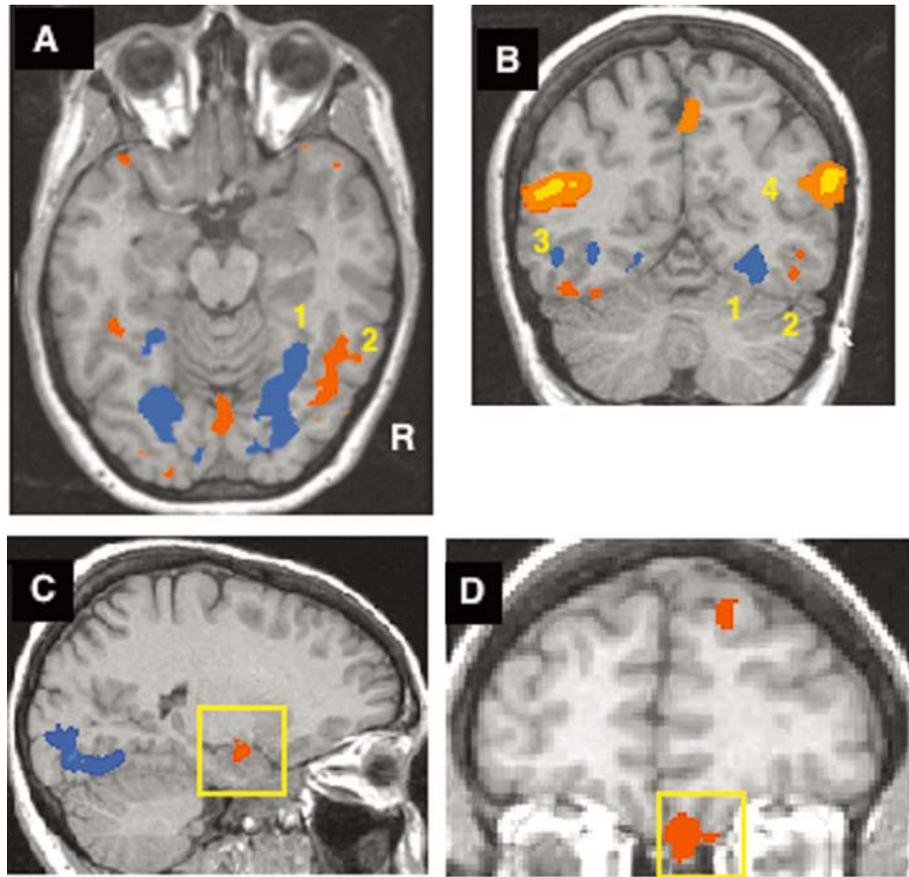


Figure 4

Group fMRI activation map showing axial view (*A*) and coronal view (*B*) of regions with greater activity associated with social (*red*) and mechanical (*blue*) interpretations of moving geometric shapes. (*1*) Medial fusiform gyrus; (*2*) lateral fusiform gyrus; (*3*) middle temporal gyrus; and (*4*) superior temporal sulcus (compare to **Figure 2**). *Yellow squares* indicate right amygdala (*C*) and ventromedial prefrontal region (*D*) more active for social than mechanical vignettes. Adapted from Martin & Weisberg 2003.