

The Functional Neuroanatomy of Thematic Role and Locative Relational Knowledge

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Abstract

■ Lexical–semantic investigations in cognitive neuroscience have focused on conceptual knowledge of concrete objects. By contrast, relational concepts have been largely ignored. We examined thematic role and locative knowledge in 14 left-hemisphere-damage patients. Relational concepts shift cognitive focus away from the object to the relationship between objects, calling into question the relevance of traditional sensory–functional accounts of semantics. If extraction of a relational structure is the critical cognitive process common to both thematic and locative knowledge, then damage to neural structures involved in such an extraction would impair both kinds of knowledge. If the nature of the relationship itself is critical, then functional neuroanatomical dissociations should occur. Using a new lesion analysis method, we found that damage to

the lateral temporal cortex produced deficits in thematic role knowledge and damage to inferior fronto-parietal regions produced deficits in locative knowledge. In addition, we found that conceptual knowledge of thematic roles dissociates from its mapping onto language. These relational knowledge deficits were not accounted for by deficits in processing nouns or verbs or by a general deficit in making inferences. Our results are consistent with the hypothesis that manners of visual motion serve as a point of entry for thematic role knowledge and networks dedicated to eye gaze, whereas reaching and grasping serve as a point of entry for locative knowledge. Intermediary convergence zones that are topographically guided by these sensory–motor points of entry play a critical role in the semantics of relational concepts. ■

INTRODUCTION

What are the neural underpinnings of thematic role and locative knowledge? Cognitive neuroscience studies of semantics have largely focused on the neural underpinnings of our knowledge of objects. For example, selective deficits in naming and recognizing objects on the basis of their category membership (such as whether or not they are animate) have led to vigorous discussions about the functional and anatomic organization of semantics (Forde & Humphreys, 1999; Caramazza & Shelton, 1998; Tranel, Damasio, & Damasio, 1997; Gainotti, Silveri, Daniele, & Giustolisi, 1995; Hart & Gordon, 1992; Hillis & Caramazza, 1991; Damasio, Damasio, Tranel, & Brandt, 1990; Warrington & Shallice, 1984). This focus on object knowledge as being central to semantics has been further bolstered by a spate of functional imaging studies (Thompson-Schill, Kan, & Oliver, 2006; Martin, Ungerleider, & Haxby, 2000; Chao, Haxby, & Martin, 1999; Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998). Only recently has attention been paid to the neural basis for knowledge of actions and spatial relations as expressed in language (Kemmerer, 2006; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003; Kable, Spellmeyer-Lease, &

Chatterjee, 2002; Chatterjee, 2001; Tranel, Adolphs, Damasio, & Damasio, 2001; Kemmerer & Tranel, 2000; Perani et al., 1999; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). Thematic role knowledge is the understanding of who is doing what to whom in an action event and is typically determined in sentences by the argument structure organized by verbs. Locative knowledge is the understanding of the spatial relationship of one object to another and is typically indicated in English sentences by prepositions. In this study, we examine the functional neuroanatomy of these kinds of knowledge as expressed in simple sentences.

Separating object knowledge from action and spatial knowledge underscores an important distinction. This distinction, emphasized by Gentner and Kurtz (2005), is that of entity and relational concepts. Entity concepts refer to objects and characteristically have a rich set of correlated intrinsic features and associations. These features and associations are the sensory–functional properties emphasized in cognitive neuroscience investigations of the meaning of objects (Martin et al., 2000). By contrast, relational concepts have a sparser set of associated features, often without an obvious set of common features (Gentner & Kurtz, 2005; Gentner, 1981). Instead, relational concepts are grounded in an underlying rule-like structure. These concepts, as the name suggests, refer to relations between things rather

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than to the things themselves. For example, action verbs might indicate who is doing what to whom, and prepositions might indicate where one thing is located in relation to another. In both instances, many entities can enter into these relations.

Framing action and spatial knowledge as relational categories highlights two fundamental points. First, relational categories introduce a level of abstraction by shifting cognitive focus away from the object itself.¹ This cognitive shift raises questions about whether the traditional sensory–functional accounts for object semantics generalize to relational concepts, questions directly relevant to our study. For example, although an apple may be understood as an apple because of its shape, color, smell, and taste, it is not clear what, with respect to sensory–functional attributes, is shared in the knowledge that apples can be eaten by a child and that worms can be eaten by a bird. The focus on the semantics of entities has rendered cognitive neuroscience largely silent on relational knowledge, the kind of knowledge that infuses cognitive systems with much of their richness and texture. Second, uncovering a relational structure provides a degree of cognitive flexibility that is not easily available when simply referring to objects in the world. This flexibility is evident in the polysemous nature of verbs. *Webster's Dictionary* shows a mean of 7.3 word senses for the 20 highest frequency nouns and a mean of 12.4 word senses for the 20 highest frequency verbs (Gentner & Kurtz, 2005). The flexibility of relational categories is also evident in metaphoric extensions of these terms. To illustrate the point, the events of a man entering an office and a lion entering a cave share few intrinsic attributes. Yet, the term “enter” highlights a relational structure that can be extended flexibly to metaphors, such as “fear entered my mind.” Although the flexible extension of spatial terms to metaphoric uses is of great interest, we will not address this issue further. Our basic point is that the cognitive neuroscience of semantics has been largely restricted to object concepts. We wish to extend the inquiry of semantics into relational concepts.

What do we know about the neural basis of actions events? Comprehension of actions is thought to be instantiated in a distributed network involving dorsolateral prefrontal, posterior parietal, and lateral temporo-occipital cortex. Tranel et al. (2003) found that damage to these three regions was associated with deficits of action knowledge. However, the specific contributions of each these areas to such deficits are still being worked out.

Human comprehension of actions is sometimes postulated as being “embodied” (Rizzolatti, Fogassi, & Gallese, 2001; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). That is, the comprehension of actions is encoded in mirror neurons within the frontal and parietal cortices, which are active both when individuals observe and when they engage in actions. Studies that link actions and language to

the prefrontal cortices are considered evidence for this embodied view (Tettamanti et al., 2005; Hauk & Pulvermuller, 2004; Pulvermuller, Harle, & Hummel, 2001).

We hypothesized that the lateral occipito-temporal cortex mediates action comprehension, in part, because of its role in processing motion. The evidence for this claim comes from the fact that the human analog of the macaque middle temporal/medial superior temporal area (area MT/MST; Dumoulin et al., 2000; Tootell et al., 1995), which specializes in processing visual motion, is active when participants view (Kourtzi & Kanwisher, 2000; Senior et al., 2000) or make semantic judgments of action pictures (Kable et al., 2002). Areas just anterior and dorsal to the MT/MST, within the posterior middle and superior temporal gyrus, are active when participants make semantic judgments of action words (verbs) (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Kable et al., 2002).

We recently reported that neural circuits within the lateral occipito-temporal cortex abstract actions away from the specific agents engaged in these actions (Kable & Chatterjee, 2006). Using a functional magnetic resonance imaging (fMRI) adaptation paradigm, we demonstrated that the posterior superior temporal sulcus, the extrastriate body area, and area MT/MST showed neural adaptation to repeated actions even when the actions were conducted by novel actors. Thus, neural circuits within the lateral occipito-temporal cortex are sensitive to specific actions and mediate an important step in the formation of relational categories, the step that shifts cognitive attention away from intrinsic features of the agent to the actions themselves. These observations suggest that parts of the posterolateral temporal cortex might also be involved in relational knowledge, specifically relational structures indexed by action verbs.

The cognitive neuroscience of spatial semantics as related to prepositions has been studied in even less detail than action semantics (for a review, see Kemmerer, 2006). In an early study, Friederici (1981) suggested that Wernicke aphasics had a semantic impairment in preposition processing. Landau and Jackendoff (1993) speculated that the parietal cortex might process prepositions. In positron emission tomography studies, the supramarginal gyrus seems to be active when people name prepositional relations (Emmorey et al., 2002; Damasio et al., 2001). Furthermore, Tranel and Kemmerer (2004) reported that comprehension of prepositional relations seems to be impaired most often by supramarginal gyrus damage. Although considerable work still needs to be done to confirm this functional–anatomic correlation, this neural organization might be related to neural circuits devoted to reaching and grasping (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). One possibility is that spatial coordinates important for such motor behaviors (knowing how to modify one’s reach for a target object in front of, as opposed to behind, another object) serve as a point of entry for language to categorize and label these relationships.

The goals of our study are twofold. The main goal is theoretical and an ancillary goal is methodological. First, we test a set of hypotheses about the neural and functional organization of thematic role and locative relational knowledge in a group of patients with focal left hemisphere damage. Second, we advocate a new approach to analyzing lesion data that strengthen the inference being made about brain–behavior relationships.

The studies presented here test relational knowledge in the context of simple sentences in patients with focal brain damage. Patients with left brain damage may have difficulty comprehending sentences describing who is doing what to whom (thematic relations) or where something is in relation to something else (locative relations). Sentence-level comprehension deficits have been investigated at many levels (Berndt, Mitchum, & Wayland, 1997), from the effects of syntactic and morphologic complexity (Caplan, Alpert, & Waters, 1998; Grodzinsky, 1988, 1989, 1995; Mauner, Fromkin, & Cornell, 1993; Caplan & Futter, 1986; Bradley, Garrett, & Zurif, 1980) to the impact of varying processing demands (Kolk, Chwilla, van Herten, & Oor, 2003; Carpenter, Miyake, & Just, 1995; Kolk & Van Grunsvan, 1985). These representation and processing considerations, although of considerable interest, are not the focus of this study. Rather, we focus on simple sentences. The fact that some patients have trouble comprehending simple sentences first noted a quarter of a century ago (Schwartz, Saffran, & Marin, 1980) has not received much scrutiny. In fact, Berndt, Mitchum, et al. (1997) pointed out that up to a third of such patients perform at chance on tasks of comprehension of simple active sentences, an observation that, to our knowledge, has not been pursued systematically.

We address a series of functional–anatomic questions about relational knowledge in the context of simple sentences. (1) Does comprehension of thematic relations dissociate from that of locative relations? On a domain-general view, a common neural system extracts relational structures, and one would predict similar functional–anatomic associations across tasks that probe these kinds of knowledge. However, if the nature of the relational structure itself (thematic or locative) is critical to its neural instantiation, then one would expect functional–anatomic dissociations. (2) Do verbal and pictorial relational knowledge of events dissociate? Finding such a dissociation might mean that conceptual understanding of spatial events is distinct from the ability to map this knowledge onto language. It would also mean that patients with a conceptual deficit would be less likely to benefit from treatment strategies that focus on mapping concepts on to words. (3) What is the relationship between thematic role knowledge, and verb and noun processing? In general, one would expect verb more than noun processing to be associated with thematic role knowledge. However, Berndt, Haendiges, and Wozniak (1997) reported dissociations between comprehension of verbs and thematic role assignments in sen-

tences leaving unresolved questions about the strength of this association.

Underlying these questions is the test of a broader organizational principle, which falls into the general family of sensory–functional accounts of semantics. On these accounts, the anatomic organization of linguistic expressions of different spatial concepts parallels the anatomic organization of corresponding sensory–motor systems, and here we suggest that the latter serve as points of entry for the former. As such, thematic relation knowledge deficits would be most associated with posterolateral temporal lobe damage on the view that visual motion is the point of entry for this kind of knowledge. By contrast, locative relation knowledge would be most associated with fronto-parietal damage as these sensory–motor systems, perhaps tied to our abilities to track paths of moving objects and to reach and grasp things in the environment, serve as the point of entry for spatial knowledge. The lexical–semantic mediation of these terms would be guided by, *without necessarily being identical to*, their sensory–motor complements.

An ancillary goal of this study is methodological. Here, we advocate a new statistical method of analyzing lesion data. Lesion analyses are poised to capitalize on statistical advances in image analyses driven by functional imaging (Chatterjee, 2005; Rorden & Karnath, 2004). The most common approach to lesion analysis has been to identify regions of overlap of lesions in patients with a defined deficit. Traditional overlap methods do not take into account how often damage to these same areas does not produce the deficit. To address this shortcoming, methods that subtract composite lesions of patients without behavioral deficits from those with behavioral deficits provide a map of areas most likely to produce the deficit. This subtraction method has been used with great effectiveness (see Tranel & Kemmerer, 2004; Tranel et al., 2003). However, subtraction methods treat each patient's performances categorically as normal or abnormal. The continuous nature of patient performance, with varying degrees of deficit severity, is not incorporated in the analysis. More recently, Saygin, Wilson, Dronkers, and Bates (2004), Wilson and Saygun (2004), and Bates et al. (2003) introduced a voxel lesion symptom mapping (VLSM) method, which does consider patients' behavioral data as a continuous variable in the analysis. An issue that remains with VLSM is dealing with the spatial coherence of lesion patterns. Contiguous voxels are not independent, given that lesions (in the case of stroke) are determined by vascular anatomy. This problem of spatial coherence gives rise to the question of how best to correct for multiple (voxel) comparisons. To address the spatial coherence issue and to treat behavioral data as continuous rather than categorical, here we use permutation analyses as an adaptation of the basic VLSM approach.

To summarize, we report our investigations of the functional and anatomic underpinnings of thematic and locative relational knowledge in patients with focal left

brain damage. We use permutation analyses, an adaptation of VLSM methods, to infer neural structures most likely to mediate these forms of knowledge.

METHODS

Participants

Nineteen patients (11 men, 8 women), ranging from 40 to 78 years in age, with chronic left hemisphere lesion (of at least six months duration), were recruited from our Focal Lesion Patient Database (University of Pennsylvania). Patients with history of other neurological disorders affecting the central nervous system or psychiatric disorders are excluded from this patient database. Seven normal control subjects (2 men, 5 women) of a similar age range (43–76 years) and education level were also tested. We report instances when individual patients' performances fell outside the range of control subjects' performances. However, an important feature of permutation analyses of lesion data is that we need not adopt a strong position on whether any individual is categorically deemed to be normal or abnormal, as the continuous nature of the patients' performances is integral to the analysis. All patients and control subjects were native English speakers and right handed. Written informed consent in compliance with the Institutional Review Board of the University of Pennsylvania was obtained for each participant before testing.

Each participant was tested individually. A native English speaker delivered all spoken materials. Two investigators recorded participants' performances independently. The tasks were administered in multiple sessions scheduled at least 1 week apart.

Initial Screening

The oral language subtests from the Western Aphasia Battery (WAB) (Kertesz, 1982) were administered, and the aphasia quotient (AQ) was computed for every patient.

In the sentence–picture matching tasks, we used stylized stick figures (see rationale below). To make sure that the participants could recognize these figures, their ability to identify circle or square stick figures was evaluated. Forty simple line drawings of an action event involving a circle and a square were presented to participants sequentially. The participants were asked to point to the circle for 20 trials and to the square for the other 20 trials. Patients unable to perform this task were not included in the rest of the study.

Relational Knowledge: Thematic and Location Sentence–Picture Matching

Two sentence–picture matching tasks were designed to assess the patients' verbal comprehension abilities using simple sentences that described thematic or location re-

lations. If the extraction of a relational structure is critical and common to both, then performance and anatomic localization across both tasks should be highly correlated. However, if thematic role knowledge is instantiated in posterolateral temporal networks and locative knowledge in fronto-parietal networks, then we would expect different brain–behavior relationships for deficits of these kinds of knowledge.

In these two tasks, participants were presented with spoken active sentences describing an action event (e.g., “The circle kicks the square.”) or a spatial relation (e.g., “The circle is above the square.”). They chose one of four possible choices of stick figure images engaged in the task (see Figure 1). The possibility that visual processing deficits would confound our results was minimized by simplifying stimuli. We used stick figures as an adaptation of the stimuli originally used by Saffran, Schwartz, and Marin (1980) and Schwartz et al. (1980). Because our focus is on the relational aspects of sentences, these stimuli are advantageous over those with images of real-world objects, which could introduce additional confounds by adding processing of the objects engaged in the events being depicted. We avoided syntactically complex sentences. Comprehension of such sentences places additional demands on working memory (Kolk et al., 2003) and involves linguistic transformations linking deep and surface sentential structures (Grodzinsky, 1995), none of which are directly relevant to our investigation. Because the direction of actions depicted can influence participant's responses (Chatterjee, Southwood, & Basilico, 1999; Chatterjee, Maher, Gonzales-Rothi, & Heilman, 1995; Chatterjee, Maher, & Heilman, 1995), the directionality of actions was counterbalanced across stimuli.

Participants pointed to one of the four pictures that best matched the spoken sentence. The pictorial materials were paired with 40 active sentences describing 10

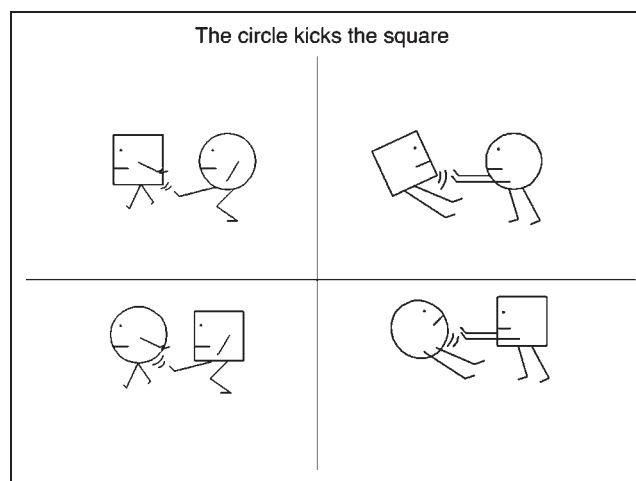


Figure 1. Example of sentence–picture matching stimuli for the thematic role knowledge task. The participant points to one of the four pictures that matches the sentence.

possible action events (brush, clean, cut, hit, kick, kiss, lift, push, shoot, spray) and 28 sentences describing 7 possible locative relations (in, on, above, below, through, next to, far from). The location of the correct response was counterbalanced across all conditions.

Linguistic and Conceptual Knowledge of Thematic Roles

This task probed participants' causal understanding of action events by examining their abilities to infer the likely consequence of the same event described in simple sentences or depicted in pictures. If access to knowledge of thematic relations varies depending on whether it is accessed pictorially or verbally, then we should see dissociations in performances and differences in brain-behavior relationships. Conceptual knowledge deficits would be expressed both pictorially and linguistically, whereas a mapping deficit would be associated with preserved pictorial knowledge of events but poor performance when this knowledge is accessed using language.

In 20 trials of this task, the participants were presented with a spoken active sentence (e.g., "The circle kicked the square."), and were asked to point to the most likely consequence following the sentence among four pictures (see Figure 2). In another 20 trials, the consequence of an event had to be inferred exclusively from a picture rather than any verbal input. No verbal response was required for either the sentence or the

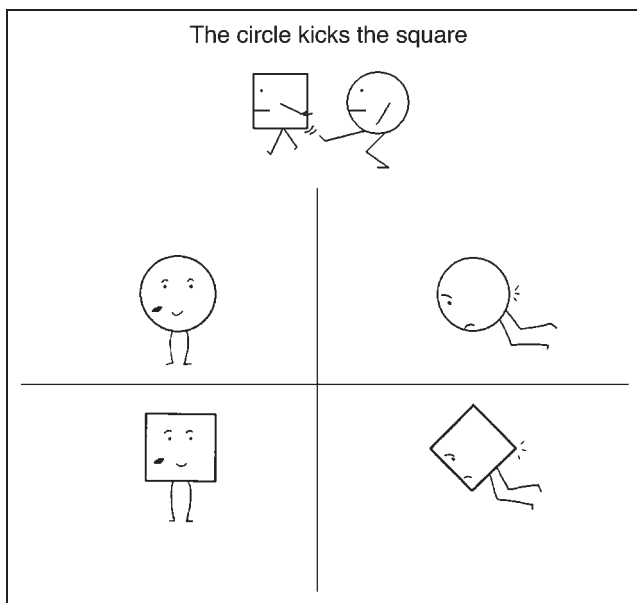


Figure 2. Example of the stimuli for the event consequence task. The participant either sees the sentence (above) or the picture depicting an event (middle), and then chooses one of the four pictures that best depicts the consequence of the event. In the stimuli presented to the participant, either the sentence or the event, but not both, is depicted.

picture consequence tasks. The two tasks were administered in different sessions.

Action and Object Knowledge: Single Words

This task was designed to assess participants' comprehension of single action and object words. The stimuli for these experiments were taken from an earlier neuroimaging study (Kable et al., 2002). The noun and verb tasks were of similar difficulty based on accuracy and reaction time performances in young normal participants. Participants were presented with 60 word triads (e.g., bed–chair–couch, shooting–aiming–punching) and were asked to perform a conceptual matching task similar to the Pyramids and Palm Tree task (Howard, 1992). In each triad, a target stimulus appeared at the top and two choice stimuli appeared at the bottom. The participants were instructed to point to one of the choice stimuli that matched the target stimulus more closely. Half of the triads consisted of three nouns, and the other half consisted of three verbs. The positions of the correct response (left/right) and the word class (nouns/verbs) were counterbalanced across the 60 trials. One patient had mild difficulty reading. For this patient, the experimenter read the stimuli out loud while pointing to the corresponding words. One patient was not tested on this task.

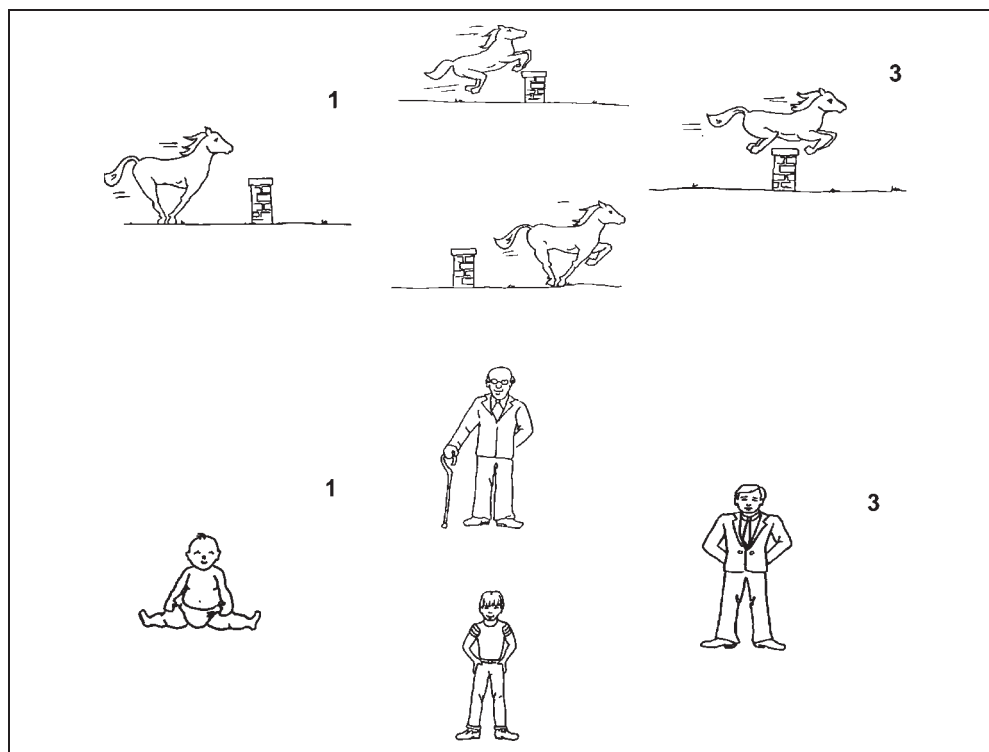
General Inferential Abilities: Selecting a Picture for Narrative Coherence

A task adapted from Saffran (unpublished material) to test participants' general inferential abilities was administered. The participants were presented with 32 trials of this task, each consisting of pictures at three serial positions, aligned horizontally. One of the three positions had two pictures, aligned vertically, and the participants were instructed to point to the picture that was a better fit with the pictures at the other two serial positions in establishing a coherent narrative. The coherence of the narrative on each trial was based on inferring the temporal order of how an event would unfold (see Figure 3), rather than being based on knowing who was doing what to whom or the consequences of such actions.

Neuroanatomical Analysis

All patients had either CT scans or MRI scans of their brains. A neurologist blind to the patients' performances on the tasks mapped the individual patients' brain lesion using the MRICRO software (Rorden & Brett, 2000; see www.sph.sc.edu/comd/rorden/mricro.html for details of the program). Lesions were drawn on templates tilted in the same axial planes of the source images. With MRI scans, the lesions were verified or modified by then comparing coronal and sagittal images of the original scans and those drawn onto the template. Each template was then realigned to a common axial angle using the

Figure 3. Examples of the stimuli used in the task of selecting a picture for narrative coherence in the unfolding sequence.



software's realignment procedures. We adapted VLSM approaches (Bates et al., 2003) to incorporate permutation analyses (Nichols & Holmes, 2002). This approach is especially effective in data with spatial correlation, such as lesion maps. In brief, a permutation test involves creating a null distribution for an arbitrary test statistic by creating a large number of random permutations of the data and regenerating the test statistic for each permutation. Given some readily satisfied assumptions (Good, 2005), this procedure yields an effective null distribution against which the "true" test statistic can be measured. Voxel-based structure function correlations were assessed by regressing behavioral scores on lesion status scores across participants independently for each voxel. Statistical significance was determined by non-parametric permutation test, with permutations generated by randomly permuting the mapping of the lesion score to the behavioral score. A maximum statistic across the entire brain is calculated for each permutation and thresholds for significance calculated from the 95th percentile of this distribution, to ensure a family-wise false-positive rate of 0.05 (Nichols & Holmes, 2002). Using the maximum statistic naturally corrects for multiple comparisons—we can say of a *t* value that exceeds a threshold derived in this way that under the null hypothesis, we would expect to observe a more extreme value *anywhere in the brain* only 5% of the time. As permutation testing avoids parametric assumptions and permits one to precisely calculate the *t* value corresponding to a specified alpha, its use is championed in many different areas of research (Good, 2005). Only

voxels that were damaged in at least two patients were included in our analyses, to minimize the effects of outlier observations.

RESULTS

Initial Screening

The patients' performance on WAB varied with AQs ranging from 21.3 to 99.3. Six patients were classified as Broca's aphasics, one as Wernicke's aphasic, one as a conduction aphasic, eight as anomic, and four performed in the normal range (i.e., AQ >93.8).

Five patients with the lowest AQ (all classified as Broca's aphasics) did not identify a circle or square reliably (average accuracy = 71%, range: 57.5–80%). These patients were excluded from further data analyses, as tests of our main hypotheses are contingent on the patients being able to reliably identify the circle and square figures. The remaining 14 patients had AQ scores that ranged from 53 to 99. These 14 patients' performances and the range of control participants' performances on individual tasks are summarized in Table 1.

Relational Knowledge: Thematic and Locative Knowledge

Performances across both thematic role and locative knowledge tasks correlated significantly ($r = .66, p < .05$). Seven patients performed outside the control participants' range on the thematic role sentence–picture

Table 1. Patients' Performances Shown as Percent Accuracy for the Experimental Conditions

	Patient No.															Control Range
	452	90	20*	412*	342	236	76	337	166*	454	384	141	480	85		
WAB AQ	53	63	72	81	81	85	87	88	89	92	94	97	99	99		
Thematic role sentence–picture matching (A)	57	35	60	98	78	100	88	73	85	78	100	98	100	100	87.5–100	
Locative sentence–picture matching (B)	43	57	96	100	89	82	96	82	79	75	100	100	100	100	89.3–100	
Sentence consequence (C)	20	42	50	98	83	90	58	58	50	83	98	100	98	100	75–100	
Picture consequence (D)	57	53	88	95	96	100	83	65	93	88	88	98	100	100	85–100	
Verb triad (E)	97	93	90	97	77	93	90	90	83	97	97	97	97	100	90–96.7	
Noun triad (F)	80	90	97	87	70	93	97	77	90	90	77	90	87	93	80–96.7	
Narrative coherence (G)	91	88	100	97	84	100	91	72	100	100	81	94	97	100	90.6–100	

Patient no. refers to their database numbers. Patients had MRI scans, unless indicated by *, in which case they had CT scans. Letters in parentheses refer to Figure 4 for the anatomic correlations for these performances. The aphasia quotients (AQs) are shown for the Western Aphasia Battery (WAB), and the last column shows the range of normal age-matched control subjects' performances.

matching task. Six patients performed outside the control participants' range on matching locative sentences to the appropriate pictures. Among them, five patients had performances that fell outside the normal range on both tasks. Importantly, two patients performed outside the normal range on the thematic role but not the on locative task, and one patient performed outside the normal range on the locative but not on the thematic role task.

Permutation analyses indicated that the *t*-statistic thresholds with a significance level of $p < .05$ for thematic role was 3.19 and for locative relations was 2.57. When mapping the patients' performance scores with their brain lesions, both thematic role and locative relation deficits were associated with damage to different anatomic regions. Thematic role knowledge deficits correlated with lesions to the mid–middle (BA 21) and anterior superior temporal gyrus (anterior BA 22) as well as white matter undercutting the superior temporal and supramarginal gyrus (Figure 4A). By contrast, locative knowledge deficits were correlated with inferior parietal (BA 39, 40), occipito-parietal junction (BA 39/19), and inferior prefrontal damage (BA 45). Parts of the very anterior superior temporal gyrus (anterior BA 22) also correlated with locative deficits (Figure 4B).

These results show that although there is a general correlation between comprehension of sentences conveying thematic and locative relations, individual dissociations in both directions occur. Furthermore, both deficits have distinct neural associations, suggesting that the type of relations being described in these sentences is relevant to their neural instantiation.

Linguistic and Conceptual Knowledge of Thematic Roles

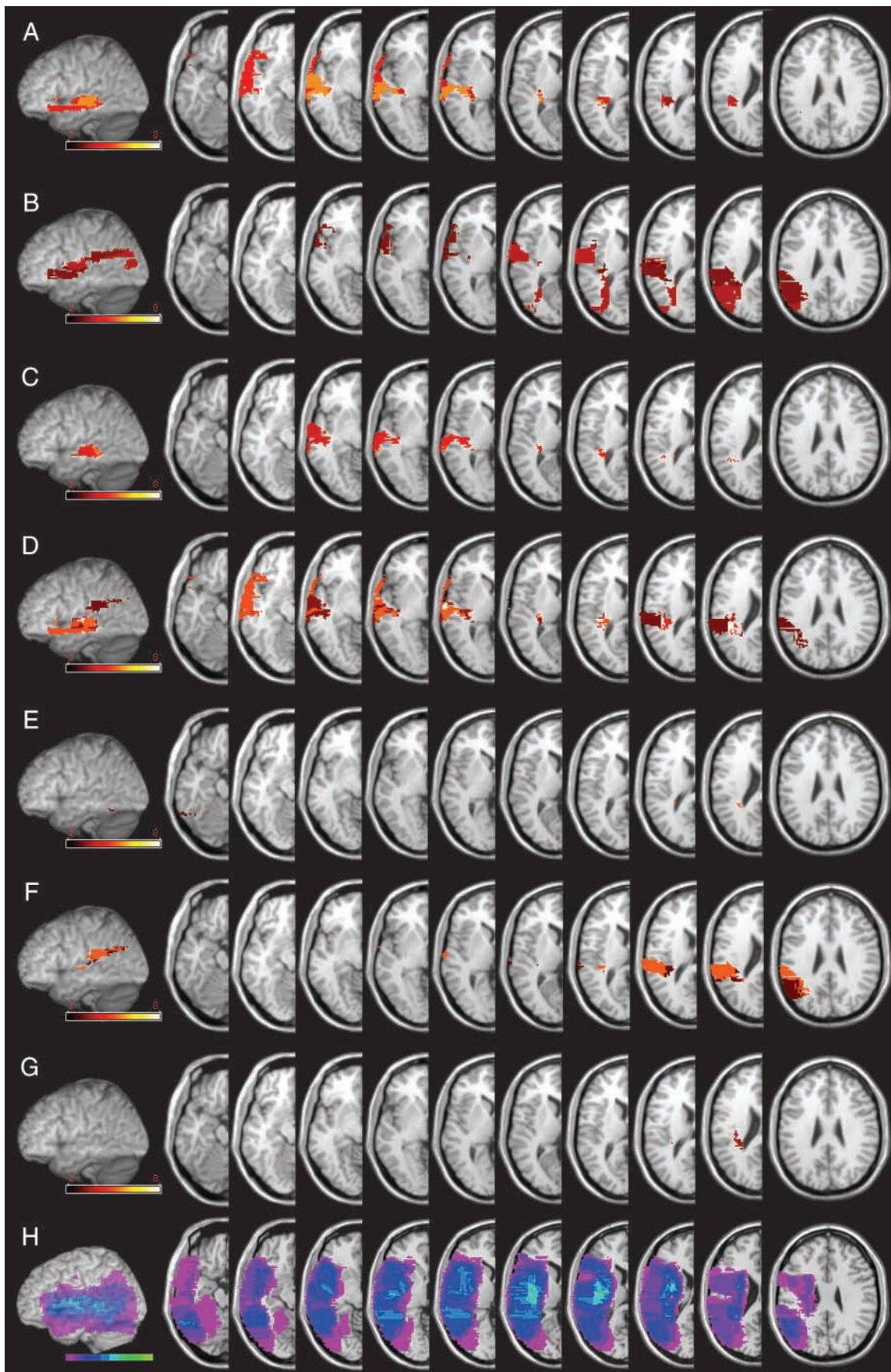
As might be expected, performance on the two tasks correlated highly ($r = .80$, $p = .001$). Six patients' performances fell outside the control participants' range when inferring consequences from sentences. Four of these six patients performed outside the control participants' range when inferring the consequences of the same actions in pictures. No patient showed the opposite dissociation, that is, a deficit in inferring consequences from pictures but not from sentences.

Permutation analyses revealed that mapwise *t*-statistic thresholds with a significance level of $p < .05$ for sentence consequence was 3.80 and for picture consequence was 2.93. Correlating patients' brain lesions with their task performance showed that deficits in inferring consequences of actions using sentences or pictures were associated with mid–middle temporal gyrus (BA 21) damage (Figure 4C and D). This localization was very similar, albeit somewhat more restricted, to that seen with the sentence–picture matching task with simple active sentences. However, deficits of the inferring consequences of actions using pictures were also associated with anterior superior temporal gyrus (anterior BA 22), supramarginal gyrus (BA 40), and inferior prefrontal (BA 45) damage (Figure 4D).

Action and Object Knowledge: Single Words

Performances on verb and noun triads did not correlate ($r = -.04$). Neither did performance correlate signifi-

Figure 4. Statistical maps (A–G) of neuroanatomic regions in which damage correlated significantly (using permutation statistics) with performances on the following tasks: (A) thematic role sentence–picture matching, (B) locative sentence–picture matching, (C) sentence consequence, (D) picture consequence, (E) verb triad, (F) noun triad, and (G) narrative coherence. (H) shows the lesion overlap of subjects in the study. Color farthest to the left of the scale is for one lesion, with each successive color representing additional lesions at that voxel.



cantly with performance on sentence–picture matching for thematic relations. Two patients performed outside the control participants’ range on the verb task, and three performed outside the control participants’ range on the noun task. Both patients with verb deficits also had sentence-level deficits. One of the three patients with noun triad deficits did not have a sentence-level deficit.

Permutation analyses indicated that *t*-statistic thresholds with a significance level of $p < .05$ for the verb task was 2.67 and for the noun task was 2.49. Verb processing deficits were associated with damage to a small region within the posterior inferior temporal gyrus (BA 37) (Figure 4E). By contrast, noun processing deficits were associated with posterior superior temporal (posterior BAS 22), supramarginal (BA 40), and angular gyrus (BA 39) lesions (Figure 4F).

General Inferential Abilities: Selecting a Picture for Narrative Coherence

Performance on the inferential tasks did not correlate significantly with sentence–picture matching of either thematic roles or locative relations. There was a trend toward a correlation with the nonverbal action consequence task ($r = .560$, $p = .06$). Four patients performed outside the normal range on this task. Two of these four patients performed poorly on the nonverbal action consequence task and two performed well. Two patients that were abnormal on the nonverbal action consequence task performed normally on this inferential task, suggesting a double dissociation in the performances on these inference tasks. Permutation analyses revealed that the mapwise *t*-statistic threshold with a significance level of $p < .05$ for this task was 3.17. Lesions to the posterior corona radiata and the medial arcuate fasciculus undercutting the supramarginal gyrus correlated most closely with deficits on this task (Figure 4G).

DISCUSSION

The current study investigated the functional neuroanatomy of relational knowledge as expressed in simple sentences. A general motivation for our investigation is sympathy for claims that understanding relational structures is a critical step in the development and organization of complex thought. Recognizing relations, *per se*, shifts cognitive focus away from objects to the relation between objects. As Gentner (2003) claims, a shift to relational thinking is “what makes us smart.” Here we examine thematic and locative relations.

The first question we addressed was whether thematic role knowledge and locative knowledge dissociate from each other behaviorally and anatomically. Relational knowledge could be organized in a domain-general or domain-specific manner. For a domain-general account,

the shift away from the object to extracting the relationship among objects is the critical cognitive operation. For a domain-specific account, the nature of the relation as reflected in the relevant sensory–motor points of entry might be critical to its neural mediation. Thus, motion might be a critical point of entry for thematic relations and spatial perceptions tied to reaching/grasping or eye-gaze behaviors might be critical points of entry for locative relations. On such an account, one would expect functional–anatomic dissociations across both kinds of tasks.

We found evidence for both domain-general and domain-specific processes in the two kinds of relational knowledge tested here. Two lines of evidence are consistent with a domain-general account. First, performance on both tasks correlated highly. Second, across both tasks, lesions to the anterior superior temporal gyrus and the inferior prefrontal cortex correlated with the degree of behavioral deficit. However, two lines of evidence also point to a domain-specific account. First, despite the correlated performances within the group across both tasks, individual participants showed double dissociations. Although the numbers of patients are small, two patients performed outside the normal range on the thematic role but not on the locative task, whereas one patient performed outside the normal range on the locative but not on the thematic role task (for a similar behavioral dissociation, see Weinrich, McCall, & Weber, 1995). Second, the anatomic correlations for these deficits differed. Most notably, thematic role assignment deficits correlated with lesions to the mid-portion of the middle temporal and superior temporal gyrus, whereas locative relation deficits correlated with damage to the inferior fronto-parietal cortex and the posterior temporo-parietal junction.

The domain-specific account is consistent with a particular form of the sensory–motor hypothesis. We argued previously that motion is processed in the temporal cortex with a posterior-to-anterior concrete-to-abstract gradient (Kable et al., 2002, 2005). Action verbs are processed more anteriorly than action pictures. This region is ventral to the classic Wernicke’s area. Neuroimaging studies find that the left posterior middle temporal cortex is involved in making judgments of the meaning of verbs (Kable et al., 2002, 2005), making lexical decisions on verbs (Perani et al., 1999), generating appropriate verbs given nouns (Warburton et al., 1996; Martin et al., 1995), and generating homonymous words when used as actions rather than objects (Tranel, Martin, Damasio, Grabowski, & Hichwa, 2005). This region is commonly impaired among patients with difficulty associating action pictures to verbs (Hillis, Tuffiash, Wityk, & Barker, 2002) and making judgments about action pictures on the basis of their attributes (Tranel et al., 2003). We now show that for the processing of action events using simple sentences, the critical region is shifted anteriorly within the mid-portion of the middle and superior temporal

gyrus. Consistent with our findings, Dronkers, Wilkins, Valin, Redfern, and Jaeger (2004) showed that lesions within the left middle temporal gyrus are associated with impaired comprehension of simple active sentences and the mid-portion of the middle and superior temporal gyrus is activated by sentence-level semantic violations (Friederici, Ruschemeyer, Hene, & Fiebach, 2003) and sentences that use motion verbs (Wallentin, Lund, Ostergaard, Ostergaard, & Roepstorff, 2005).

Locative relations, as described by sentences, seem to be mediated by inferior fronto-parietal cortices. We found that damage to the inferior frontal gyrus, inferior premotor, and supramarginal gyrus, along with the temporo-parietal junction, was most closely associated with severity of the locative deficit. These findings are remarkably consistent with Tranel and Kemmerer's (2004) anatomic observations of the neural correlates of locative prepositions (e.g., see their Figure 3 for the correlates of preposition–picture matching task, using subtraction lesion analyses). We speculate that neural circuits dedicated to complex motor behavior, including reaching, grasping, and eye-gaze behavior (Wu, Morganti, & Chatterjee, 2004; Binkofski et al., 1998; Grafton, Fagg, Woods, & Arbib, 1996; Gonzalez-Rothi, Heilman, & Watson, 1985), are the sensory–motor points of entry of spatial knowledge expressed by locative relations.² On this view, prepositional relationships label the kind of spatial knowledge needed to track paths of motion, reach, or navigate (which itself may integrate visual and proprioceptive and vestibular input) in and around things in our environment.

Our observations are not consistent with the prominent hypothesis that knowledge of actions engages abstract motor representations mediated by prefrontal neurons. Tranel et al. (2003) found that damage to the white matter underlying the left frontal operculum and the anterior portion of the insula was associated with impaired retrieval of action knowledge, in addition to the association with posterior middle temporal gyrus damage. Hauk and Pulvermuller (2004) employed verb stimuli that preferentially describe actions of the leg, arm, or mouth in both fMRI and event-related potential studies, and reported a somatotopic distribution over frontal cortices of engagement by these verb classes. Incidentally, they also found posterior temporal activation for these verbs.

The association of action knowledge to posterior frontal regions of the brain is interpreted as indicating that one comprehends actions by mapping them to a mirror neuron system. Our previous findings (Kable & Chatterjee, 2006; Kable et al., 2002, 2005) and the current ones do not provide strong support for this dominant view. We suggest that the mirror neuron system contributes to the comprehension of only a subset of actions. Buccino et al. (2004), in an fMRI study, found that prefrontal activations were only present when the observed actions are within the motor reper-

toire of the observer. Furthermore, some action events, such as “slithering snake” or “swarming bees,” cannot, in principle, be instantiated in human motor systems. In the current study, lesions to the posterior frontal region and anterior superior temporal gyrus were associated with deficits in both thematic and locative knowledge. Thus, damage to these areas does not appear to produce specific deficit in action event comprehension. Rather, these areas may be related to domain-general processing (e.g., Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997) or to extracting a syntactic structure (Humphreis, Binder, Medler, & Liebenthal, 2006) that is independent of the semantic content of that structure.

The second question we addressed was whether conceptual and linguistic knowledge of thematic relations dissociate. Similar questions have been addressed in the context of object knowledge (Vignolo, 1999; Chertkow, Bub, Deaudon, & Whitehead, 1997; Gainotti, Miceli, & Caltagirone, 1979). We found that deficits of conceptual knowledge of thematic relations dissociated from deficits of linguistic access to this knowledge. Four patients' performances fell outside the range of normal performances across both tasks. However, two patients did well judging the consequence of events depicted in pictures, and poorly with sentences. Damage to the middle temporal and parts of the anterior superior temporal gyrus correlated most closely with the linguistic deficits. In addition, damage to the supramarginal and inferior frontal gyrus correlated with conceptual-level deficits. Saygin et al. (2004) also assessed linguistic and nonlinguistic deficits in action comprehension in a series of aphasic patients. They also found conceptual and linguistic dissociations. Their patients with linguistic deficits also had lesions in the superior temporal gyrus, and patients with nonlinguistic deficits had more distributed damage including inferior frontal and postcentral gyrus lesions.

The observation that some patients have trouble comprehending simple sentences as a downstream consequence of an underlying conceptual disorder has important practical implications. Mapping treatments assume preserved conceptual representations and patients are trained on rules to map language on to this conceptual knowledge (Byng, Nickels, & Black, 1994). Our study suggests that the subgroup of patients with intact conceptual representations is more likely to benefit from mapping treatments than those with conceptual deficits.

The third question we address is the relationship between thematic role comprehension and noun and verb processing. Given the many reports of noun–verb processing dissociations in aphasic individuals (Berndt, Haendiges, Mitchum, & Sandson, 1997; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Damasio & Tranel, 1993; Caramazza & Hillis, 1991; Zingeser & Berndt, 1990; Miceli, Silveri, Nocentini, & Caramazza, 1988), it is not surprising that noun and verb processing deficits did not correlate.

However, performances on both tasks also correlated poorly with the thematic role sentence–picture matching task. Brain–behavior correlations revealed that the posterior inferior temporal gyrus was critical to verb processing. This region is just anterior to area MT, although it is located slightly ventral to where we observed greater activation for verbs than nouns in our previous fMRI study (Kable et al., 2002). By contrast, posterior parietal damage correlated with noun processing. The relationship of verb to sentence processing is complex. Berndt, Haendiges, and Wozniak (1997) suggested that verb retrieval difficulty might contribute to sentence processing impairments in some, but not all, patients.

The deficits of thematic and locative relational knowledge are not explained by a general deficit in making inferences. On a task in which patients made inferences about the temporal order of an unfolding event, there were no significant correlations with deficits on this task and either the locative or the thematic relation sentence–picture matching tasks. Again, we interpret this lack of correlations cautiously because they are based on relatively few subjects. Two patients' performances fell outside the normal range on the consequence task but not on the inference task, whereas two other patients showed the reverse pattern. The only area that correlated with deficits on this inference task was within the white matter affecting the corona radiata, and possibly, the arcuate fasciculus (Catani, Jones, & Ffytche, 2005). In this regard, it should be noted that damage to this general subcortical region was correlated with deficit severity in almost every task (Figure 4), suggesting that integrity of the connecting fibers, perhaps those linking posterior temporal–parietal and inferior prefrontal regions, may be critical to a broad range of reasoning tasks.

As a final comment, we return to the functional–anatomic organization of relational knowledge. We have suggested that the relevant sensory–motor processing serves as a guide to the linguistic organization of this knowledge. This is consistent with the view that spatial terms are grounded in interactions with the environment as mediated neurally by specific sensory–motor networks (Chatterjee, 2001; Regier & Carlson, 2001; Talmy, 2000; Chatterjee et al., 1999; Chatterjee, Maher, & Heilman, 1995; Hayward & Tarr, 1995; Landau & Jackendoff, 1993). At issue, however, is the nature of this “grounding.” We have been careful *not* to claim that these early sensory–motor cortices are necessarily engaged by the linguistic mediation of this knowledge. For action events, visual motion areas in area MT are not activated by verbs (Kable et al., 2002, 2005). The posterior middle temporal and, perhaps, the inferior temporal gyri instantiate processing of verbs, and we now show that damage within more anterior portions of the middle and superior temporal gyri is associated with deficits of processing sentences that describe action events. Thus, there appears to be a gradient along the temporal cortex, with area MT/MST and the posterior superior

temporal sulcus serving as points of entry for the linguistic instantiation of action concepts, which are processed progressively more anteriorly along the lateral temporal cortex.

Within the family of sensory–functional accounts of semantics, we wish to highlight an important difference between relational concepts and object concepts. In object concepts, early sensory–motor processing is considered integral to the meaning of entities (Simmons & Barsalou, 2003; Martin et al., 2000; Martin, Wiggs, Ungerleider, & Haxby, 1996; Warrington & Shallice, 1984). As mentioned in the Introduction, the link between lexical semantics and sensory–motor processing for relational terms differs from that of object terms. Relational terms have a sparser semantic organization with a shallower hierarchical structure (Miller & Fellbaum, 1991). Verbs, unlike nouns, tend to have more of a matrix-like organization with less defined levels of structure (Vigliocco, Vinson, Lewis, & Garrett, 2004; Huttenlocher & Lui, 1979). Verbs are less dependent than nouns on precise features for their meaning (Gentner & Kurtz, 2005; Graesser, Hopkinson, & Schmid, 1987; Gentner, 1981; Huttenlocher & Lui, 1979) and tend to be more abstract than nouns (Bird, Lambdon Ralph, Patterson, & Hodges, 2000).

Damasio (1989) proposed that convergent intermediary zones instantiate the neural bases for semantics by reactivating early sensory–motor cortices. We suggest that these intermediary zones are topographically aligned with the relevant sensory–motor cortices (also see Simmons & Barsalou, 2003). Importantly, the relative importance of intermediary convergence zones and early sensory–motor networks may not be the same for relational and entity terms. For relational terms, the intermediary zones play a role in abstracting relations from the complementary sensory–motor networks. These sensory–motor networks serve as critical points of entry, without being intrinsic, to the lexical semantics of relational terms. In fact, the relative importance of such intermediary zones over early sensory–motor points of entry in the neural mediation of relational concepts may be exactly what gives these terms the freedom to be used flexibly.

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Notes

1. Some nouns are also relational. Thus, the noun “predator” is understood specifically in a relational context. We are not aware of empirical study of the neural underpinnings of relational nouns per se.
2. Motion can be segregated into manners and paths of motion. In English, manners of motion (gallop, trot, canter) are described primarily by verbs, whereas paths of motion (into, around) are described primarily by prepositional phrases (Talmy, 2000). We have made preliminary observations suggesting that regions within the posterior inferior temporal cortex preferentially process manners of motion and that posterior parietal cortices preferentially process paths of motion (Wu et al., 2004). In this article, manner of motion is being linked to verb processing.

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