

Neural Substrates of Action Event Knowledge

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Abstract

■ Human concepts can be roughly divided into entities (prototypically referred to in language by nouns) and events (prototypically referred to in language by verbs). While much work in cognitive neuroscience has investigated how the brain represents different categories of entities, less attention has been given to the more basic distinction between entities and events. We used functional magnetic resonance imaging to examine brain activity while subjects performed a conceptual matching task that required them to access knowledge of objects and actions, using either pictures or words. Since action events involve movement through space, we hypothesized that accessing knowledge of actions would cause greater activation in brain regions involved in motion or spatial processing. In comparison to objects, accessing knowledge of

actions through pictures was accompanied by increased activity bilaterally in the human MT/MST and nearby regions of the lateral temporal cortex. Accessing knowledge of actions through words activated areas just anterior and dorsal to area MT/MST on the left, within the posterior aspect of the middle and superior temporal gyri. We propose that the lateral occipital–temporal cortex contains a mosaic of neural regions that processes different kinds of motion, ranging from the perception of objects moving in the world to the conception of movement implied in action verbs. The lateral occipital–temporal cortex mediates the perceptual and conceptual features of action events, similar to the way that the ventral occipital–temporal cortex processes the perceptual and conceptual features of entities. ■

INTRODUCTION

Human concepts (and the words that refer to them) seem to fall into a manageable and consistent set of categories. A fundamental conceptual distinction is between the categories of entities and events. Entities are things such as people, animals, and objects, and are prototypically referred to in language by nouns. Events are what happens to things, including actions (spatial and temporal changes to entities), prototypically referred to in language by verbs, and thematic relationships (who does what to whom), prototypically referred to in language by the syntactic location of nouns.

That human concepts seem to fall into distinct categories suggests that the brain may represent these categories differently. Cognitive neuroscientists have considered this possibility over the past 25 years. Most of this work has focused on how the brain represents different categories of concrete entities (Gainotti, Silveri, Daniele, & Giustolisi, 1995). For example, brain damage may produce the selective disruption of knowledge about living things or animate objects (Caramazza & Shelton, 1998; Tranel, Damasio, & Damasio, 1997; Hillis & Caramazza, 1991; Hart, Berndt, & Caramazza, 1985; Warrington & Shallice, 1984). Though less common, brain damage may also produce the reverse dissociation, loss of knowledge about man-made arti-

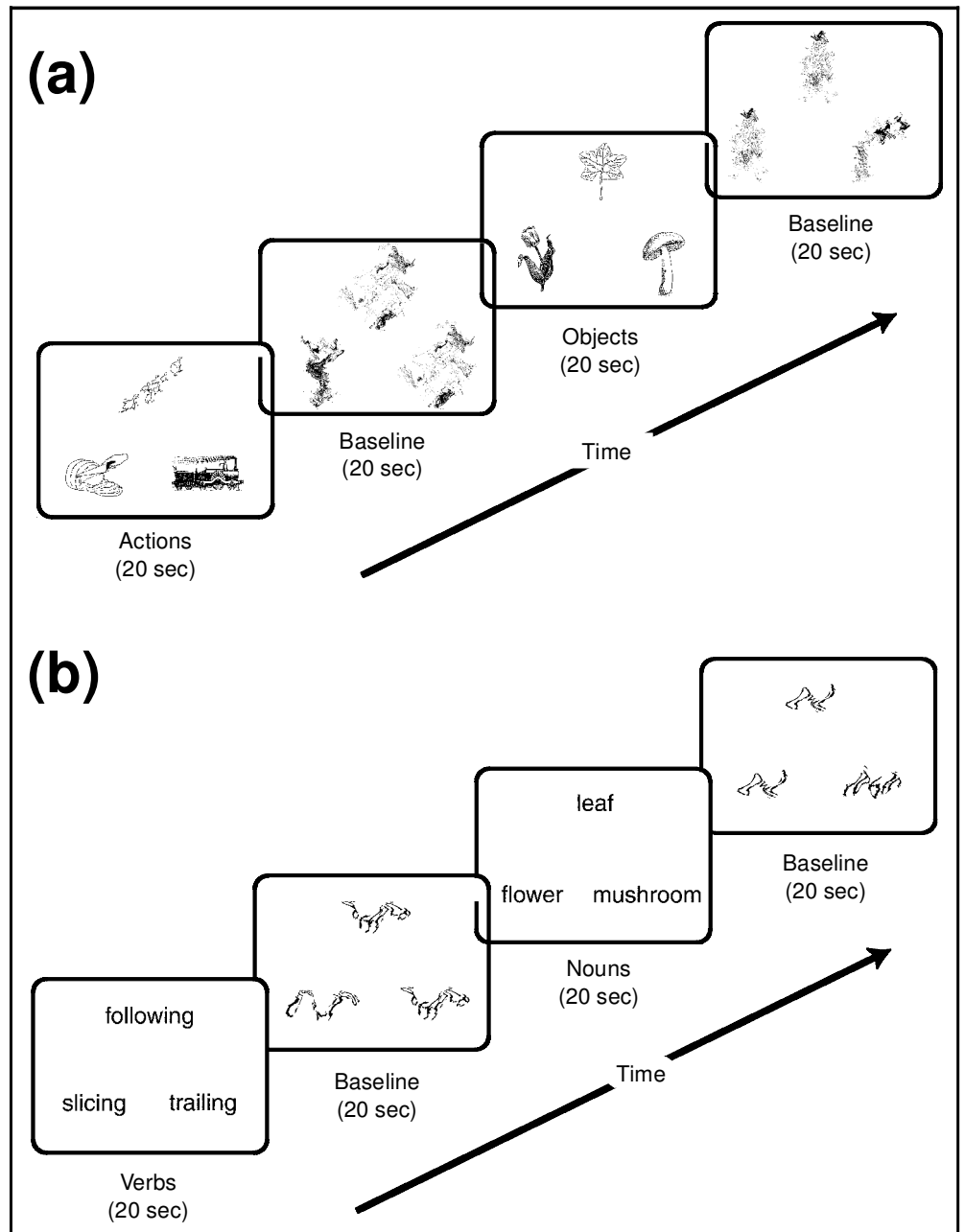
facts or inanimate objects (Tranel et al., 1997; Sacchett & Humphreys, 1992; Hillis & Caramazza, 1991; Warrington & McCarthy, 1983). Functional neuroimaging has provided converging evidence that distinct neural networks represent living things and man-made artifacts, using animals and tools as examples of each category (Chao, Haxby, & Martin, 1999; Perani et al., 1999; Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin, Wiggs, Ungerleider, & Haxby, 1996). A common explanation for these results is that knowledge of animate and inanimate objects incorporates different features of those objects (Saffran & Schwartz, 1994). Knowledge of animate objects depends more on visual features such as shape and color, while knowledge of inanimate objects depends more on functional features such as characteristic uses. According to this view, distinct neural structures are not specialized for processing different semantic categories on their own, rather they are specialized for processing particular features (such as color or shape) which might be more critical for knowledge of particular semantic categories (although see Caramazza & Shelton, 1998 for an opposing view).

Despite the wealth of research on how the brain represents different categories of concrete entities, less attention has been given to the more basic distinction between entities and events. Some patients with brain damage may have selective difficulty in naming pictures

of actions in comparison to pictures of objects, while others may have object-naming deficits with spared action naming (Berndt, Haendiges, Mitchum, & Sandson, 1997; Berndt, Mitchum, Haendiges, & Sandson, 1997; Silveri & Di Betta, 1997; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Damasio & Tranel, 1993; McCarthy & Warrington, 1985). For at least some of these patients, the deficit may be at the conceptual level, rather than simply one of lexical retrieval (Silveri & Di Betta, 1997; Daniele et al., 1994; McCarthy & Warrington, 1985). Conceptual deficits for event knowledge have also been demonstrated within a subset of agrammatic aphasic patients who demonstrate difficulties with

understanding thematic relations in sentences (Chatterjee, Southwood, Calhoun, & Thompson, 1999). Behavioral data suggest that knowledge of action events incorporates spatial features similar to the way that knowledge of entities might incorporate features of shape or color or functional uses (Chatterjee, Maher, Gonzalez Rothi, & Heilman, 1995; Chatterjee, Maher, & Heilman, 1995; Chatterjee, Southwood, & Basilico, 1999; Maher, Chatterjee, Gonzalez Rothi, & Heilman, 1995), and linguists have made a similar argument on theoretical grounds (Talmy, 1996; Jackendoff, 1990). However, the neural substrate mediating this knowledge of events is not well understood.

Figure 1. Schematic of the experimental paradigm. (a) Conceptual matching task with pictures and corresponding baseline task. (b) Conceptual matching task with words and corresponding baseline task.



A consideration of the spatial features of action events suggests several hypotheses about cortical regions more important for the knowledge of events than entities. Events, unlike entities, often involve motion through space and may form a conceptual category where linguistic and spatial representations make contact (Chatterjee, 2001). One hypothesis is that action concepts depend on motion features represented by visual motion areas (MT/MST). A second hypothesis is that action concepts involve spatial maps represented by the parietal cortex. The third hypothesis is that action concepts (because they can involve self-movement) engage motor engrams represented by the motor and premotor cortex. Finally, it is possible that the conceptual distinction between objects and actions is not realized at a large-scale neural level.

The available evidence bearing on these hypotheses is not conclusive. In a large series of brain-damaged patients, action-naming deficits were most often associated with left inferior frontal or left lateral occipital-temporal lesions (Kemmerer & Tranel, 2000). Some investigators have found that left prefrontal damage specifically impairs action naming more than object naming (Daniele et al., 1994; Damasio & Tranel, 1993), although others have disputed this claim (Tyler, Russell, Fadili, & Moss, 2001; Bird, Howard, & Franklin, 2000). In a recent PET study, action naming produced greater activity than tool naming in bilateral occipital-temporal cortex near the location of human MT/MST (Damasio et al., 2001). Thus, studies of action naming provide some support for the “motor” and “motion” hypotheses, although interpretation of these studies is complicated by the fact that naming requires lexical retrieval processes as well as access to conceptual knowledge. In contrast, Tyler et al. (2001) found no differences between nouns and verbs in a recent PET study. Using a lexical decision and a semantic categorization task, they found robust activation extending from the left inferior frontal cortex to the inferior temporal lobe, but they did not find any differences as a function of word class. Consequently, they propose that conceptual knowledge is represented in distributed neural systems, but that this knowledge is not differentiated by conceptual category within these networks.

We used functional magnetic resonance imaging (fMRI) to investigate the various hypotheses about cortical regions preferentially involved in the conceptual knowledge of actions over objects. Two groups of subjects performed a matching task with line drawings (Figure 1). This task required subjects to access conceptual knowledge about objects and actions, with minimal demands on lexical retrieval processes. Three pictures were presented simultaneously, and subjects decided which of two pictures at the bottom of the stimulus was most related to the one at the top. In different blocks of the trials, the pictures were of objects or actions (Figure 1a). If action concepts are

preferentially mediated by premotor, parietal, or posterior temporal areas, then these areas should show more activity during matching action pictures than matching object pictures.

The second group of subjects also performed the same matching task with words instead of pictures (Figure 1b). In this case, the object words were nouns and the action words were verbs. The word-matching task allowed us to test for differences in activity depending on whether conceptual knowledge of actions was accessed by pictures or by words. If conceptual knowledge of actions is not material-specific (pictures vs. words), then areas involved in action picture matching should also be more active during verb matching than during noun matching. These tasks also allowed us to test for areas involved in making conceptual judgments, irrespective of conceptual category (objects or actions) or material (pictures or words).

RESULTS

Behavioral Results

For the first group of 5 subjects, there was no significant difference between object and action picture matching in either accuracy or reaction time ($82 \pm 4\%$ and 1541 ± 78 msec for objects, $78 \pm 3\%$ and 1636 ± 89 msec for actions). For the second group of 6 subjects, there was no significant difference in accuracy between object and action picture matching ($79 \pm 2\%$ for objects and $76 \pm 4\%$ for actions), but reaction times for action matching were slower [1516 ± 50 msec for objects and 1720 ± 80 msec for actions, $t(5) = 2.9$, $p = .03$]. For this group, there were also no significant differences in either accuracy or reaction time for word matching ($87 \pm 4\%$ and 1495 ± 69 msec for nouns and $91 \pm 3\%$ and 1469 ± 65 msec for verbs).

Imaging Results

We conducted all of our analyses of the imaging data in each individual subject without normalization to a common space, and then tested whether the effects obtained in individual subjects were consistent across a group of subjects (see Methods). Our first group of five subjects performed the conceptual matching task with pictures. In comparison to the baseline task, conceptual matching of object or action pictures activated bilateral areas in the inferior frontal, premotor, inferior parietal, inferior temporal and occipital, and lateral temporal cortical areas in most of the subjects. Of these regions, the only areas that showed greater activation for actions than objects were lateral occipital-temporal regions near the location of human MT/MST.

To directly test the hypothesis that the MT/MST was involved, we identified the MT/MST in each of 6 subjects in a second group using a localizer scan

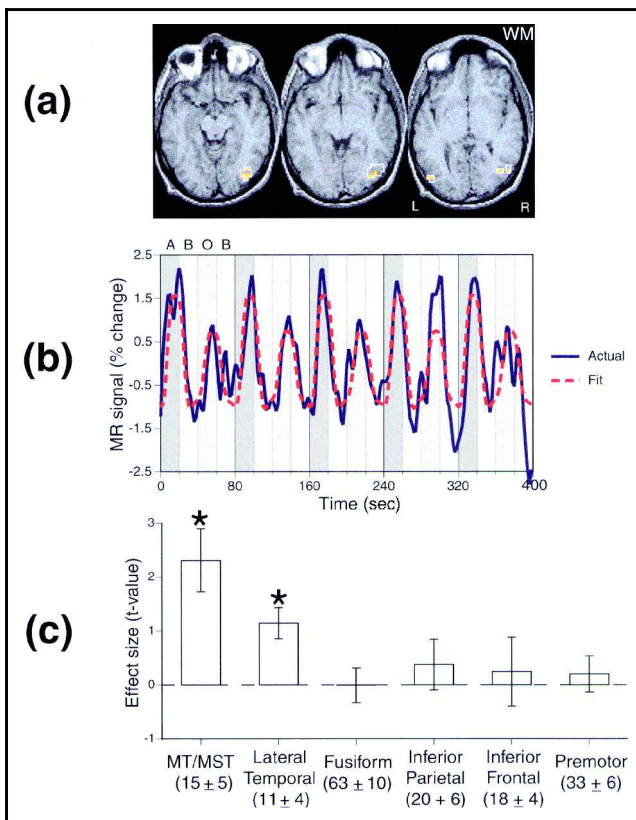


Figure 2. Brain areas showing greater activity during matching action pictures than during matching object pictures. In all anatomical images, the left side of the brain is shown on the left. (a) Three slices from a representative subject (WM) showing the location of voxels in the MT/MST with a significant main effect for picture matching (objects and actions) as compared to baseline ($p < .05$, one-tailed, corrected for multiple comparisons within ROI). Functional data are overlaid on T1 anatomical images. Active voxels are shown in yellow, and the ROI is outlined in white. (b) Data, averaged across the voxels in (a), showing greater activity during conceptual matching of action pictures. Solid lines indicate time course of MR signal and dashed lines indicate the fit of object- and action-matching covariates. Task blocks are labeled: A = action picture matching, B = baseline task, O = object picture matching. Data are filtered to remove low-frequency drift. (c) Average effect size across subjects ($n = 6$) for the action picture matching minus object matching comparison in different ROIs. Error bars represent the standard error of the mean. The numbers in parentheses are the average number of voxels in each ROI considered for this analysis (those significant for the main effect of picture matching minus baseline). Asterisks indicate that effect size is significantly different from zero ($p < .05$, two-tailed). ROIs are bilateral.

(see Methods) (Kourtzi & Kanwisher, 2000; Tootell, Reppas, Kwong et al., 1995). We successfully identified the MT/MST in both the right and the left hemispheres in all 6 subjects. The MT/MST was consistently located near the lateral extent of the occipital lobe (posterior to the anterior occipital sulcus) at the level of the lateral occipital sulcus, which separates the inferior and superior parts of the middle occipital gyrus. The average size of the MT/MST was 25 ± 5 voxels in the right hemisphere (range: 10–36) and 12 ± 3 voxels in the left hemisphere (range: 2–24 voxels). These subjects also performed the conceptual matching task

with pictures. Activity in the MT/MST bilaterally was indeed consistently greater for matching action pictures than matching object pictures across subjects, whether considering all voxels in the MT/MST [$t(5) = 4.6$, $p < .01$] or just those voxels with a significant main effect for the picture matching task (objects and actions) compared to baseline [$t(5) = 3.6$, $p = .02$, Figure 2a–b]. There was no correlation between the size of this effect and the size of the MT/MST across subjects ($R^2 = .19$).

To determine if other regions were differentially active for object or action picture matching, we defined 5 bilateral anatomical regions-of-interest (ROIs) based on the results in the first 5 subjects: inferior frontal gyri (Brodmann's areas 44, 45, and 47), premotor cortex

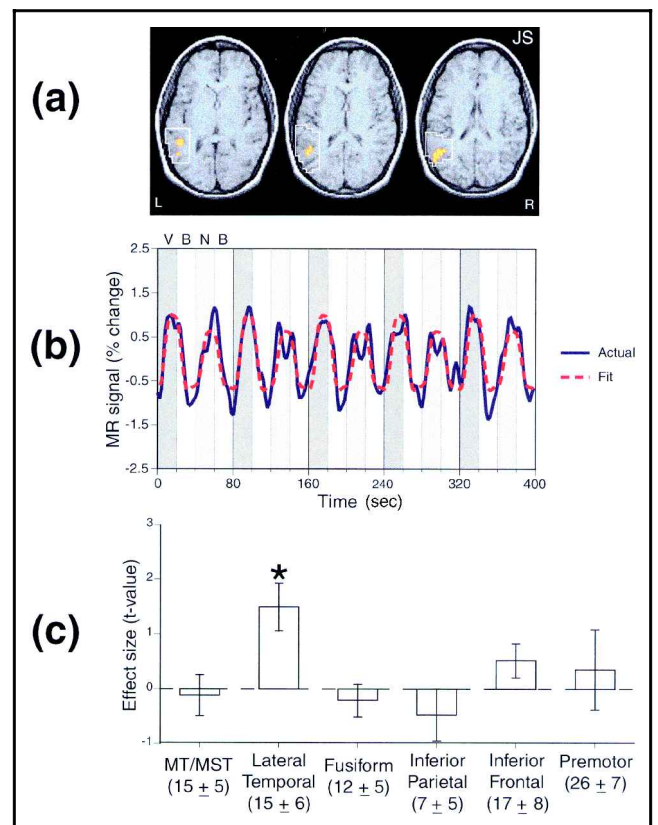
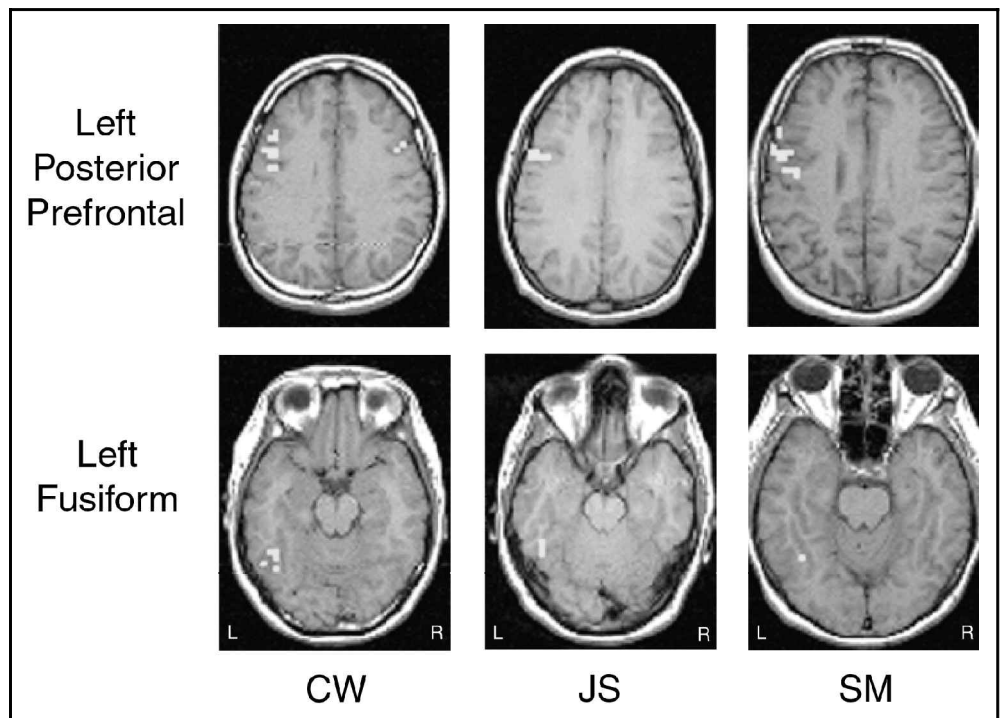


Figure 3. Brain area showing greater activity during matching action words (verbs) than during matching object words (nouns). (a–b) Data from a representative subject (JS) showing greater activity in the lateral posterior temporal cortex during conceptual matching of verbs. Same format as in Figure 2a–b. (c) Average effect size across subjects ($n = 6$) for the verb matching minus noun matching comparison in different ROIs. Error bars represent the standard error of the mean. The numbers in parentheses are the average number of voxels in each ROI considered for this analysis (those significant for the main effect of word matching minus baseline). Asterisk indicates that effect size is significantly different from zero ($p < .05$, two-tailed). Since no voxels in the MT/MST in any subject were significant for the main effect of word matching minus baseline, effect sizes in the MT/MST are shown for voxels that were significant for the main effect of picture matching minus baseline (for direct comparison to Figure 2). All other ROIs are restricted to the left hemisphere.

Figure 4. Brain areas showing significant activation during both the picture-matching and word-matching tasks. One slice from each of three subjects is presented, showing the location of voxels that were significantly active for both the picture matching (objects and actions) as compared to the baseline comparison and the word matching (nouns and verbs) as compared to the baseline comparison (both $p < .05$, one-tailed, corrected for multiple comparisons).



(Brodmann's area 6), fusiform gyrus, posterior middle and superior temporal gyri, and inferior parietal cortex (Brodmann's areas 39 and 40). In each ROI, we identified voxels within each subject that had significantly greater activity during the conceptual task (collapsing across object and action matching) compared to the baseline task. Combining data from all the active voxels within an ROI, we then examined the difference between action and object matching and tested whether this difference was consistent across subjects. Using this analysis, the only significant difference was in the posterior lateral temporal regions bilaterally, where activity was consistently greater for matching action pictures than matching objects [$t(5) = 3.6$, $p = .02$, Figure 2c].

These subjects also performed the conceptual matching task with words instead of pictures. In contrast to the picture version, there was no consistent difference in MT/MST activity between verb and noun matching across subjects, when considering all voxels in the MT/MST. In addition, there were no voxels in the MT/MST in any subject that were significant for the main effect of word matching (nouns and verbs) minus baseline. We also performed an ROI analysis to identify areas that showed differential activity for noun or verb matching. Since few voxels in the right hemisphere were active in the word-matching task, we only considered the left hemisphere in each ROI (although statistical results did not differ if the right hemisphere was included). Similar to the picture version, voxels in the posterior lateral temporal cortex showed consistently greater activity during verb matching compared to noun matching across subjects [$t(5) =$

3.1, $p = .03$, Figure 3]. In 2 of 6 subjects, there was an overlap of the voxels considered for this analysis in the lateral temporal cortex across the picture and word versions of the task. For the remaining subjects, the voxels considered in the word version were located anterior and dorsal to the ones considered in the picture version, in the posterior part of the middle and superior temporal gyri. Again, similar to the picture version, no other region showed differential activity for nouns or verbs.

Finally, in each subject, we searched for voxels that were significantly active in both the picture and word versions, collapsing across conceptual category (objects and actions). We tested whether any voxels passed the joint hypothesis tests for greater activity during object and action picture matching as compared to baseline and for greater activity during noun and verb matching as compared to baseline. Using this test, we found significant voxels in the left posterior prefrontal cortex in five of six subjects (11 ± 4 voxels, range: 2–20 voxels) and in the left fusiform gyrus (4 ± 1 voxels, range: 1–9 voxels) in a different 5 of 6 subjects (Figure 4). We did not find significant voxels in any other region in a majority of subjects. Within the voxels that were jointly significant in the left fusiform, the effect size was larger in the picture-matching scan for all subjects.

DISCUSSION

The main purpose of this study was to establish that the neural mediation of the conceptual category of events differs from that of entities in the normal human brain. We found that conceptual matching of actions caused

greater activation in areas of the lateral occipital-temporal cortex. When subjects matched action pictures, in comparison to objects, there was greater activity in human MT/MST bilaterally. When subjects matched action words (verbs), in comparison to object words (nouns), there was greater activity anterior and dorsal to the MT/MST on the left, within the posterior aspect of the middle and superior temporal gyri. In contrast, we found no evidence for greater activity during action matching in either prefrontal or parietal regions. Finally, areas in the left posterior prefrontal cortex and the left fusiform gyrus were activated across both the picture- and word-matching tasks, irrespective of the category of stimuli (objects or actions).

The greater activation for action than object matching in the MT/MST and adjoining regions in the posterior temporal lobe is consistent with the idea that conceptual knowledge of actions incorporates motion features. Furthermore, the pattern of action-specific activations suggests a mosaic of cortical areas that processes different senses of motion, from the visual association cortex (more perceptual) to the perisylvian regions (more linguistic). Action-specific activations in the picture-matching task primarily centered on the MT/MST, extending into the middle temporal gyrus, while action-specific activations in the word-matching task were dorsal and anterior to those in the picture task, across both the middle and superior temporal gyri.

Other findings provide converging support for a mosaic of regions processing different kinds of motion along the lateral occipital-temporal surface. Naming actions that involve an implement produces more activity bilaterally near the MT/MST than does naming implements (Damasio et al., 2001), and lesions in a similar area of the left hemisphere are associated with action-naming deficits (Kemmerer & Tranel, 2000). In addition, generating a corresponding verb in response to an object picture produces more activity than generating a corresponding color name in the left posterior temporal regions anterior to the MT/MST (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). When the stimulus is a word instead of a picture, verb generation produces activation that extends more anteriorly into perisylvian regions (Martin et al., 1995). Finally, imagining actions (compared to a passive baseline) activates parts of the lateral temporal cortex, as does observing semantically meaningful actions (compared to meaningless actions) (Ruby & Decety, 2001; Decety et al., 1997).

Converging support can also be found in previous findings concerning the neural basis of conceptual knowledge of concrete entities. Naming or viewing pictures of tools, in comparison to animal pictures, consistently activates portions of the left posterior temporal cortex (Chao et al., 1999; Damasio et al., 1996; Martin et al., 1996). This tool-specific activation is also present in verbal tasks in which no pictures are pre-

sented (Chao et al., 1999; Perani et al., 1999; Cappa et al., 1998). Lesions in this area of the inferior temporal gyrus are associated with deficits in tool naming as well as retrieval of conceptual knowledge about tools (Tranel et al., 1997; Damasio et al., 1996). Since characteristic motions may be more important for tool concepts than animal concepts, these results are consistent with the idea that conceptual categories that incorporate motion recruit posterior temporal cortices.

Our findings also provide additional insight into the functional significance of MT/MST activity, which may occur in the absence of moving stimuli. For example, MT/MST activity increases when subjects perceive motion in illusions or when they imagine a moving stimulus (Goebel, Khorrām-Sefat, Muckli, Hacker, & Singer, 1998; Tootell, Reppas, Dale et al., 1995; Zeki, Watson, & Frackowiak, 1993). Still pictures with implied motion (e.g., athletes, natural scenes, or objects in motion) also activate the MT/MST (Kourtzi & Kanwisher, 2000; Senior et al., 2000). However, none of these tasks explicitly involve semantics. Our results are consistent with the interpretation that activity in the MT/MST can be modulated by high-level inferences about stimuli (such as conceptual categorization), as suggested by Kourtzi & Kanwisher (2000).

Our failure to find greater activity in either the prefrontal or the parietal cortex during action matching with either pictures or words does not support the idea that the semantics of actions are preferentially mediated by these areas. How can this finding be reconciled with the action-naming deficits found in patients with left frontal brain damage (Kemmerer & Tranel, 2000; Daniele et al., 1994; Damasio & Tranel, 1993)? One possibility is that these action-naming deficits result from lexical rather than semantic or conceptual factors. Bird et al. (2000) recently demonstrated that action-naming deficits were no longer evident in their patients when concreteness was balanced across objects and actions. Alternatively, verbs play a more crucial role than nouns in syntax. Left prefrontal regions may be important in using verbs to establish a syntactic frame (Chatterjee & Maher, 2000). Since our task did not involve syntactic structures explicitly, perhaps the prefrontal cortex was not preferentially activated.

Furthermore, our data do not support the proposal of Tyler et al. (2001) that conceptual knowledge is represented within nondifferentiated distributed neural networks. The stimuli in their study were divided along grammatical class rather than conceptual category, and included both abstract and concrete words. Sensorimotor features, such as motion or form, are not likely to be as critical for the concepts embodied by abstract nouns or verbs. In addition, there was variability across subjects in the location of the activations we found in the lateral temporal cortex in the word-matching task. Because PET data from different subjects must be combined within a normalized reference frame, PET

may be less sensitive than fMRI to detect the changes we found.

We found no evidence for greater activity in any cortical region during object matching than action matching. However, in the picture version of the task, all of the action stimuli included objects. Similarly, in the word version of the task, semantic processing of an action word may automatically evoke references to objects participating in those actions. The most likely candidate for a region important for object knowledge is the ventral surface of the temporal lobe. If this region is object-specific, then the category-specific activity demonstrated in this region (Chao et al., 1999; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Aguirre, Zarahn, & D'Esposito, 1998a; Epstein & Kanwisher, 1998; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997) should be insensitive to whether the object is participating in an action or not.

While the MT/MST and the posterior temporal areas were preferentially activated by action matching, the left posterior prefrontal cortex and the left fusiform gyrus were activated by the semantic-matching task regardless of the conceptual category (objects or actions) or the material (pictures or words). Many previous findings have implicated these two regions in language or semantic processing (Tyler et al., 2001; Gabrieli, Poldrack, & Desmond, 1998; Binder et al., 1997; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Luders et al., 1991; Burnstine et al., 1990). Using PET, Vandenberghe et al. (1996) found that the same two areas were activated in both the picture and word versions of a similar object-matching task. Our results replicate their finding for objects and demonstrate that similar activation occurs more generally across semantic domains, including actions. The effect size within the left posterior prefrontal cortex was similar for the picture and word versions, a pattern suggesting that this region plays a more general role in semantic processing. Recent fMRI and patient studies suggest that left prefrontal regions have a role in selecting information from semantic memory (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill et al., 1998; Thompson-Schill, D'Esposito, & Kan, 1999). Since selection demands should be similar across the picture and word versions of the matching task, our results are consistent with this hypothesis. In contrast, the effect size within the left fusiform gyrus was greater during the picture version of the task, a pattern that suggests that this region plays a greater role in visual representations. The activation in the fusiform was close to regions implicated in category-specific visual representations of objects (sometimes referred to as structural descriptions) (Chao et al., 1999; Ishai et al., 1999; Aguirre et al., 1998a; Epstein & Kanwisher, 1998; Kanwisher et al., 1997; McCarthy et al., 1997). Since it may be hard to consider actions in the absence of objects involved in the actions, this area may remain active across all versions of the matching task.

While the left posterior prefrontal and the left fusiform activations were present in both the picture- and word-matching tasks, the general pattern of activation diverged across the two versions of the task. As discussed above, the action-specific voxels in picture and word versions did not overlap in all subjects. In addition, activations in picture matching were bilateral in all subjects, while activations in word matching were predominantly left lateralized. Chatterjee (2001) recently proposed that the right hemisphere might be more involved in representing or interpreting specific imagistic instances of a concept (a particular picture), while the left hemisphere might be more involved in representing or interpreting prototypical instances of a concept (a word or schematic that could apply to a number of pictures). Our data are consistent with this proposal.

In summary, while left prefrontal regions were robustly activated in all conditions in the present study, activity in the posterior cortex diverged across the different conceptual category (objects or actions) and material (pictures or words) manipulations. In particular, parts of the lateral occipital-temporal cortex, including the MT/MST, were differentially activated when subjects accessed their conceptual knowledge of actions through pictures or words. These results are consistent with the hypotheses that knowledge of events incorporates motion features. Much previous work in the cognitive neuroscience of semantic memory has stressed the importance of a mosaic of regions within the ventral occipital-temporal surface, which processes different perceptual and conceptual features of objects. The current study suggests the existence of another mosaic of regions within the lateral occipital-temporal surface, which processes perceptual and conceptual features of motion, including the perception of moving objects, the implied motion in action pictures, and the implied motion of action verbs.

METHODS

Subjects

Two men and 3 women from the university community participated in Experiment 1 (mean age = 22.2 years). Three men and 3 women subjects participated in Experiment 2 (mean age = 20.7 years). All subjects were right-handed and English was their only language before school age. None had a history of neurologic or psychiatric symptoms. All subjects gave informed consent in accordance with the procedures of the University of Pennsylvania.

Behavioral Task and Design

During a scan, subjects performed a conceptual matching task similar to the Pyramids and Palm Trees task

(Howard & Patterson, 1992). On each trial, a target stimulus was presented at the top of the screen and two choice stimuli were presented at the bottom. Subjects indicated which of the choices matched the target with a button press (right or left hand). On experimental trials, the correct choice was semantically linked to the target. For example, “leaf” matched with “flower” rather than “mushroom,” or “following” matched with “trailing” rather than “slicing.” In baseline trials, the stimuli were distorted forms (distorted versions of pictures used in the experimental condition), and subjects indicated which of the choices was the same as the target (Figure 1). A perceptual task was used instead of a resting baseline because of previous evidence that brain regions involved in conceptual processing are active during “rest” (Binder et al., 1999).

The second group of subjects performed two versions of the conceptual matching task, one with picture stimuli and one with corresponding word stimuli. The first group of subjects performed only the picture version. In all cases, experimental and baseline trials were presented in alternating blocks of 20 sec. Each block consisted of a 2-sec instruction and six trials of 3 sec each. Further, experimental blocks alternated between object stimuli and action stimuli. The order of object and action blocks, as well as picture- and word-version scans, was counterbalanced across subjects.

Picture triads were adapted from the Florida Semantics Battery (Raymer & Gonzalez Rothi, 2000). Thirty object stimuli and 30 action stimuli were selected through pilot testing such that normal subjects responded with similar accuracy and reaction time. We chose to equate stimuli on accuracy and reaction time, as opposed to other possible variables, such as visual complexity, since performance parameters seemed more directly linked to brain activity. Equal numbers of left and right matches were chosen in each condition, and no individual pictures were repeated.

Word triads were constructed by substituting an appropriate name for each picture. Object and action words did not differ in either frequency or regularity of words. Because many English words can refer to objects or actions, all action words were presented in the present participle form, ending in “-ing.” Although such a consistent ending might create a potential confound (by making action words longer, for instance), we felt it was necessary to ensure that subjects understood the words as clearly referring to actions.

Baseline triads were created by distorting picture or word stimuli with the “ripple” and “wave” filters in Adobe Photoshop, and replacing the distorted match with the distorted target (see Figure 1 for examples). Baseline stimuli were the same size as experimental stimuli and contained limited shape information, but lacked any information about object parts or letters. Baseline stimuli were pilot tested to ensure that none of the distorted pictures or words were recognizable.

Subjects were familiarized with the tasks before the scanning session. During the scanning session, stimuli were back-projected onto a screen at the foot of the subject gurney and subjects viewed the stimuli through a mirror mounted on the head coil. Stimulus presentation and recording of responses were controlled by Psycoscope software (psycoscope.psy.cmu.edu) for the language tasks and Pixx software (psychology.concordia.ca/departement/CVLab/CVLab.html) for the visual motion task.

MRI Acquisition

BOLD-sensitive, T2*-weighted fMRI data were acquired using a gradient-echo, echo-planar pulse sequence on a 1.5-T GE signa scanner (TR = 2000 msec, TE_{eff} = 50 msec, flip angle = 90°, 64 × 64 matrix in a 24-cm field of view, resulting in 3.75 by 3.75 mm within slice resolution). The scanner was equipped with a quadrature radio-frequency head coil and a prototype fast gradient system. Head motion was minimized using foam padding. Data were acquired in twenty-one 5-mm axial slices, covering the entire cortex but omitting lower portions of the cerebellum and brainstem. Subjects performed no task during the first 20 sec of each scan as steady-state magnetization was achieved. Subjects completed each version of the task in one 7-min scan, resulting in 200 observations per voxel per subject. High-resolution, T1-weighted axial and sagittal scans were also acquired for each subject using a spin-echo sequence (TR = 600 msec, TE = 14 msec, 192 × 256 matrix).

Data Analysis

Data processing was performed using software developed at the University of Pennsylvania (www.voxbo.org). Before statistical analysis, data were corrected for staggered slice acquisition by sinc-interpolation in time, realigned to the first image acquired for each subject using a six-parameter motion-correction algorithm, and thresholded to exclude extra-parenchymal voxels from subsequent analyses. No spatial smoothing or normalization to a common space was performed.

Voxel-wise analysis within each subject was performed using a general linear model for serially correlated error terms. Included in this model were covariates modeling different task components (e.g., “object matching” or “action matching”), an estimate of the intrinsic temporal autocorrelation, and sine and cosine regressors for frequencies below those of the task. Task covariates were boxcar waveforms convolved with an estimate of the BOLD hemodynamic transfer function empirically derived from the motor cortex in a large group of subjects (Aguirre, Zarahn, & D’Esposito, 1998b). To improve specificity, data were also smoothed in time with the hemodynamic transfer function. This method has been empirically demonstrated to control the

map-wise false-positive rate (Aguirre, Zarahn, & D'Esposito, 1997; Zarahn, Aguirre, & D'Esposito, 1997).

Group analyses focused on identifying regions of the brain where activity differed significantly between object and action conditions. Group analyses were performed as random-effects models, rather than fixed-effects models, so that the results could be generalized from the sample to the population (Woods, 1996). Initially, voxels were identified within each subject where activity was significant for the main effect of experimental (objects plus actions) compared to baseline conditions ($p < .05$, corrected for multiple comparisons within an ROI). This main effect contrast would detect voxels that were significantly active in either the object or the action conditions compared to the baseline condition (one exception is discussed below). Then, the fMRI time series was averaged for all significant voxels within a defined ROI in each subject. Next, a measure of the effect size for the orthogonal contrast of actions minus objects was extracted from the averaged ROI time series in each subject. We used t values as a measure of effect size rather than percent signal change, because the residual error term in the denominator of the t value most effectively corrects the effect size for scaling effects due to differences in overall MR signal intensity across scanning sessions (Postle, Zarahn, & D'Esposito, 2000). Finally, paired t tests addressed whether this effect was consistently greater for objects or actions in that ROI across subjects. Thus, a significant difference in this random-effects analysis indicates that activity in that ROI was consistently greater for actions compared to objects across subjects (for example), but merits no conclusion as to whether that region was exclusively active in only one condition compared to the baseline.

The above group analysis can detect effects that are reliable across subjects, but may be too subtle to detect at the voxel level in an individual subject. Thus, the logic of this analysis is similar to a random-effects analysis at the voxel level after normalizing and smoothing each subject's data. However, this analysis compares favorably to a random-effects analysis at the voxel level in two ways. First, by reducing the effect size in each ROI to one value, this analysis avoids the need to correct for multiple comparisons across voxels, increasing sensitivity. Second, because the voxels being compared across subjects are defined functionally by the main effect comparison, this analysis avoids the assumption that brain areas in the same coordinates of normalized space are functionally homologous across subjects, as well as the assumption that all voxels within an ROI are homologous. This point is particularly critical when considering the temporal cortex, where large subject-to-subject variability in the location of activations has previously been reported (Thompson-Schill et al., 1999). One drawback of this analysis, in comparison to a random-effects analysis at the voxel level, is the loss of spatial resolution that results from averaging across all active voxels within an ROI.

This analysis would miss differences occurring in voxels that do not show a significant main effect. For example, activity within a voxel might be greatest for action matching, intermediate for the baseline task, and least for object matching, such that there was no main effect for object and action matching compared to the baseline. However, such a pattern of activity would be peculiar, because it would imply that a given region responds positively to one semantic task compared to the baseline, and negatively to the other semantic task compared to the baseline. Such a pattern would be detected by a direct contrast between the action and object conditions for both the word and picture versions. The results of these direct contrasts did not change the interpretation of our main-effects analyses.

ROIs were defined by either anatomical or functional criteria. The locations of anatomical ROIs were chosen on the basis of a priori hypotheses, as well as the results seen in the first group of subjects. Anatomical ROIs were traced on each subject's high-resolution, T1-weighted image according to the following boundaries, including both gray and white matter. The inferior frontal ROI included the pars triangularis, pars opercularis, and pars orbitalis, corresponding to Brodmann's areas 44, 45, and 47 (362 ± 32 voxels bilaterally). The premotor cortex ROI corresponded to Brodmann's area 6, which includes the posterior half of the superior frontal gyrus medially and the cortex surrounding the precentral sulcus laterally (973 ± 86 voxels). The fusiform ROI included both the occipital and temporal portions of this gyrus (338 ± 26 voxels). The posterior temporal ROI included the posterior two-thirds of the middle and superior temporal gyri (873 ± 54 voxels). The inferior parietal ROI included the angular and supramarginal gyri, corresponding to Brodmann's areas 39 and 40 (729 ± 50 voxels).

To functionally identify the visual motion cortex, subjects participated in a separate localizer scan. In this scan, subjects viewed alternating 16-sec blocks of radially moving dots and stationary dots. The radially moving dots alternated between inward and outward motion every 2 sec. In accordance with previous studies, the visual motion cortex was defined as all contiguous voxels in the lateral occipital-temporal cortex with significantly greater activity during presentation of moving dots (Kourtzi & Kanwisher, 2000; Tootell, Reppas, Kwong et al., 1995). The region identified by this contrast appears to be the human homologue of motion-sensitive cortical areas in the macaque, including the MT and the MST (Tootell, Reppas, Kwong, et al., 1995).

For the second group of subjects, we also identified voxels that had significantly greater activity during conceptual matching in both the picture and word versions of the experiment ($p < .05$, corrected for multiple comparisons, for both the main effect of picture matching minus baseline and the main effect of word matching minus baseline).

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The data reported in this experiment have been deposited in The fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2002-11GN.

REFERENCES

- Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1997). Empirical analyses of BOLD fMRI statistics: II. Spatially smoothed data collected under null-hypothesis and experimental conditions. *Neuroimage*, *5*, 199–212.
- Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998a). An area within human ventral cortex sensitive to “building” stimuli: Evidence and implications. *Neuron*, *21*, 373–383.
- Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998b). The variability of human, BOLD hemodynamic responses. *Neuroimage*, *8*, 360–369.
- Berndt, R. S., Haendiges, A. N., Mitchum, C. C., & Sandson, J. (1997). Verb retrieval in aphasia: 2. Relationship to sentence processing. *Brain and Language*, *56*, 107–137.
- Berndt, R. S., Mitchum, C. C., Haendiges, A. N., & Sandson, J. (1997). Verb retrieval in aphasia: 1. Characterizing single word impairments. *Brain and Language*, *56*, 68–106.
- Binder, J. R., Frost, J. A., Hammeke, T. A., Cox, R. W., Rao, S. M., & Prieto, T. (1997). Human brain language areas identified by functional magnetic resonance imaging. *Journal of Neuroscience*, *17*, 353–362.
- Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S., Rao, S. M., & Cox, R. W. (1999). Conceptual processing during the conscious resting state. A functional MRI study. *Journal of Cognitive Neuroscience*, *11*, 80–95.
- Bird, H., Howard, D., & Franklin, S. (2000). Why is a verb like an inanimate object? Grammatical category and semantic category deficits. *Brain and Language*, *72*, 246–309.
- Burnstine, T. H., Lesser, R. P., Hart, J., Uematsu, S., Zinreich, S. J., Krauss, G. L., Fisher, R. S., Vining, E. P., & Gordon, B. (1990). Characterization of the basal temporal language area in patients with left temporal lobe epilepsy. *Neurology*, *40*, 966–970.
- Cappa, S. F., Perani, D., Schnur, T., Tettamanti, M., & Fazio, F. (1998). The effects of semantic category and knowledge type on lexical–semantic access: A PET study. *Neuroimage*, *8*, 350–359.
- Caramazza, A., & Shelton, J. R. (1998). Domain-specific knowledge systems in the brain the animate–inanimate distinction. *Journal of Cognitive Neuroscience*, *10*, 1–34.
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*, 913–919.
- Chatterjee, A. (2001). Language and space: Some interactions. *Trends in Cognitive Sciences*, *5*, 55–61.
- Chatterjee, A., & Maher, L. (2000). Grammar and agrammatism. In S. E. Nadeau, L. J. Gonzalez Rothi, & B. Crosson (Eds.), *Aphasia and language: Theory to practice* (pp. 133–156). New York: Guilford Press.
- Chatterjee, A., Maher, L. M., Gonzalez Rothi, L. J., & Heilman, K. M. (1995). Asyntactic thematic role assignment: The use of a temporal–spatial strategy. *Brain and Language*, *49*, 125–139.
- Chatterjee, A., Maher, L. M., & Heilman, K. M. (1995). Spatial characteristics of thematic role representation. *Neuropsychologia*, *33*, 643–648.
- Chatterjee, A., Southwood, M. H., & Basilico, D. (1999). Verbs, events and spatial representations. *Neuropsychologia*, *37*, 395–402.
- Chatterjee, A., Southwood, M. H., Calhoun, J., & Thompson, K. A. (1999). Conceptual and linguistic knowledge of thematic roles in aphasia. *Neurology Abstracts*, *52*, A458.
- Damasio, A. R., & Tranel, D. (1993). Nouns and verbs are retrieved with differently distributed neural systems. *Proceedings of the National Academy of Sciences, U.S.A.*, *90*, 4957–4960.
- Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D., & Damasio, A. R. (1996). A neural basis for lexical retrieval. *Nature*, *380*, 499–505.
- Damasio, H., Grabowski, T. J., Tranel, D., Ponto, L. L., Hichwa, R. D., & Damasio, A. R. (2001). Neural correlates of naming actions and of naming spatial relations. *Neuroimage*, *13*, 1053–1064.
- Daniele, A., Giustolisi, L., Silveri, M. C., Colosimo, C., & Gainotti, G. (1994). Evidence for a possible neuroanatomical basis for lexical processing of nouns and verbs. *Neuropsychologia*, *32*, 1325–1341.
- Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F., & Fazio, F. (1997). Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain*, *120*, 1763–1777.
- Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, *392*, 598–601.
- Gabrieli, J. D., Poldrack, R. A., & Desmond, J. E. (1998). The role of left prefrontal cortex in language and memory. *Proceedings of the National Academy of Sciences, U.S.A.*, *95*, 906–913.
- Gainotti, G., Silveri, M. C., Daniele, A., & Giustolisi, L. (1995). Neuroanatomical correlates of category-specific semantic disorders: A critical survey. *Memory*, *3*, 247–264.
- Goebel, R., Khorrám-Sefat, D., Muckli, L., Hacker, H., & Singer, W. (1998). The constructive nature of vision: Direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. *European Journal of Neuroscience*, *10*, 1563–1573.
- Hart, J., Jr., Berndt, R. S., & Caramazza, A. (1985). Category-specific naming deficit following cerebral infarction. *Nature*, *316*, 439–440.
- Hillis, A. E., & Caramazza, A. (1991). Category-specific naming and comprehension impairment: A double dissociation. *Brain*, *114*, 2081–2094.
- Howard, D., & Patterson, K. (1992). *Pyramids and palm trees: A test of semantic access from pictures and words*. Bury St. Edmunds, UK: Thames Valley Test Company.
- Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, U.S.A.*, *96*, 9379–9384.
- Jackendoff, R. (1990). *Semantic structures* (vol. 18). Cambridge: MIT Press.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Kemmerer, D., & Tranel, D. (2000). Verb retrieval in brain-damaged subjects: 1. Analysis of stimulus, lexical, and conceptual factors. *Brain and Language*, *73*, 347–392.

- Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, *12*, 48–55.
- Luders, H., Lesser, R. P., Hahn, J., Dinner, D. S., Morris, H. H., Wyllie, E., & Godoy, J. (1991). Basal temporal language area. *Brain*, *114*, 743–754.
- Maher, L. M., Chatterjee, A., Gonzalez Rothi, L. J., & Heilman, K. M. (1995). Agrammatic sentence production: The use of a temporal–spatial strategy. *Brain and Language*, *49*, 105–124.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, *270*, 102–105.
- Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, *379*, 649–652.
- McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997, September). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, *9*, US, <http://mitpress>.
- McCarthy, R., & Warrington, E. K. (1985). Category specificity in an agrammatic patient: The relative impairment of verb retrieval and comprehension. *Neuropsychologia*, *23*, 709–727.
- Perani, D., Schnur, T., Tettamanti, M., Gorno-Tempini, M., Cappa, S. F., & Fazio, F. (1999). Word and picture matching: A PET study of semantic category effects. *Neuropsychologia*, *37*, 293–306.
- Postle, B. R., Zarahn, E., & D'Esposito, M. (2000). Using event-related fMRI to assess delay-period activity during performance of spatial and nonspatial working memory tasks. *Brain Research, Brain Research Protocols*, *5*, 57–66.
- Raymer, A. M., & Gonzalez Rothi, L. J. (2000). The semantic system. In S. E. Nadeau, L. J. Gonzalez Rothi, & B. Crosson (Eds.), *Aphasia and language: Theory to practice* (pp. 108–132). New York: Guilford Press.
- Ruby, P., & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: A PET investigation of agency. *Nature Neuroscience*, *4*, 546–550.
- Sacchetti, C., & Humphreys, G. W. (1992). Calling a squirrel a squirrel but a canoe a wigwam: A category-specific deficit for artefactual objects and body parts. *Cognitive Neuropsychology*, *9*, 73–86.
- Saffran, E. M., & Schwartz, M. F. (1994). Of cabbages and things: Semantic memory from a neuropsychological perspective—a tutorial review. In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance: XV. Conscious and nonconscious information processing* (pp. 507–536). Cambridge: MIT Press.
- Senior, C., Barnes, J., Giampietro, V., Simmons, A., Bullmore, E. T., Brammer, M., & David, A. S. (2000). The functional neuroanatomy of implicit-motion perception or representational momentum. *Current Biology*, *10*, 16–22.
- Silveri, M. C., & Di Betta, A. M. (1997). Noun–verb dissociations in brain-damaged patients: Further evidence. *Neurocase*, *3*, 477–488.
- Talmy, L. (1996). Fictive motion in language and “ception.” In P. Bloom, & M. A. Peterson, L. Nadel, & M. F. Garrett (Eds.), *Language and space. Language, speech, and communication* (pp. 211–276). Cambridge: MIT Press.
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences, U.S.A.*, *94*, 14792–14797.
- Thompson-Schill, S. L., D'Esposito, M., & Kan, I. P. (1999). Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron*, *23*, 513–522.
- Thompson-Schill, S. L., Swick, D., Farah, M. J., D'Esposito, M., Kan, I. P., & Knight, R. T. (1998). Verb generation in patients with focal frontal lesions: A neuropsychological test of neuroimaging findings. *Proceedings of the National Academy of Sciences, U.S.A.*, *95*, 15855–15860.
- Tootell, R. B., Reppas, J. B., Dale, A. M., Look, R. B., Sereno, M. I., Malach, R., Brady, T. J., & Rosen, B. R. (1995). Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature*, *375*, 139–141.
- Tootell, R. B., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., Rosen, B. R., & Belliveau, J. W. (1995). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *Journal of Neuroscience*, *15*, 3215–3230.
- Tranel, D., Damasio, H., & Damasio, A. R. (1997). A neural basis for the retrieval of conceptual knowledge. *Neuropsychologia*, *35*, 1319–1327.
- Tyler, L. K., Russell, R., Fadili, J., & Moss, H. E. (2001). The neural representation of nouns and verbs: PET studies. *Brain*, *124*, 1619–1634.
- Vandenberghe, R., Price, C., Wise, R., Josephs, O., & Frackowiak, R. S. (1996). Functional anatomy of a common semantic system for words and pictures. *Nature*, *383*, 254–256.
- Warrington, E. K., & McCarthy, R. (1983). Category specific access dysphasia. *Brain*, *106*, 859–878.
- Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain*, *107*, 829–854.
- Woods, R. P. (1996). Modeling for intergroup comparisons of imaging data. *Neuroimage*, *4*, S84–S94.
- Zarahn, E., Aguirre, G. K., & D'Esposito, M. (1997). Empirical analyses of BOLD fMRI statistics: I. Spatially unsmoothed data collected under null-hypothesis conditions. *Neuroimage*, *5*, 179–197.
- Zeki, S., Watson, J. D., & Frackowiak, R. S. (1993). Going beyond the information given: The relation of illusory visual motion to brain activity. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *252*, 215–222.