



Neuroanatomical distribution of five semantic components of verbs: Evidence from fMRI

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Abstract

The Simulation Framework, also known as the Embodied Cognition Framework, maintains that conceptual knowledge is grounded in sensorimotor systems. To test several predictions that this theory makes about the neural substrates of verb meanings, we used functional magnetic resonance imaging (fMRI) to scan subjects' brains while they made semantic judgments involving five classes of verbs—specifically, Running verbs (e.g., *run, jog, walk*), Speaking verbs (e.g., *shout, mumble, whisper*), Hitting verbs (e.g., *hit, poke, jab*), Cutting verbs (e.g., *cut, slice, hack*), and Change of State verbs (e.g., *shatter, smash, crack*). These classes were selected because they vary with respect to the presence or absence of five distinct semantic components—specifically, ACTION, MOTION, CONTACT, CHANGE OF STATE, and TOOL USE. Based on the Simulation Framework, we hypothesized that the ACTION component depends on the primary motor and premotor cortices, that the MOTION component depends on the posterolateral temporal cortex, that the CONTACT component depends on the intraparietal sulcus and inferior parietal lobule, that the CHANGE OF STATE component depends on the ventral temporal cortex, and that the TOOL USE component depends on a distributed network of temporal, parietal, and frontal regions. Virtually all of the predictions were confirmed. Taken together, these findings support the Simulation Framework and extend our understanding of the neuroanatomical distribution of different aspects of verb meaning.

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1. Introduction

An important new multidisciplinary movement in the mind/brain sciences is an approach to conceptual representation that is often referred to as the Embodied Cognition Framework or, as we will call it, the Simulation Framework. The central tenet of this approach is that semantic

knowledge is not entirely amodal in character, but is instead grounded in sensorimotor systems that are automatically engaged during online conceptual processing so as to re-enact modality-specific patterns of activity that are normally evoked during perception and action. The Simulation Framework has been receiving increasing attention from researchers in numerous areas of inquiry, including linguistics (Bergen, 2007; Hampe, 2005), psychology (Barsalou, 1999, 2005, in press; Gibbs, 2006; Glenberg, de Vega, & Graesser, in press-a; Pecher & Zwaan, 2005), neuroscience (Damasio, 1989; Gainotti, 2007; Gallese & Lakoff, 2005; Goldberg, Perfetti, & Schneider, 2006; James

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& Gauthier, 2003; Jeannerod, 2006; Kemmerer, in press; Keysers & Gazzola, 2006; Simmons et al., 2007), and philosophy (Gallagher, 2005; Lakoff & Johnson, 1999; Prinz, 2002). Although much of the work conducted so far has focused on the types of object concepts that are usually encoded by nouns (Martin, 2007), a growing number of studies have explored the types of action concepts that are usually encoded by verbs (Fischer & Zwaan, in press).

The goal of this paper is to extend recent research on action concepts within the Simulation Framework by reporting a new study that employed functional magnetic resonance imaging (fMRI) to investigate the neuroanatomical distribution of five distinct semantic components of verbs. This study builds on previous work both empirically and theoretically. On the empirical side, we describe a complex set of findings that adds to the existing database in a variety of novel ways, converging with the results of some prior studies while diverging from those of others. On the theoretical side, we attempt to enrich the Simulation Framework, as it has hitherto been applied to action concepts, by linking it with—or, more precisely, subsuming it within—a more general theory of the linguistic encoding of events that has been supported for over 20 years and that continues to be highly influential.

The model we are referring to is sometimes called the Two-Level Theory because it maintains that the meanings of verbs have two separate levels of semantic structure (e.g., Davis, 2001; Iwata, 2005; Pinker, 1989; Rappaport Hovav & Levin, 1998; Van Valin, 2005, 2006; for a review see Levin & Rappaport Hovav, 2005; see also Pinker, 2007, chap. 2). The first level consists of an austere representation, referred to variously as the “event structure template” (Rappaport Hovav & Levin, 1998), the “thematic core” (Pinker, 1989), or the “logical structure” (Van Valin, 2005, 2006), that is (a) common to all the verbs in a given class, (b) composed primarily of schematic predicates and variables for arguments, (c) relevant to the syntactic properties of all the verbs in a given class, and (d) within the theoretical scope of “constructionist” approaches to language (e.g., Fried & Boas, 2005; Goldberg, 1995, 2006; Goldberg & Jackendoff, 2004; Jackendoff, 2002; Kako, 2006; Östman & Fried, 2005). The second level reflects the uniqueness of every verb and has been dubbed the “constant” (Rappaport Hovav & Levin, 1998) because it captures idiosyncratic semantic features that (a) distinguish each verb in a given class from all the others, (b) are often modality-specific in format, (c) have no influence on the syntactic properties of verbs, and (d) fall within the theoretical scope of the Simulation Framework. According to the Two-Level Theory, the composite meaning of a verb involves the association of a particular constant with a particular event structure template. For example, so-called Running verbs (Levin, 1993, pp. 265–267) encode different ways in which animate entities (typically humans) locomote, and while all the verbs in this class share the same template, as shown in (1), they differ with respect to the unique constants that instantiate the “manner” component of that template, as

shown in (2). In other words, the template in (1) represents a schematic or skeletal event structure in which an agent X performs a generic action of the locomotion type, with the details left unspecified. The three verbs in (2) share this semantic scaffolding, but the unique constant of each one fleshes out the “manner of locomotion” variable in an idiosyncratic way (symbolized by the verb in quotation marks), indicating not only how each particular kind of gait is executed (i.e., how it feels in the body) but also how it appears when seen by an observer (Jackendoff, 2002, p. 350).

(1) Template [x ACT <MANNER OF LOCOMOTION>]

(2) a. *stroll* [x ACT <MANNER OF LOCOMOTION>] (e.g., Susan strolled down the sidewalk)

|
“stroll”

b. *strut* [x ACT <MANNER OF LOCOMOTION>] (e.g., Bill strutted across the street)

|
“strut”

c. *sashay* [x ACT <MANNER OF LOCOMOTION>] (e.g., Ashley sashayed up to Steve)

|
“sashay”

Based on the Simulation Framework and the broader Two-Level Theory, we conducted an fMRI study that focused on five distinct classes of verbs—Running, Speaking, Hitting, Cutting, and Change of State—that vary systematically with respect to the presence or absence of five distinct semantic components—ACTION, MOTION, CONTACT, CHANGE OF STATE, and TOOL USE. Table 1 lists 20 verbs belonging to each class, and Table 2 provides a matrix illustrating the five semantic components, organized as a function of verb class. The aim of our study was to test a set of hypotheses about the neural substrates of the five semantic components. These hypotheses are expressed in Table 2 and elaborated in detail below. It is important to clarify at the outset, however, that the five semantic components addressed by our study are represented, albeit in different ways, at both levels of verb meaning posited by the Two-Level Theory (see especially Pinker, 1989; see also Levin & Rappaport Hovav, 2005; Van Valin, 2005). On the one hand, abstract symbols for these components, *qua* components, are among the basic conceptual elements in the event structure templates associated with the five verb classes; these symbols interface with syntax, and they differentiate entire classes of verbs, not individual verbs. On the other hand, concrete, modality-specific, idiosyncratic, lexically discriminative instantiations of the components are specified by the constants of individual verbs; these semantic structures are plausible candidates for sensorimotor re-enactment during online processing, according to the Simulation Framework. Crucially, our hypotheses about the neural substrates of the five semantic components apply to this second level of verb meaning, and the predictions about patterns of brain activation that we derive from these hypotheses reflect the Simulation Framework. In Section 4.2, we return to the issue of how the two distinct levels of verb meaning relate to each other, both linguistically and neurobiologically.

Table 1
Twenty verbs from each of five different classes

	Running (51.3.2)	Speaking (37.3)	Hitting (18)	Cutting (21)	Change of state (45)
1	walk	yell	batter	snip	break
2	amble	shout	hit	clip	shatter
3	stroll	holler	knock	cut	smash
4	saunter	bellow	pound	hack	chip
5	strut	scream	slap	scrape	crack
6	march	shriek	smack	scratch	fracture
7	stomp	wail	strike	slash	split
8	limp	cry	whack	slit	snap
9	trudge	bawl	tap	nick	rip
10	stagger	chant	clobber	gouge	tear
11	stumble	whisper	pummel	gash	bend
12	sprint	murmur	spank	chop	fold
13	run	mumble	jab	dice	crease
14	jog	mutter	poke	mince	crumple
15	skip	groan	prod	grate	crumble
16	sneak	whine	prick	shred	bloom
17	tiptoe	grumble	caress	slice	blossom
18	leap	chatter	stroke	carve	sprout
19	jump	whimper	pat	grind	wilt
20	hop	sing	pinch	sever	wither
Frequency	45.4 (8.4)	47.4 (7.1)	42.7 (10.6)	42.7 (7.9)	46.5 (6.2)
Length	4.9 (1.3)	5.4 (1.2)	4.7 (1.1)	4.6 (0.9)	5.3 (1.4)

The number beside the name of each class indicates the corresponding class in Levin's (1993) taxonomy. For frequency, cells indicate means and, in parentheses, standard deviations, based on Carroll et al. (1971). For length, cells indicate means and, in parentheses, standard deviations, in terms of number of letters.

1.1. Component 1: ACTION

The ACTION component is incorporated in the meanings of verbs of Running, Speaking, Hitting, and Cutting (Tables 1 and 2). Verbs of Running encode specific leg actions, verbs of Speaking encode specific vocal actions, and verbs of Hitting and Cutting encode specific arm/hand actions, with the latter class also implying skilled manipulation of a sharp tool. Within each of these classes, individual verbs contrast with each other semantically by making distinctions, often of a remarkably fine-grained nature, along a number of motor-related dimensions. For example, verbs of Running designate different types of rapid locomotion (e.g., *jog*, *run*, *sprint*), leisurely locomotion (e.g., *amble*, *stroll*, *mosey*), furtive locomotion (e.g., *sneak*, *tiptoe*, *sidle*), and awkward locomotion (e.g., *stagger*, *stumble*, *lurch*)

(Slobin, 2000). In fact, relative to many of the other 6000+ languages in the world (Levinson & Wilkins, 2006; Malt et al., in press; Slobin, 2004), English has a fairly rich inventory of locomotion verbs, with the class provided by Levin (1993) containing 124 members.

On the other hand, verbs of Change of State are marked in Table 2 as *not* incorporating the ACTION component. This is because, strictly speaking, the most basic event structure template for this class of verbs consists of a single-argument predicate which indicates that an object—often instantiated as an inanimate entity—shifts from one state or condition to another, as expressed by intransitive—or, more precisely, unaccusative—sentences like *The glass broke*, *The plate shattered*, and *The twig snapped* (Kuno & Takami, 2004; Levin, 1993; Levin & Rappaport Hovav, 1995, 2005; Pinker, 1989). It is true that the first fifteen Change of State verbs listed in Table 1 can also occur in transitive sentences with agentive subjects—i.e., sentences like *Bill broke the glass*, *Bill shattered the plate*, and *Bill snapped the twig*. However, this reflects the addition of a causal semantic component through a process that is sometimes called “template augmentation” (Rappaport Hovav & Levin, 1998; see also Dixon, 2000; Van Valin, 2005). Moreover, the idiosyncratic semantic features of these verbs do not specify the particular kind of action that the agent executes to alter the state of the affected object; instead, they focus on different types of object transformation. Finally, the last five Change of State verbs listed in Table 1 do not even allow template augmentation (e.g., *The flowers bloomed* vs. **Bill bloomed the flowers*), since they belong to a narrowly defined subclass referred to as verbs of Internally Caused Change of State (Levin, 1993; McKoon & MacFarland, 2000; Wright, 2001).

Turning to the brain, many studies utilizing a variety of techniques suggest that the primary motor and premotor cortices are engaged not only when familiar actions are executed, but also when they are imagined, observed, and heard (for reviews see Fadiga, Craighero, & Olivier, 2005; Jeannerod, 2006; Wilson & Knoblich, 2005; for more recent studies see Assmus, Giessing, Weiss, & Fink, 2007; Caetano, Jousmäki, & Hari, 2007; Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006; Filimon, Nelson, Hagler, & Sereno, 2007; Gazzola, Aziz-Zadeh, & Keysers, 2006; Pobric & Hamilton, 2006; Saygin, 2007; Van Schie et al., 2007). In addition, and in keeping with the Simulation

Table 2
Five semantic components of verbs and their hypothesized neural substrates, organized as a function of verb class

Verb classes	Hypotheses regarding semantic components and their neural substrates				
	(H1) Action = M1, M2	(H2) Motion = PLTC	(H3) Contact = IPS, IPL	(H4) Change of State = VTC	(H5) Tool use = Network
Running	+	+	–	–	–
Speaking	+	+	–	–	–
Hitting	+	+	+	–	–
Cutting	+	+	+	+	+
Change of State	–	+	–	+	–

Abbreviations: H1–H5, Hypotheses 1–5; M1, primary motor cortex; M2, premotor cortex; PLTC, posterolateral temporal cortex; IPS, intraparietal sulcus; IPL, inferior parietal lobule; VTC, ventral temporal cortex; (+) the component is necessarily incorporated by the verb class; (–) the component is not necessarily incorporated by the verb class.

Framework, a growing number of studies employing fMRI (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Hauk, Johnsrude, & Pulvermüller, 2004; Rüschemeyer, Brass, & Friederici, 2007; Tettamanti et al., 2005), transcranial magnetic stimulation (TMS; Buccino et al., 2005; Glenberg et al., in press-b; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005a), magnetoencephalography (MEG; Pulvermüller, Shtyrov, & Ilmoniemi, 2005b), high-density electroencephalography (EEG; Hauk & Pulvermüller, 2004), and purely behavioral methods (Borreggine & Kaschak, in press; Boulenger et al., 2006; Glenberg & Kaschak, 2002; Klatzky, Pellegrino, McClosky, & Doherty, 1989; Scorolli & Borghi, 2007; Zwaan & Taylor, 2006) provide evidence that the processing of spoken or written verbs for leg/foot actions (e.g., *kick*), arm/hand actions (e.g., *pick*), and mouth actions (e.g., *lick*) engages somatotopically mapped sectors of the primary motor and premotor cortices (for reviews see Pulvermüller, 2005; Fischer & Zwaan, in press; Glenberg, in press). One might suppose that the reason why hearing or seeing an action verb engages the motor system is because the person voluntarily conjures up a motor image (Ehrsson, Geyer, & Naito, 2003; Michelon, Vettel, & Zacks, 2006) of the linguistically encoded action after having already understood the verb's meaning. However, according to the strongest version of the Simulation Framework, the rapid, possibly automatic activation of the motor cortices actually constitutes an essential part of the comprehension process itself—specifically, the part that involves retrieval of the uniquely elaborated ACTION component of the verb's meaning. This position has been receiving increasing support, but it remains controversial, and further investigation is necessary to illuminate the many complex issues surrounding the topic. With the aim of contributing to this line of research, we formulated the following hypothesis: *Hypothesis 1 (H1): Semantic processing of the ACTION component of verbs of Running, Speaking, Hitting, and Cutting engages somatotopically organized primary motor and/or premotor cortices (Table 2).*

1.2. Component 2: MOTION

All five verb classes incorporate the MOTION component (Tables 1 and 2). Within the Running class, individual verbs elaborate this component by indicating how certain patterns of dynamic locomotion appear from the point of view of an observer. Similarly, verbs of Speaking specify how various vocal-communicative actions appear,¹ and verbs of Hitting and Cutting specify how various arm/hand actions appear, with verbs of Cutting including information about two other kinds of motion as well—namely, the movement patterns of the tools that are characteristically used to perform the actions (e.g., the distinctive double-bladed movement of scissors encoded by *snip*), and the

movement patterns of the objects that undergo different sorts of material separations (e.g., the breaking up into small fragments encoded by *shatter*). Finally, verbs of Change of State also incorporate the MOTION component, but they focus primarily (in many cases exclusively) on the distinctive ways in which objects move while shifting from one physical condition to another.

It is well established that the middle temporal area (MT or MT+, also known as V5 or hOc5) is critically involved in all manner of motion processing tasks (e.g., Smith, Greenlee, Singh, Kraemer, & Hening, 1998). This area is located at the borders of lateral BA² 37 and 19, in the anterior part of the occipital lobe at the continuation of the inferior temporal sulcus (Dumoulin et al., 2000; Malikovic et al., 2006; Tootell et al., 1995; Watson et al., 1993; Zeki et al., 1991). MT receives input along multiple parallel pathways from V1 (Nassi & Callaway, 2006), and it partially overlaps the extrastriate body area (EBA; Downing, Wiggett, & Peelen, 2007), which responds preferentially to the sight of human bodies and body parts (Downing, Jiang, Shuman, & Kanwisher, 2001; Pourtois, Peelen, Spinelli, Seeck, & Vuilleumier, 2007; Saxe, Jamal, & Powell, 2006; Urgesi, Candidi, Ionta, & Aglioti, 2007) and is also involved in a number of additional body-related operations, including naming body parts (Kemmerer & Tranel, in press), observing body actions (Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Kable & Chatterjee, 2006; Peelen, Wiggett, & Downing, 2006), executing body actions without visual feedback (Astafiev, Stanley, Shulman, & Corbetta, 2004), and locating one's self within one's body (Arzy, Thut, Mohr, Michel, & Blanke, 2006). MT, and probably also the EBA, projects to higher-order areas of the posterolateral temporal cortex (PLTC) that subserve more complex forms of motion processing, not only for human actions (for reviews see Giese & Poggio, 2003; Blake & Shiffrar, 2007) but also for tools (for reviews see Lewis, 2006; Beauchamp & Martin, 2007). Observing the movements of different human body parts elicits substantially overlapping activation maps in the PLTC; however, there is also evidence for some degree of body-part-based segregation, predominantly in the right hemisphere (for a review of the pre-2000 literature, see Allison, Puce, & McCarthy, 2000). Specifically: (a) observation of human walking evokes activity concentrated in the posterior superior temporal sulcus (STS; e.g., Pelphrey et al., 2003); (b) observation of mouth movements evokes activity concentrated more anteriorly in the mid-posterior STS (e.g., Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005); and (c) observation of hand actions evokes activity concentrated in the posterior and inferior STS (e.g., Pelphrey et al., 2005).

With regard to linguistic meaning, support for the Simulation Framework comes from several recent studies which suggest that the visual motion features encoded by verbs

¹ These verbs also encode information about sound quality, and we return to this topic in Section 4.1.2.

² BA stands for Brodmann area, and we follow the conventional numbering system.

depend on MT (Damasio et al., 2001; Rüschemeyer, Glenberg, Kaschak, & Friederici, submitted for publication; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003; Tranel, Martin, Damasio, Grabowski, & Hichwa, 2005; Tranel, Manzel, Asp, & Kemmerer, in press; Wallentin, Lund, Ostergaard, Ostergaard, & Roepstorff, 2005) and the PLTC anterior and dorsal to it (Kable, Lease-Spellmeyer, & Chatterjee, 2002, 2005; Noppeney, Josephs, Kiebel, Friston, & Price, 2005; Pirog, Aslin, & Tannenhaus, submitted for publication; Tettamanti et al., 2005), especially in the left hemisphere (for convergent behavioral work, see Kaschak et al., 2005; Zwaan, Madden, Yaxley, & Aveyard, 2004). We are not aware, however, of any studies that have focused specifically on the narrower question of whether these motion features are cortically mapped in a body-part-based fashion. Taking all of these considerations into account, we formulated the following hypothesis: *Hypothesis 2 (H2): Semantic processing of the MOTION component of verbs of Running, Speaking, Hitting, Cutting, and Change of State engages left MT and/or left posterolateral temporal cortex (PLTC), possibly with a body-part-based organization (Table 2).*

1.3. Component 3: CONTACT

The CONTACT component is incorporated by only two of the five verb classes—namely, verbs of Hitting and Cutting (Tables 1 and 2). The verbs in these classes denote multifarious types of agentive arm/hand actions that are directed toward objects, and it is for this reason that they are used almost exclusively in transitive sentences (In fact, we consider the CONTACT component to capture one of the basic elements of the semantic prototype of transitivity, as discussed in the classic paper by Hopper & Thompson, 1980; see also Dixon, 2000 and Ackerman & Moore, 2001). For example, within the Hitting class, *slap* describes a hard blow made with an open palm, *pat* describes a gentle touch made with an open palm, and *poke* describes a type of forceful contact made with an outstretched finger. While many verbs of Hitting can *optionally* be used to refer to actions involving tool use, most verbs of Cutting can *only* be used to refer to actions involving tool use—specifically, manipulation of a sharp tool suitable for creating a certain kind of incision in an object. Thus, *hack* implies a heavy tool such as a cleaver or an axe, *nick* implies a smaller blade such as a razor, and *grate* implies a specialized kitchen device. Verbs of Running and Speaking clearly do not involve actions in which an agent necessarily contacts an object with any body part. Verbs of Change of State do not incorporate the CONTACT component either, because as noted earlier, they are basically single-argument predicates.³

³ Syntactic support for this analysis comes from the fact that the body-part possessor ascension construction, which is sensitive to the CONTACT component (Levin, 1993; see also Kemmerer, 2003), licenses verbs of Hitting (e.g., *Bill hit Bob on the arm*) as well as verbs of Cutting (e.g., *Bill cut Bob on the arm*), but excludes verbs of Change of State (e.g., **Bill broke Bob on the arm*). We return to this point in Section 4.2.

The visuomotor coordination of object-directed arm and hand actions is subserved, in part, by a network of areas in the parietal cortex. In particular, recent evidence suggests that the control of reaching depends on the posterior intraparietal sulcus (pIPS), the control of grasping depends on the anterior intraparietal sulcus (aIPS), and the planning of visually guided actions depends on the inferior parietal lobule (IPL; for a review see Culham & Valyear, 2006; see also Glover, 2004). Many of these regions are also engaged during the observation and imagination of object-directed actions (e.g., Buccino et al., 2001; Fillion et al., 2007; Shmuelof & Zohary, 2005, 2006). In addition, recent research suggests that the aIPS may contribute to representing the intended goal of an action (for a review see Tunik, Rice, Hamilton, & Grafton, 2007; see also Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Hamilton & Grafton, 2006; Tunik, Frey, & Grafton, 2005). Furthermore, there is a large literature relating functional and manipulative knowledge of tools with the IPL, primarily in the left hemisphere (for reviews see Johnson-Frey, 2004; Lewis, 2006; see also Buxbaum, Kyle, Grossman, & Coslett, 2007; Canessa et al., 2007; Ebisch et al., 2007; Imazu, Sugio, Tanaka, & Inui, 2007; Mahon et al., 2007). It has even been shown that the process of learning to use a tool (e.g., a rake) to contact and manipulate objects in certain ways is accompanied by a form of neural plasticity which is consistent with the notion that the tool becomes an extension of the body schema, as if the agent's hand were elongated to the tip of the tool (for reviews see Maravita & Iriki, 2004; Farné, Serino, & Ladavas, 2007).

With respect to semantic issues, a recent fMRI study by Tettamanti et al. (2005) provided support for the Simulation Framework by demonstrating that relative to transitive sentences describing abstract events (e.g., *I appreciate sincerity*), transitive sentences describing bodily actions directed at objects in peripersonal space engaged portions of the left intraparietal sulcus and IPL, with substantially overlapping but also partially distinct activation maps for sentences describing actions executed with different body parts. Most relevant to the current study is their finding that listening to sentences expressing object-directed arm/hand actions (e.g., *I grasp the knife*) activated both anterior and posterior sectors of the left intraparietal sulcus as well as the adjacent IPL. This discovery, together with other convergent findings (Noppeney et al., 2005; Saccuman et al., 2006), led us to formulate the following hypothesis: *Hypothesis 3 (H3): Semantic processing of the CONTACT component of verbs of Hitting and Cutting engages the left intraparietal sulcus (IPS) and inferior parietal lobule (IPL) (Table 2).*

1.4. Component 4: CHANGE OF STATE

Like the CONTACT component, the CHANGE OF STATE component is incorporated by only two verb classes—in this case, verbs of Cutting and, by definition, verbs of Change of State (Tables 1 and 2). Within the Cutting

class, each verb specifies an idiosyncratic way in which an agent brings about a separation in the material integrity of an object by means of acting on it with a sharp tool, and the CHANGE OF STATE component in each verb's semantic structure elaborates the precise nature of the separation that is induced. To take a few illustrative examples, *slit* specifies making a long straight incision in something, *gouge* specifies creating a hole or groove in something, and *dice* specifies cutting something into small cube-shaped pieces. With regard to Change of State verbs, as already mentioned, they encode unique forms of physical transformation that objects undergo as the result of either external causes (verbs 1–15 in Table 1) or internal causes (verbs 16–20 in Table 1). Thus, *shatter* denotes the sudden fragmentation of an object into shards, *chip* denotes the breaking off of a small part of an object, and *bend* denotes the taking on of a curved or angled shape. Interestingly, verbs of Cutting and Change of State exhibit many crosslinguistic differences (Majid, Bowerman, van Staden, & Boster, 2007). For instance, in Yeli Dnye, just three verbs cover most of the semantic domain of “cutting and breaking,” and as shown by Levinson (2007), “they are all based on ‘exotic’ distinctions in the mode of severance—coherent severance with the grain vs. against the grain, and incoherent severance (regardless of grain).”

The CHANGE OF STATE component focuses on dynamic shifts in the visual appearance of objects. Shape transformations are most important, but changes in surface properties like color and texture are also specified by some verbs. It is well established that the perceptual processing of these visual attributes of objects depends on the ventral occipitotemporal stream (for a review see Milner & Goodale, 2006; see also Cant & Goodale, 2007). In addition, consistent with the Simulation Framework, numerous studies employing a diversity of brain mapping methods support the notion that the retrieval of conceptual knowledge of the form and surface properties of objects depends on various regions of the ventral temporal cortex (VTC), especially in the fusiform gyrus (for reviews see Kemmerer, in press; Martin, 2007). From a linguistic perspective, this cortical territory has been associated much more with the meanings of nouns than verbs (e.g., Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Shapiro, Moo, & Caramazza, 2006; Vandenbulcke, Peeters, Fannes, & Vandenbergh, 2006; for a review see Shapiro, Hillis, & Caramazza, 2007). However, a recent fMRI study by Bedny and Thompson-Schill (2006) found that activity in the left fusiform gyrus increased as the visual imageability ratings for both nouns and verbs increased (for a follow-up study see Bedny, Aguirre, & Thompson-Schill, 2007; and for convergent data see Vigliocco et al., 2006). Moreover, there are a few hints that, as the Simulation Framework predicts, the VTC plays a role in representing the visual aspects (perhaps the initial and final states) of the unique types of object transformations encoded by many verbs (Lu et al., 2002; Wolk, Coslett, & Glosser, 2005). With a view toward exploring these issues in greater depth, we formulated the

following hypothesis: *Hypothesis 4 (H4): Semantic processing of the CHANGE OF STATE component of verbs of Cutting and Change of State engages the ventral temporal cortex (VTC), predominantly in the left hemisphere (Table 2).*

1.5. Component 5: TOOL USE

Finally, the TOOL USE component is incorporated by just one of the five verb classes—namely, verbs of Cutting (Tables 1 and 2). As we have already pointed out, each of the verbs in this class specifies a type of action that involves the skilled use of a particular kind of sharp instrument. Although some verbs of Hitting and Change of State can occur in sentences that express instruments in oblique *with* phrases (e.g., *Bill hit Sam with a golf club*, *Bill broke the window with a rock*; see Schlesinger, 1995), these are arguably cases of template augmentation. In contrast, the TOOL USE component of verbs of Cutting is an inherent element of the shared event structure template, and is fleshed out in different ways by different verbs (Levin, 1993).

The main reason why we are interested in the TOOL USE component is because the neural substrates of tool knowledge have been the topic of intense investigation in recent years, with data from many diverse approaches supporting the idea that such knowledge is implemented in a primarily left-lateralized (but see Lewis, Phinney, Brefczynski, & DeYoe, 2006) multimodal system that is anatomically distributed over several interconnected cortical regions, including the following: the medial fusiform gyrus (visual form information); the PLTC (motion information); the IPL (functional and manipulative information); and portions of the lateral premotor/prefrontal cortex, particularly the upper hand-related sector of the ventral premotor cortex (functional and manipulative information) (for reviews see Johnson-Frey, 2004; Lewis, 2006; Beauchamp & Martin, 2007). It is also noteworthy that several neuropsychological studies suggest that “instrumental verbs” have a special status in the brain, relative to other types of verbs that do not necessarily encode tool use (Jonkers & Bastiaanse, 2006, 2007; Kambanaros & van Steenbrugge, 2006; Kemmerer & Tranel, 2000). Based on this literature, we formulated the following hypothesis: *Hypothesis 5 (H5): Semantic processing of the TOOL USE component of verbs of Cutting engages a complex network of left temporal, parietal, and frontal regions (Table 2).*

1.6. The current approach

The hypotheses outlined above focus on the neural correlates of five semantic components of verbs—namely, ACTION, MOTION, CONTACT, CHANGE OF STATE, and TOOL USE—and are formulated in terms of whether each component is present or absent in the event structure templates of five classes of verbs—namely,

Running, Speaking, Hitting, Cutting, and Change of State. In addition, the hypotheses addressing the first two components take into account one possible factor underlying the cortical organization of the within-class, uniquely defining or “constant” semantic features of verbs—namely somatotopy, i.e., body-part-based segregation. Thus, taken together, the entire set of hypotheses reflects issues that are relevant to both the Simulation Framework and the Two-Level Theory of verb meaning. To test the hypotheses, we observed subjects’ brain activity with fMRI while they performed a task requiring analytic processing of the idiosyncratic semantic features that differentiate between the verbs in each class. A baseline task involving strings of characters in Wingdings font was also included, and the principal contrasts involved subtracting the activation map evoked by this baseline condition from the activation maps evoked by each of the five verb class conditions.

2. Methods

2.1. Participants

Sixteen young adults (8 male and 8 female; mean age = 24.7 years, $SD = 3.8$), most of whom were university students, participated in the study for pay after giving written informed consent in accord with the Institutional Review Board at Purdue University. All of the participants were right-handed, had no history of head injury or other neurological problems, had normal or corrected-to-normal vision, and were monolingual native English speakers.

2.2. Experimental design

We developed the Semantic Similarity Judgment Test (SSJT), which requires participants to retrieve and compare relatively subtle aspects of the meanings of verbs. Each test item consists of 3 verbs in a triangular array—1 at the top and 2 at the bottom—and the task is to indicate, as quickly and accurately as possible, which of the 2 bottom verbs is more similar in meaning to the 1 on top.⁴ For example:

	trudge	
limp		stroll

For each item, all 3 verbs come from the same semantic class, and the “odd one out” is only moderately different from the other 2, so performing the task requires participants to think carefully about how the verbs relate to each other. The SSJT contains a total of 120 items—24 from each of the 5 classes described in Section 1. To create the items for each class, we used the verbs shown in Table 1.⁵ We did not attempt to balance the classes according to either imageabil-

ity ratings or homonymy with nouns. However, we did ensure that the classes are not significantly different with respect to both verb frequency (mean = 44.9, $SD = 8.0$, $p = .24$; see Table 1; frequency data drawn from Carroll, Davies, & Richman, 1971) and letter length (mean = 5.0, $SD = 1.2$, $p = .14$; see Table 1). In order to have a baseline condition against which we could evaluate performance on the SSJT, we also designed a task in which strings of characters in Wingdings font are presented in a triangular array—1 at the top and 2 at the bottom—and participants must indicate which of the 2 bottom strings is identical to the 1 on top (see Footnote 4). For example:

	☒ℳ∂⊖□	
☒ℳ∂⊖□		☒⊖∂⊗□

The experiment consisted of 4 runs, each of which had the same organization of blocks lasting a total of 345 s (Fig. 1). Each run began and ended with a 15-s block during which participants viewed a flashing fixation cross; these blocks were included to achieve equilibrium signal levels. In between were 9 blocks, each 35 s in duration, presented in the following order: verbs, Wingdings, verbs, rest, verbs, Wingdings, verbs, rest, verbs. Each of these blocks began with a 5-s visually-presented instruction (“Verbs,” “Wingdings,” or “Rest”). For each block of verbs, the instruction was followed by 6 consecutive items from the SSJT, with each item being shown for 4 s followed by 1 s of blank screen. The verbs comprising the 6 items within a given block were all from the same class (e.g., 6 consecutive trials involving Running verbs). Each of the 5 classes was represented by 1 block in each run, but the order of class-specific blocks varied across the 4 runs in an unpredictable way. Appendix A provides a complete list of the stimuli comprising the 5 blocks of verb trials in each of the 4 runs. For each block of Wingdings, the instruction was followed by 6 consecutive items, with each item being shown for 4 s followed by 1 s of blank screen. For each block of rest, the instruction was followed by 30 s of a flashing fixation cross. Finally, in presenting the runs to our subjects, we employed a Latin square design such that subject 1 received run sequence 1, 2, 3, 4, subject 2 received run sequence 2, 3, 4, 1, subject 3 received run sequence 3, 4, 1, 2, and so on.

The stimuli were back-projected onto a screen placed at the foot of the patient bed. Participants could see the stimuli clearly through a mirror placed above their eyes. Stimulus presentation and response collection were controlled using MacStim (<http://www.brainmapping.org/WhiteAnt>). Participants responded to the stimuli by pressing buttons with their left hand, using their index finger to indicate that, for a given triangular array of either verbs or Wingdings, the bottom right one was the correct answer, and using their middle finger to indicate that the bottom left one was correct (the MRI-compatible response box was

⁴ For a similar approach to investigating the neural substrates of verb meanings with fMRI, see Kable et al. (2002, 2005).

⁵ For details see Appendix A. This is discussed further in the next paragraph of the main text.

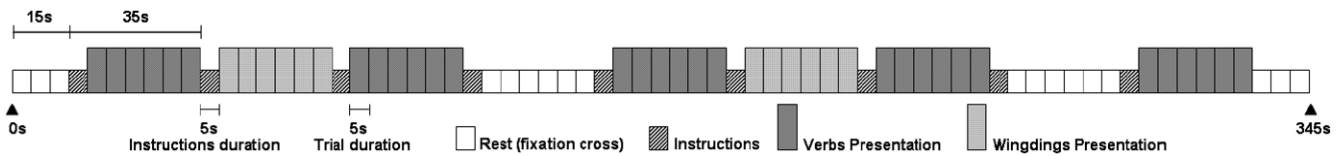


Fig. 1. Temporal course of one run.

Current Designs Model HH-1x4-L, <http://www.forp.us>). To familiarize participants with the experimental tasks, just one run was administered with a laptop computer outside the magnet at least 1 week prior to the scanning session; this practice run always corresponded to the run that was administered last during that subject's scanning session.

2.3. Data acquisition

Scans were acquired on a 1.5 T General Electric Signa CVi scanner (InnerVision Advanced Medical Imaging, Lafayette, Indiana). Subjects were lying in a supine position and their heads were stabilized with adjustable padding to minimize head movement during the scans. T₁-weighted SPGR high-resolution anatomical images (124 sagittal slices, FOV = 24 cm, slice thickness = 1.2 mm) were acquired for each subject prior to the functional runs. Functional scans were collected using a blipped echo-planar imaging sequence (TE = 40 ms, FOV = 24 cm, slice thickness = 4.4 mm). For each subject a total of 138 volumes were collected with a repetition time (TR) of 2.5 s. Volumes contained 25 (12 subjects) or 26 (4 subjects) axial slices with an in-plane resolution of 3.75 × 3.75 mm.

2.4. Data analyses

Data were analyzed using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm>). Each subject's data were motion corrected to the first functional scan. The data from 3 subjects were eliminated due to excessive head movement (more than 2 mm in a single run and/or 2 or more within-TR—i.e., from one image acquisition to the next—shifts larger than 0.5 mm). In addition, the data from 1 subject were eliminated due to a 10% shift in signal baseline occurring in the middle of the imaging session, likely due to loose contact between the coil adapter box and the imager. For the remaining 12 subjects, motion corrected functional scans were aligned to each subject's anatomical scan. The data were then normalized to the standard MNI space using the T₁-weighted template provided by the SPM5 software. The last pre-processing step consisted of smoothing the data with an isotropic Gaussian filter (FWHM = 8 mm) to compensate for anatomical inter-subject variability and to match the statistical requirements of the general linear model.

In order to identify the areas of the brain activated by the different verb classes, individual and group analyses were performed. At the individual level, statistical maps were computed using a general linear model in SPM5 with

motion parameters as regressors. Responses for each verb class were contrasted against activations for the first block of Wingdings in each functional run (i.e., Running vs. Wingdings, Speaking vs. Wingdings, etc.). For the group results, the individual contrasts of each verb class against Wingdings were used as the input to five independent one-sample *t*-test random-effects analyses in SPM5.

Tridimensional inflated surface representations were rendered with AFNI/SUMA (<http://www.nimh.nih.gov/afni>). This software provides ready-to-use cortical surfaces in the Talairach and Tournoux coordinate system. When required for presentation purposes, statistical maps were transformed from MNI space into Talairach space using the automatic transformation mechanisms provided by AFNI software 3dWarp.

3. Results

3.1. Behavioral results

The behavioral results for both accuracy and response time (RT) are shown in Table 3. Regarding accuracy, the subjects achieved a high overall level of performance on the SSJT (mean = 93.0%, *SD* = 2.8%). Furthermore, the subjects' average accuracy for the Wingdings (mean = 93.5%, *SD* = 5.2%) was almost identical to that for the verbs in the SSJT. Regarding RTs, the subjects were slightly faster for the verbs (mean = 1.6 s, *SD* = 0.2 s) than the Wingdings (mean = 1.9 s, *SD* = 0.2 s).

3.2. Imaging results

Each of the five verb conditions was contrasted with the baseline (i.e., Wingdings) condition. The anatomical regions, maximum *t* values, MNI coordinates, and cluster sizes of the significant activations (random-effects analyses, *p* < .001, uncorrected) are shown in Tables 4–8 for verbs of

Table 3
Behavioral results

Condition	Accuracy (%)	Response time (s)
<i>Verb classes</i>		
Running	95.5 (4.8)	1.6 (0.2)
Speaking	94.3 (5.1)	1.5 (0.2)
Hitting	92.9 (4.5)	1.6 (0.2)
Cutting	89.3 (6.7)	1.7 (0.3)
Change of state	92.9 (4.7)	1.6 (0.2)
Mean	93.0 (2.8)	1.6 (0.2)
<i>Wingdings</i>	93.5 (5.2)	1.9 (0.2)

Table 4

Anatomical regions, maximum t values, MNI coordinates, and cluster sizes for activations associated with the contrast between Running verbs and Wingdings (random-effects analyses, $p < .001$, uncorrected)

Side	Anatomical region	BA	Peak t value	MNI coordinates (x, y, z)			Cluster size
Activations in hypothesized regions							
<i>Frontal lobe</i>							
L	Dorsal precentral gyrus	4	4.48	–28	–32	60	5
R	Dorsal precentral gyrus	4	7.07	24	–32	62	16
<i>Temporal lobe</i>							
L	Posterolateral temporal cortex	21/22	8.39	–60	–36	0	294
Activations in other regions							
<i>Frontal lobe</i>							
L	Inferior frontal gyrus	45	5.80	–54	24	28	49
L	Inferior frontal gyrus	45	4.64	–54	32	16	7
L	Inferior frontal gyrus	44/45	4.33	–46	16	36	2
L	Inferior frontal gyrus	47/10	4.94	–44	30	–16	35
L	Dorsomedial prefrontal cortex	8	6.42	–6	44	46	65
<i>Temporal lobe</i>							
L	Superior temporal gyrus	22	4.60	–60	–42	22	25
L	Superior temporal gyrus	22	4.71	–58	–52	18	11
L	Anterolateral temporal cortex	21	6.83	–60	–4	–12	20
L	Middle temporal gyrus	21	4.22	–50	–22	–10	2
L	Inferior temporal gyrus	20	5.62	–46	–14	–30	26
R	Temporal pole	38	5.44	46	12	–18	41
R	Anterolateral temporal cortex	21	4.86	58	–6	–12	8
R	Anterolateral temporal cortex	21	4.73	60	2	–10	6
<i>Parietal lobe</i>							
R	Dorsal postcentral gyrus	2	4.19	24	–48	72	2
<i>Occipital lobe</i>							
R	Calcarine fissure and cuneus	17/18	5.26	14	–84	26	7
R	Calcarine fissure	17	4.32	12	–70	20	4
<i>Other regions</i>							
M	Posterior corpus colosum	–	5.49	10	–40	22	32
L	Hippocampus	27	5.61	–34	–30	–6	8
L	Hippocampus	27	4.52	–30	–42	2	7
L	Insula	13	5.10	–36	–20	24	2

Voxel size: 2 mm × 2 mm × 2 mm.

Running (Table 4), Speaking (Table 5), Hitting (Table 6), Cutting (Table 7), and Change of State (Table 8). In each table, activations in hypothesized regions are listed first, followed by additional activations in other regions. Below we focus on results that are relevant to testing our hypotheses about the neural correlates of the five semantic components that are manifested in cross-cutting patterns across the different verb classes.

3.2.1. Component 1: ACTION

Hypothesis 1 maintains that the ACTION component of verbs of Running, Speaking, Hitting, and Cutting depends on somatotopically organized primary motor and/or premotor cortices; furthermore, it assumes that this semantic component is not incorporated by Change of State verbs (Table 2). Fig. 2 shows the activations for all five verb classes, relative to baseline, rendered on three different sets of contiguous axial sections ($p < .001$).

Panel (a) depicts a set of contiguous axial sections with the MNI z values of 64, 62, and 60, revealing several areas of activation for both the Running and Hitting

classes. Verbs of Running were associated with two relatively symmetrical bilateral activations in the dorsal precentral gyrus (left: –28, –32, 60; right: 24, –32, 62). Verbs of Hitting were also associated with two relatively symmetrical bilateral activations in the dorsal precentral gyrus (left: –28, –30, 62; right: 14, –26, 62). For both classes of verbs, the right-sided activations were larger than the left-sided ones. The maxima of all of these activations are in the heart of the probabilistic map for primary motor cortex (M1) provided by Mayka, Corcos, Leurgans, and Vaillancourt (2006). Panel (b) shows a set of contiguous axial sections with the MNI z values of 44, 42, and 40, revealing activation in the left mid-precentral gyrus for verbs of Cutting (–46, 10, 40). The peak fell at the anterior, superior edge of Mayka et al.'s (2006) probabilistic map for the ventral premotor cortex. Panel (c) shows a set of contiguous axial sections with the MNI z values of 24, 22, and 20. We selected these z values for two reasons: first, Tettamanti et al. (2005) found that listening to sentences describing mouth actions elicited an activation peak at MNI –44, 2, 24;

Table 5

Anatomical regions, maximum t values, MNI coordinates, and cluster sizes for activations associated with the contrast between Speaking verbs and Wingdings (random-effects analyses, $p < .001$, uncorrected)

Side	Anatomical region	BA	Peak t value	MNI coordinates (x, y, z)			Cluster size
Activations in hypothesized regions							
<i>Temporal lobe</i>							
L	Posterolateral temporal cortex	21/22	7.80	−54	−38	2	212
L	Posterolateral temporal cortex	21/22	4.50	−48	−30	−8	7
Activations in other regions							
<i>Frontal lobe</i>							
L	Inferior frontal gyrus	45	6.18	−50	18	20	16
L	Inferior frontal gyrus	47	4.76	−50	24	−12	7
L	Inferior frontal gyrus	47/10	4.38	−46	34	−2	2
L	Dorsomedial prefrontal cortex	9	4.97	−4	56	36	9
L	Ventromedial prefrontal cortex	11	5.52	−2	48	−14	63
<i>Other regions</i>							
R	Hippocampus	27	4.76	34	−40	2	2

Voxel size: 2 mm × 2 mm × 2 mm.

Table 6

Anatomical regions, maximum t values, MNI coordinates, and cluster sizes for activations associated with the contrast between Hitting verbs and Wingdings (random-effects analyses, $p < .001$, uncorrected)

Side	Anatomical region	BA	Peak t value	MNI coordinates (x, y, z)			Cluster size
Activations in hypothesized regions							
<i>Frontal lobe</i>							
L	Dorsal precentral gyrus	4/6	5.78	−28	−30	62	17
R	Dorsal precentral gyrus	6	7.94	14	−26	62	50
R	Dorsal precentral gyrus	4	4.43	10	−34	68	2
<i>Temporal lobe</i>							
L	Posterolateral temporal cortex	21/22	4.67	−54	−38	2	15
L	Posterolateral temporal cortex	21	4.39	−66	−36	2	2
L	Posterolateral temporal cortex	37	4.82	−58	−34	−10	6
Activations in other regions							
<i>Frontal lobe</i>							
L	Inferior frontal gyrus	45/47	4.92	−46	40	4	26
L	Inferior frontal gyrus	47/11	4.41	−32	40	−14	6
L	Orbital cortex	11	4.67	−42	46	−14	8
<i>Temporal lobe</i>							
L	Anterolateral temporal cortex	21	6.82	−58	−4	−14	18
R	Temporal pole	38	4.67	60	4	−8	5
<i>Parietal lobe</i>							
R	Postcentral gyrus	2/1	5.11	24	−48	72	4
R	Precuneus	31	5.67	14	−58	32	18
<i>Other regions</i>							
M	Ventral anterior cingulate	25	4.46	0	28	−20	3

Voxel size: 2 mm × 2 mm × 2 mm.

and second, [Hauk et al. \(2004\)](#) found that reading verbs describing mouth actions elicited an activation peak at MNI −50, 10, 20. Both of those peaks are within [Mayka et al.'s \(2006\)](#) probabilistic map for the ventral premotor cortex. In the current study, we found that making semantic similarity judgments about verbs of Speaking elicited an activation peak at the same axial level as in [Hauk et al.'s \(2004\)](#) study, namely $z = 20$; however, contrary to our hypothesis and to both of the previous studies, this peak was not within [Mayka et al.'s \(2006\)](#)

probabilistic map for the ventral premotor cortex, but was instead centered more anteriorly in BA 45 (−50, 18, 20), a region that was also engaged by all four of the other verb classes (see Section 3.2.6).

3.2.2. Component 2: MOTION

Hypothesis 2 maintains that the MOTION component of verbs of Running, Speaking, Hitting, Cutting, and Change of State depends on left MT and/or left PLTC, possibly with a body-part-based organization ([Table 2](#)).

Table 7

Anatomical regions, maximum *t* values, MNI coordinates, and cluster sizes for activations associated with the contrast between Cutting verbs and Wingdings (random-effects analyses, $p < .001$, uncorrected)

Side	Anatomical region	BA	Peak <i>t</i> value	MNI coordinates (<i>x, y, z</i>)			Cluster size
Activations in hypothesized regions							
<i>Frontal lobe</i>							
L	Inferior frontal, middle frontal, and precentral gyri	45/44/9/6	6.23	−46	28	24	253
L	Middle frontal and precentral gyri	9/6	4.21	−46	10	40	In cluster above
<i>Temporal lobe</i>							
L	Posterolateral temporal cortex	21/22	6.91	−54	−40	2	178
L	Posterolateral temporal cortex	22	4.48	−60	−42	16	9
L	Posterolateral temporal cortex	21	4.69	60	−58	−8	6
L	Posterolateral temporo-occipital cortex	37	6.83	−44	−60	12	87
L	Fusiform gyrus	20	5.12	−46	−14	−30	5
<i>Parietal lobe</i>							
L	Angular gyrus	39	6.53	−36	−68	42	37
L	Angular gyrus	39	4.57	−38	−60	38	6
Activations in other regions							
<i>Frontal lobe</i>							
L	Inferior frontal gyrus	45	4.73	−52	36	18	5
L	Inferior frontal gyrus	44	4.23	−58	16	−12	2
L	Inferior frontal gyrus	47/11	6.29	−28	38	−12	20
L	Inferior frontal gyrus	47	5.14	−50	38	−2	17
L	Inferior frontal gyrus	47	4.32	−54	26	−4	2
L	Ventromedial prefrontal cortex	11	6.54	−4	48	−18	91
L	Orbital cortex	11	4.37	−36	40	18	5
R	Rolandic operculum	4	5.16	70	−8	16	6
<i>Temporal lobe</i>							
R	Middle temporal gyrus	4	4.43	54	−72	26	2
<i>Parietal lobe</i>							
R	Dorsal postcentral gyrus	1	4.47	24	−50	72	2
R	Precuneus	31	4.44	10	−58	30	2
<i>Occipital lobe</i>							
R	Calcarine fissure	17	5.08	16	−66	12	9
R	Calcarine fissure	17	4.37	10	−70	20	2
<i>Other regions</i>							
R	Insula	13	5.67	44	−16	4	12

Voxel size: 2 mm × 2 mm × 2 mm.

According to Malikovic et al. (2006), the mean location of MT in the left hemisphere is centered at MNI −43, −73, 10 (although there is considerable variation across subjects in the size and extent of the area). None of the five verb conditions, relative to baseline, revealed activation at those coordinates at either $p < .001$ or $p < .005$. Before reporting the imaging results for the left PLTC, it is worth addressing the question of whether any of the verb classes led to significant activation in the left EBA, which partially overlaps MT. According to Downing et al. (2007), the mean location of the EBA (for body parts rather than whole bodies) in the left hemisphere is centered at MNI −46, −70, 4 (transformed from Talairach and Tournoux −46, −70, 4). Again, none of the five verb conditions, relative to baseline, revealed activation at those coordinates at either $p < .001$ or $p < .005$.

Turning now to the left PLTC, Fig. 3 shows the activations for all five verb classes, relative to baseline, ren-

dered on the left lateral surface of an inflated 3D brain ($p < .001$).

Each of the verb classes was associated with extensive activation in the left PLTC; however, as illustrated in panel (c), verbs of Running, Speaking, and Cutting evoked the largest areas of activity, verbs of Change of State evoked a somewhat more restricted pattern of activity, and verbs of Hitting evoked the smallest region of activity. There were many complex combinations of overlap among the activation patterns triggered by the five verb classes; to limit the complexity of the figure, all overlaps are depicted as yellow in panels (a) and (b). An advantage to collapsing all overlaps into a single category is that this helps bring into sharp relief the fact that several of the verb classes were uniquely linked with certain sectors of the left PLTC, as indicated by the magnified class-specific color patterns in panel (b). Most notably, verbs of Running uniquely engaged the medial portion of the mid-posterior superior temporal sulcus (STS), verbs of Speaking uniquely engaged

Table 8
Anatomical regions, maximum *t* values, MNI coordinates, and cluster sizes for activations associated with the contrast between Change of State verbs and Wingdings (random-effects analyses, $p < .001$, uncorrected)

Side	Anatomical region	BA	Peak <i>t</i> value	MNI coordinates (<i>x, y, z</i>)			Cluster size
Activations in hypothesized regions							
<i>Temporal lobe</i>							
L	Posterolateral temporal cortex	21/22	9.79	−56	−38	0	147
L	Fusiform gyrus	20	4.28	−44	−16	−28	2
L	Inferior temporal gyrus	20	4.15	−52	−26	−22	2
Activations in other regions							
<i>Frontal lobe</i>							
L	Inferior frontal gyrus	45	6.40	−46	18	22	122
L	Inferior frontal gyrus	45	4.32	−38	30	22	2
L	Dorsomedial prefrontal cortex	8	5.56	−4	46	50	22
<i>Temporal lobe</i>							
L	Anterolateral temporal cortex	21	5.79	−58	−6	−14	8
L	Superior temporal gyrus	22	5.13	−58	−44	18	14
<i>Occipital lobe</i>							
R	Calcarine fissure	17	4.19	10	−68	18	2

Voxel size: 2 mm × 2 mm × 2 mm.

a more anterior portion of the STS, and verbs of Cutting uniquely engaged the most posterior portion of the STS extending into the posterolateral temporo-occipital cortex. In contrast, Hitting verbs and Change of State verbs were not uniquely linked with particular areas of the left PLTC; instead, their activation patterns overlapped almost completely with those of the other verb classes.

It is worth emphasizing that the imaging data shown in Fig. 3 represent group effects. To further explore the possibility of a body-part-based organization within the left PLTC, we investigated each individual subject's activation patterns in this region for verbs of Running (leg actions), verbs of Speaking (mouth actions), and verbs of Hitting (arm/hand actions), all relative to baseline. Fig. 4 presents these results for five subjects. A threshold of $p < .05$ was used in order to better illustrate the patterns, and the five subjects were selected because they appeared to exhibit the strongest degree of body-part-based cortical segregation. The data are plotted on an axial section of each subject's own brain, with coordinates centered at MNI −56, −37, 1, which is the average of the activation maxima in the left PLTC for the three verb classes. The results have been masked so as to exclude areas with overlapping activation for either two or all three of the verb classes; hence each image shows only those areas that were activated uniquely by each class.

3.2.3. Component 3: CONTACT

Hypothesis 3 maintains that the CONTACT component of both Hitting and Cutting verbs depends on the left IPS and IPL; furthermore, the hypothesis assumes that the CONTACT component is not incorporated by the other three verb classes (Table 2). As shown in Tables 6 and 7, when examined at the $p < .001$ level, the left IPS was not significantly activated, relative to baseline, by either Hitting or Cutting verbs; nor was it engaged by any of the other

verb classes. However, the left IPL—in particular, a large area within the angular gyrus (−36, −68, 42)—was significantly activated, relative to baseline, by verbs of Cutting ($p < .001$). These findings are portrayed in Fig. 5. None of the other verb classes elicited significantly above-baseline activation in this region.

3.2.4. Component 4: CHANGE OF STATE

Hypothesis 4 maintains that the CHANGE OF STATE component of verbs of Cutting and verbs of Change of State depends on the VTC, predominantly in the left hemisphere; it also assumes that this semantic component is not incorporated by any of the other verb classes (Table 2). As indicated in Tables 7 and 8, for each of the two target verb classes—namely Cutting and Change of State—several areas in the middle portion of the left VTC were significantly activated at the $p < .001$ level, compared to the baseline task. In particular, a small area in the left fusiform gyrus was engaged by both Cutting verbs (−46, −14, −30) and Change of State verbs (−44, −16, −28); in addition, a small area in the left inferior temporal gyrus (ITG) was uniquely engaged by Change of State verbs (−52, −26, −22). These findings are illustrated in Fig. 6, which shows the activations for all five verb classes, relative to the baseline task, rendered on three sagittal sections of the left hemisphere with the MNI *x* values of −52, −46, and −44. The image depicting the section with $x = -52$ reveals the ITG activity unique to Change of State verbs. The images depicting the sections with $x = -46$ and $x = -44$ show the overlapping activity in the fusiform gyrus for both Cutting verbs and Change of State verbs. Notably, this overlap also includes verbs of Running, which unexpectedly engaged the region as well (see Table 4). None of the other verb classes elicited significantly above-baseline activation in the left VTC.

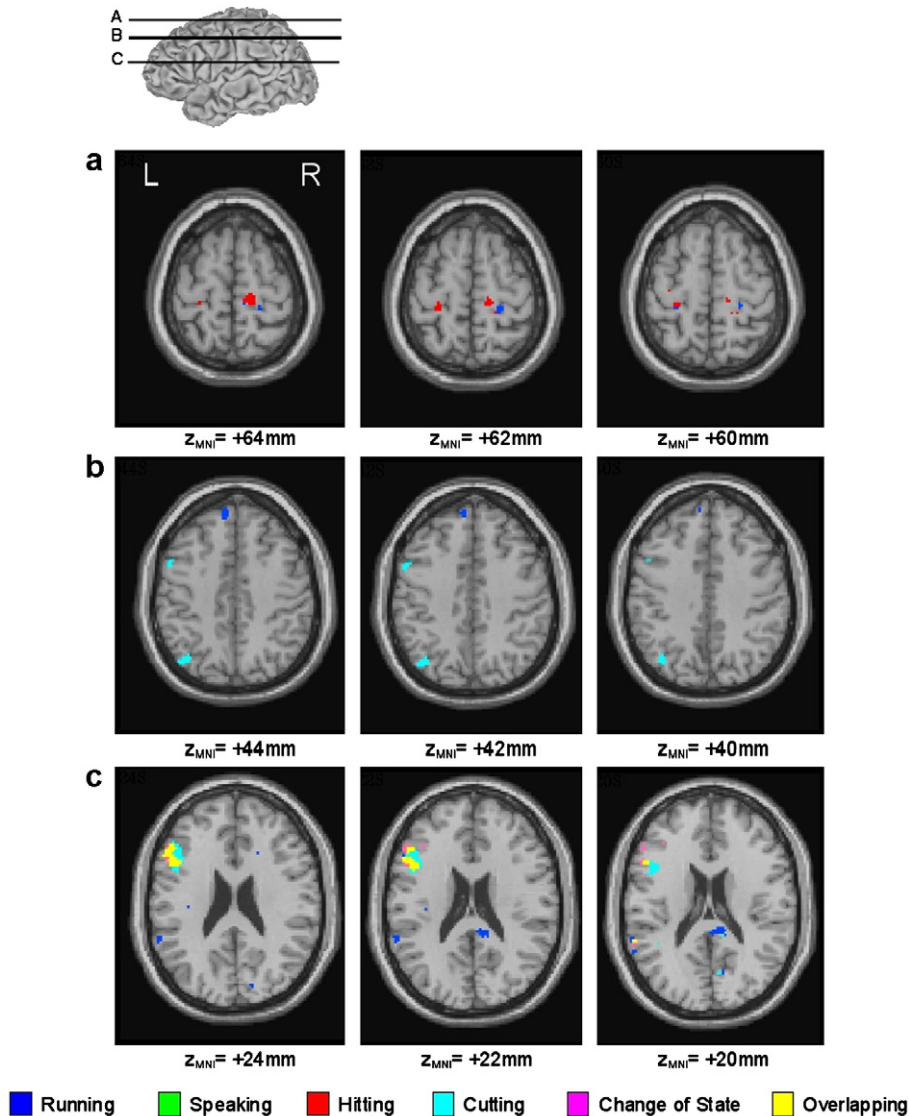


Fig. 2. Group results relevant to the ACTION component. Differential activations (random-effects analyses, $p < .001$, uncorrected) for each verb class versus Windings are shown on three separate sets of contiguous axial sections of a representative brain. (Top) Left lateral view indicating the planes of the three sets of axial sections. (Panel a) Bilateral activations for Running verbs and Hitting verbs in the dorsal precentral gyri. (Panel b) Activation for Cutting verbs in the left mid-precentral gyrus. (Panel c) No activation for Speaking verbs in the left ventral primary motor or premotor cortices; however, overlapping activations for all five verb classes more anteriorly in BA 45.

3.2.5. Component 5: TOOL USE

Hypothesis 5 maintains that the TOOL USE component of verbs of Cutting depends on a complex network of left parietal, frontal, and temporal structures that have been strongly associated with various aspects of tool knowledge (Table 2). Many of these brain areas were in fact only significantly activated at the $p < .001$ level for Cutting verbs, relative to the baseline task: (1) the left angular gyrus ($-36, -68, 42$; see Fig. 5); (2) the left posterolateral temporal-occipital cortex, especially the most posterior sector ($-44, -60, 12$; see Fig. 3); and (3) the upper portion of the left ventral premotor cortex ($-46, 10, 40$; see Fig. 2b) together with a large cluster of activated voxels that, while centered in the posterior inferior frontal gyrus ($-46, 28, 24$), extended superiorly into the posterior middle frontal gyrus.

3.2.6. Broca's area

This study yielded a number of additional findings that were not explicitly predicted by Hypotheses 1–5. We would like to highlight just one of these findings. Relative to the baseline task, BA 45 in the left inferior frontal gyrus—traditionally considered to be part of Broca's area, but see Lindenberg, Fangerau, and Seitz (2007)—was activated by all five verb classes, and the adjacent BA 47 was activated by all of the classes except Change of State at the $p < .001$ level (these activations are visible in Figs. 2c and 3a).

3.2.7. Summary

A synopsis of the major imaging results, indicating how they relate to Hypotheses 1–5, is provided in Table 9. This is identical to Table 2, except confirmed predictions are

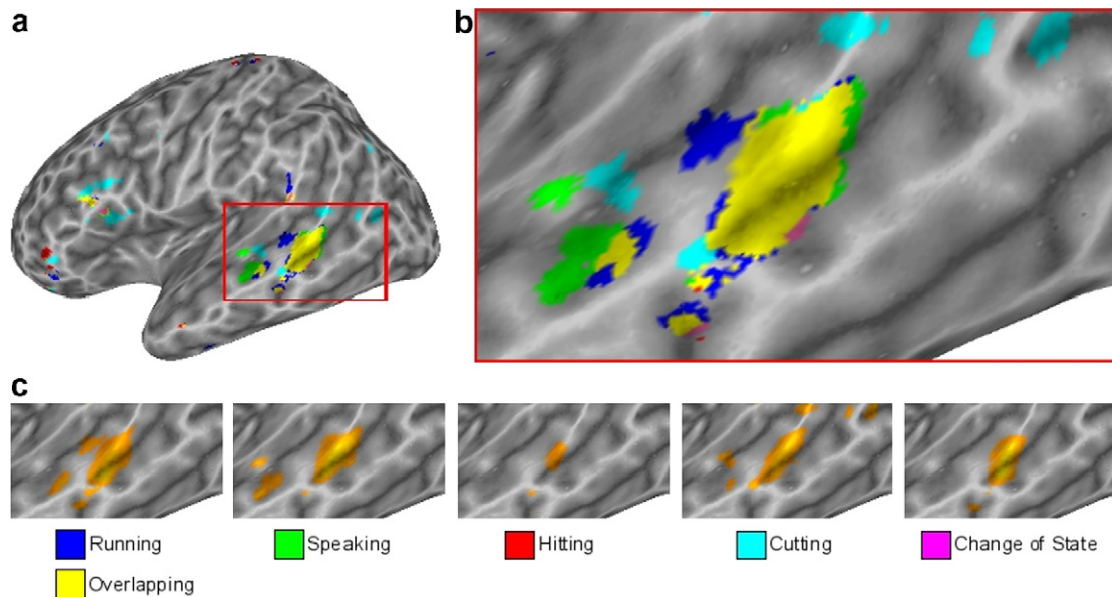


Fig. 3. Group results relevant to the MOTION component. Differential activations (random-effects analyses, $p < .001$, uncorrected) for each verb class versus Wingdings are shown on an inflated 3D brain seen from the left side. (a) The red box indicates activation patterns across verb classes in the posterolateral temporal cortex (PLTC). Yellow patches signify areas of overlapping activation for two or more verb classes. Other colored patches signify areas of activation unique to particular verb classes, according to the color key in (c). (b) Enlargement of the red box in (a). (c) Activations for each separate verb class in the territory of the PLTC indicated by the red box in (a). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

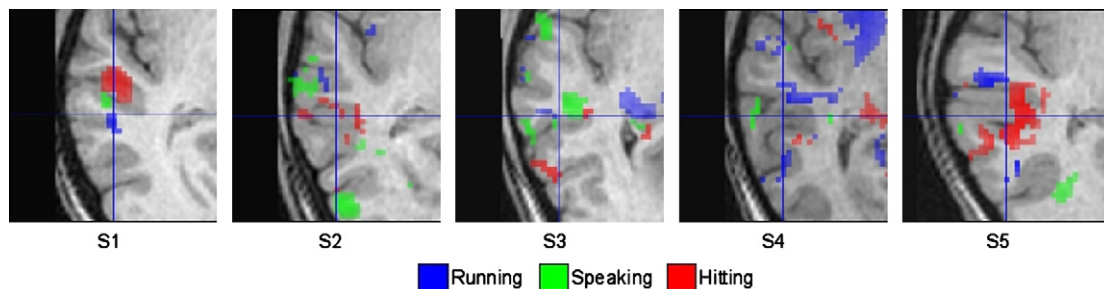


Fig. 4. Individual subject results relevant to the MOTION component. Non-overlapping differential activations ($p < .05$, uncorrected) for verbs of Running, Speaking, and Hitting, relative to Wingdings, are shown on axial sections of the individual brains of five subjects, with coordinates (blue crosshairs) centered at MNI $-56, -37, 1$, which is the average of the activation maxima in the left posterolateral temporal cortex (PLTC) for the three verb classes. Areas of overlapping activation for two or more verb classes have been excluded so that segregated activation patterns pertinent to somatotopic organization can be clearly visualized. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

indicated by cells with grey shading, while unconfirmed predictions are indicated by cells with white background. As can be seen, of the 25 cells in the table, all but 3 have grey shading, which reflects the fact that most of our predictions were supported.

4. Discussion

The experimental aim of this fMRI study was to identify the neuroanatomical distribution of five distinct components of action concepts that are manifested in cross-cutting patterns across five distinct classes of verbs. More generally, our goal was to test several predictions derived from the Simulation Framework and to connect that model with the Two-Level Theory of verb meaning. Virtually all

of the predictions were confirmed. In what follows, we first discuss the implications of our results for the Simulation Framework, and then we turn to broader issues concerning the Two-Level Theory.

4.1. Implications for the Simulation Framework

4.1.1. Component 1: ACTION

Consistent with Hypothesis 1, we found that the retrieval and strategic comparison of subtle semantic features of Running verbs, Hitting verbs, and Cutting verbs activated somatotopically organized sectors of the primary motor and premotor cortices. More precisely: (1) areas in or near the leg sector of the motor homunculus were engaged when subjects made fine-grained semantic similar-

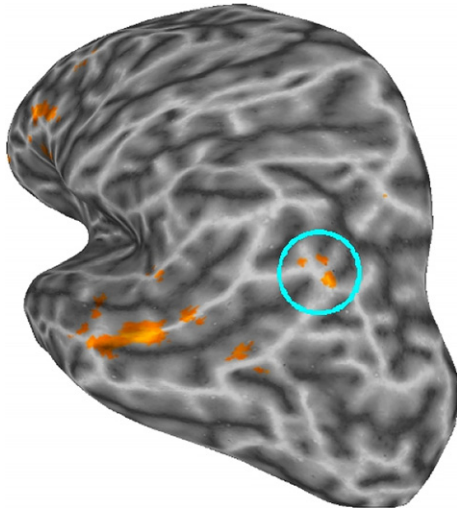


Fig. 5. Group results for Cutting verbs versus Wingdings (random effects analysis, $p < .001$, uncorrected), rendered on the left hemisphere of an inflated 3D brain seen from a posterior viewpoint. The circle indicates significant activation in the left angular gyrus.

ity judgments about triads of Running verbs (e.g., determining that *stagger* is more like *limp* than *tiptoe*); (2) areas in or near the arm sector were engaged when subjects made such judgments about triads of Hitting verbs (e.g., determining that *pound* is more like *pummel* than *prod*); and (3) areas in or near the hand sector⁶ were engaged when subjects made such judgments about triads of Cutting verbs (e.g., determining that *hack* is more like *chop* than *carve*). These results bolster the Simulation Framework insofar as they suggest that paying close attention to the motoric aspects of the meanings of verbs may involve covertly recapitulating the kinematics of the linguistically designated actions within the motor system itself, as opposed to relying entirely on an abstract, amodal representational format. In this regard, the current study adds to the growing body of literature supporting the view that “effector congruent motor resonance” may be integral to understanding the ACTION component of verbs (for reviews see Fischer & Zwaan, in press; Glenberg, in press; Pulvermüller, 2005; see also Rüschemeyer et al., 2007).

An important caveat is that we have only mapped brain regions activated during the semantic processing of action

⁶ It is actually an oversimplification to refer to a single hand sector, since the lateral precentral gyrus of the macaque brain contains at least three separate hand representations (one in primary motor cortex, a second in ventral premotor cortex, and a third in dorsal premotor cortex) whose topographic partitioning reflects multiple, conflicting mapping requirements, including the need to encode distinct repertoires of complex, ethologically relevant movements, such as climbing/leaping behaviors, reaching behaviors, hand-to-mouth behaviors, defensive behaviors, and central space/manipulation behaviors (for a review see Graziano, 2006). Regarding the motor representation of hand actions in the lateral precentral gyrus of the human brain, yet another mapping requirement may involve the development of neurons tuned to the idiosyncratic types of hand actions that are expressed by verbs in different languages (Majid et al., 2007).

verbs, and have not gone on to investigate whether the very same regions are, as the Simulation Framework would predict, also activated during the execution and observation of the corresponding actions. However, it is noteworthy that the regions we have identified do appear to reside within the primary motor and premotor cortices (Mayka et al., 2006), which are known to contribute to action execution and observation (for a review see Jeannerod, 2006). In addition, these regions are close to those that previous fMRI studies have found to respond not only to the semantic processing of action verbs, but also to the execution (Hauk et al., 2004) and observation (Aziz-Zadeh et al., 2006) of effector congruent behaviors.

Another issue that warrants consideration revolves around the fact that our study utilized a task that requires not only automatic (bottom-up, implicit) but also controlled (top-down, explicit) processing of the idiosyncratic semantic properties of verbs. An opponent of the Simulation Framework—that is, someone who is skeptical of the view that conceptual knowledge is grounded in the brain’s modality-specific systems—might argue that because the task was partially controlled, the motor activations we observed might reflect non-semantic imagery (of the kind reported by, e.g., Ehrsson et al., 2003 and Michelson et al., 2006) rather than intrinsically semantic content. The design of our study prevents us from ruling out this possibility. However, it is important to note that other studies have provided strong support for the Simulation Framework by employing tasks that probe automatic processing. First, drawing on a variety of highly time-sensitive brain mapping methods and behavioral paradigms, a number of studies have shown that effector congruent motor resonance can occur extremely quickly—in some cases within 200 ms (Boulenger et al., 2006)—after subjects have read or heard verbs describing human actions performed with different body parts (Borreggine & Kaschak, in press; Hauk & Pulvermüller, 2004; Pulvermüller, Härle, & Hummel, 2001, 2005b; Scorolli & Borghi, 2007; Zwaan & Taylor, 2006). Second, a few additional studies have used TMS to reveal functional links between the motor system on the one hand and the semantic processing of action verbs on the other (Buccino et al., 2005; Glenberg et al., in press-b; Pulvermüller et al., 2005a; see also Pobric & Hamilton, 2006). Still, the question of whether, and how, effector congruent motor resonance is sensitive to task variables has only recently begun to receive close attention (Tomasino, Werner, Weiss, & Fink, 2007). Furthermore, it is unknown whether the primary motor and premotor cortices are *necessary* for understanding the ACTION component of verb meanings, although an increasing number of lesion studies suggest that they may be (e.g., Bak et al., 2006; Bak & Hodges, 2003; Kemmerer & Tranel, 2003; Saygin, 2007; Silveri & Ciccarelli, 2007; Tranel et al., 2003).

So far we have only discussed the three verb classes that did engage the primary motor and premotor cortices, namely verbs of Running, Hitting, and Cutting. We turn

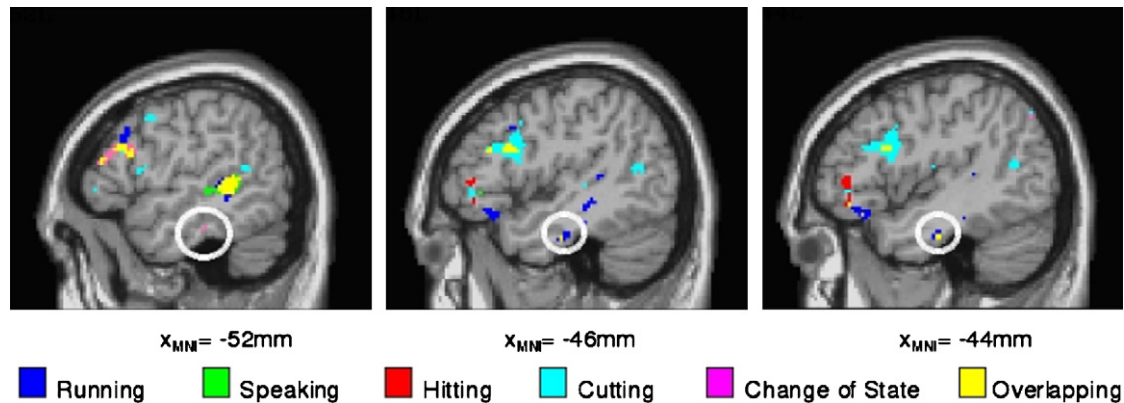


Fig. 6. Group results relevant to the CHANGE OF STATE component. Differential activations (random-effects analyses, $p < .001$, uncorrected) for each verb class versus Wingdings are shown on three sagittal sections of a representative brain. The circle in the left panel indicates significant activation (pink patch) in the left inferior temporal gyrus for Change of State verbs. The circles in the middle and right panels indicate overlapping activations (yellow patches) in the left fusiform gyrus for Change of State verbs, Cutting verbs, and Running verbs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

Table 9
Comparison of results and hypotheses

Verb classes	Hypotheses regarding semantic components and their neural substrates				
	(H1) Action = M1, M2	(H2) Motion = PLTC	(H3) Contact = IPS, IPL	(H4) Change of state = VTC	(H5) Tool use = Network
Running	+ (legs/feet)	+ (legs/feet)	–	–	–
Speaking	+ (mouth)	+ (mouth)	–	–	–
Hitting	+ (arm/hand)	+ (arm/hand)	+ (arm/hand)	–	–
Cutting	+ (arm/hand)	+ (arm/hand)	+ (arm/hand)	+	+
Change state	–	+	–	+	–

This table is identical to Table 2, except confirmed predictions are indicated by shaded cells, and unconfirmed predictions are indicated by unshaded cells.

now to the two verb classes that did not engage those brain regions, namely verbs of Speaking and Change of State. Contrary to our expectations, semantic judgments involving verbs of Speaking did not elicit significant activation in the mouth sector of either the primary motor cortex or the premotor cortex. A follow-up region-of-interest-based one-way ANOVA conducted on the mean activation for each class of verbs also revealed no significant difference between the mean for Speaking verbs and the means for the other four verb classes, relative to Wingdings ($p = .42$).⁷ This is in marked contrast to the fMRI studies reported by Hauk et al. (2004), Tettamanti et al. (2005), and Aziz-Zadeh et al. (2006). It is not clear why we did not observe significant engagement of the mouth region; however, one possibility is that this was due to task differences between our study and the previous studies. None of the previous studies presented a list of the linguistic stimuli that were employed, but it is not unreasonable to assume that they used a fairly wide range of material, including

verbs (e.g., *lick*; Hauk et al., 2004), sentences (e.g., *I bite the apple*; Tettamanti et al., 2005), and verb–object phrases (e.g., *biting the peach*; Aziz-Zadeh et al., 2006) that express motorically complex object-directed mouth actions.⁸ Perhaps such stimuli trigger effector congruent motor resonance more readily than verbs of Speaking (e.g., *shout*, *whine*, *mumble*, *whisper*, etc.; see Table 1) because the latter place less emphasis on motoric information than on other types of semantic information such as appearance, sound quality, and affective valence (see below).

Finally, in keeping with our hypothesis, verbs of Change of State did not activate primary motor or premotor cortices. We predicted this outcome because the meanings of these verbs focus on multifarious types of object transformation and do not indicate what sorts of agentive actions instigate those changes; in fact, verbs in the specialized subclass called Internally Caused Change of State (e.g., *bloom*, *blossom*, *wither*, *decay*, etc.) require inanimate grammatical subjects (Kuno & Takami, 2004; Levin, 1993; McKoon & MacFarland, 2000; Wright, 2001).

⁷ The region of interest was a 6-mm radius sphere, centered at MNI coordinates $-47, 6, 22$ based on previous literature (Hauk et al., 2004 and Tettamanti et al., 2005) and falling within Mayka et al.'s (2006) probabilistic map for the ventral premotor cortex.

⁸ The examples given for the various studies are drawn from the articles.

4.1.2. Component 2: MOTION

Unlike several previous functional neuroimaging studies of verb semantics (Damasio et al., 2001; Rüschemeyer et al., submitted for publication; Tranel et al., 2005; Wallentin, Lund, Ostergaard, Ostergaard, & Roepstorff, 2005), the current study did not reveal significant activation in the left MT area. However, consistent with a number of other functional neuroimaging studies of verb semantics (Kable et al., 2002, 2005; Noppeney et al., 2005; Pirog et al., submitted for publication; Tettamanti et al., 2005), we did find that all five classes of verbs robustly engaged the higher-order left PLTC anterior and dorsal to MT, thus providing partial support for Hypothesis 2. It is not obvious why some studies have obtained activation in left MT while others have not, and this issue deserves brief discussion. In two of the studies that did discover left MT activation (Damasio et al., 2001; Tranel et al., 2005), subjects retrieved verbs to name static pictures of actions (for pertinent lesion studies of action naming that also implicate left MT, see Tranel, Adolphs, Damasio, & Damasio, 2001; Tranel et al., in press). One might suppose that this MT activation reflected the visual processing of the pictorial stimuli rather than the semantic processing of the corresponding verbs, because the observation of action “stills” or “snapshots” that imply movement has been shown to engage MT rapidly and independently of naming tasks (Assmus et al., 2007; David & Senior, 2000; Kourtzi & Kanwisher, 2000; Olson, Gatenby, Leung, Skudlarski, & Gore, 2003; Senior et al., 2000; Senior, Ward, & David, 2002; but see Alford, van Donkelaar, Dassonville, & Marrocco, 2007). However, in the second study (Tranel et al., 2005), the MT activation was significant even after subtracting out a condition in which subjects performed a different naming task with the very same pictorial stimuli (specifically, naming the tools used to perform the actions). Furthermore, in the other two studies that discovered left MT activation during verb processing (Rüschemeyer et al., submitted for publication; Wallentin et al., 2005), subjects were not shown pictures of actions; instead, they listened to sentences containing motion verbs, which suggests that the comprehension of such linguistic expressions may be sufficient to recruit MT. Contradicting this view, however, is the fact that in one of the studies that found left PLTC activation but not—or at least not definitively—left MT activation (Tettamanti et al., 2005), subjects also listened to sentences containing motion verbs. Moreover, in the remaining studies that found left PLTC activation but not left MT activation (Kable et al., 2002, 2005; Noppeney et al., 2005), subjects made semantic judgments about either printed or spoken verbs, much like in the current study. Overall, these considerations suggest that the degree to which left MT is activated during tasks that probe verb semantics may be modulated by several complex factors that are not yet understood. Further research is needed to investigate these factors in greater detail, while also taking into account recent evidence for inter-subject variability in the precise anatomical location of MT (Malikovic et al., 2006).

Shifting our focus to the PLTC, it is well established that this region plays an important role in representing the complex motion patterns of not only people and animals (for reviews see Blake & Shiffrar, 2007; Giese & Poggio, 2003), but also non-living things like tools (for reviews see Beauchamp & Martin, 2007; Lewis, 2006). Against this background, the left PLTC activation that was elicited by all of the verb classes in our study could be interpreted within the context of the Simulation Framework as reflecting the evocation of the unique types of dynamic movement patterns encoded by specific verbs—e.g., the similar yet distinct appearances of the gaits encoded by *stroll*, *strut*, and *sashay*. As in the discussion of the ACTION component above, however, we must acknowledge that we did not directly address the question of whether the left PLTC areas that were engaged by our semantic processing task are also engaged during the execution and observation of the actions denoted by the verbs. Moreover, as before, an advocate of the amodal theory could argue that the left PLTC activation may not be the neural signature of the MOTION component of verb meanings, but may instead reflect post-comprehension mental imagery. Although this alternative type of interpretation cannot be completely ruled out, support for the notion that the left PLTC is necessary for understanding the MOTION component of verbs comes from a neuropsychological study which found that a group of brain-damaged patients with impaired performance on several tasks evaluating knowledge of action concepts tended to have lesions that included the left PLTC and underlying white matter (Tranel et al., 2003; see also Saygin, 2007).

Although there was substantial overlap among the left PLTC activation patterns associated with the five classes of verbs, there was also some evidence, at the group level as well as at the level of individual subjects, for class-specificity, perhaps indicating a rough body-part-based organization. Interestingly, some aspects of this strongly left-lateralized PLTC parcellation are analogous to the strongly right-lateralized PLTC parcellation that has been found in tasks involving the observation of different body-part movements. For example, at the group level, semantic judgments for Running verbs engaged a posterior area of the left PLTC in our study, and Pelphrey et al. (2003) found a comparable region of activity, only in the right hemisphere, during observation of human walking. In addition, at the group level, semantic judgments for Speaking verbs engaged an anterior area of the left PLTC in our study, and observation of mouth movements (relative to hand and eye movements) similarly engaged an anterior portion of the right PLTC in a study by Pelphrey et al. (2005).

It is noteworthy, however, that much of the left PLTC has been implicated not only in the representation of motion patterns, but also in the representation of environmental sounds (Dick et al., 2007; Lewis et al., 2004; see also Bidet-Caulet, Voisin, Bertrand, & Fonlupt, 2005). This is especially relevant to our condition involving verbs of

Speaking because it raises the possibility that the left anterior PLTC area that was selectively engaged by these verbs may reflect not only information about how different styles of speech appear to an observer (e.g., the open mouth action associated with *shout* vs. the small lip movements associated with *murmur*), but also information about how different styles of speech vary along multiple auditory dimensions such as loudness, pitch, and timbre. As suggested above in connection with the lack of motor activation for verbs of Speaking, it may be the case that these verbs assign greater semantic importance to visual and auditory information than to motoric information. Modest support for this view comes from several studies that have linked the perception of emotional vocalizations with the left PLTC (Grandjean et al., 2005; Morris, Scott, & Dolan, 1999; Phillips et al., 1998; for a review see Schirmer & Kotz, 2006). Further research is necessary, however, to understand the precise nature of the left PLTC activation elicited by verbs of Speaking.

4.1.3. Component 3: CONTACT

We found that Cutting verbs significantly activated a portion of the angular gyrus in the left IPL just below the IPS. This discovery provides partial support for Hypothesis 3, but from a semantic perspective it may be more closely related to the TOOL USE component than to the CONTACT component, and for this reason we discuss it in Section 4.1.5.

Unexpectedly, our whole brain analyses revealed that neither Hitting verbs nor Cutting verbs significantly activated the left IPS, despite the fact that this region has been strongly implicated in the visuomotor coordination of exactly the types of object-directed arm and hand actions that are encoded by those verb classes (for reviews see Culham & Valyear, 2006; Milner & Goodale, 2006). A follow-up region-of-interest-based one-way ANOVA conducted on the mean activation for each class of verbs also revealed no significant difference between the means for Hitting and Cutting verbs contrasted with the other verb classes, relative to Windings ($p = .82$).⁹ This is inconsistent with Hypothesis 3, and it is also inconsistent with several previous fMRI studies of semantic processing. Most importantly, Noppeney et al. (2005) found that the left aIPS, which has been linked with grasping (for a review see Tunik et al., 2007), was engaged when subjects performed a semantic similarity judgment task that was very much like ours insofar as it required explicit discriminations among triads of transitive verbs encoding goal-oriented arm/hand actions (e.g., determining that *tickle* is more like *touch* than *pierce*). In addition, as noted in Section 1, Tettamanti et al. (2005) observed even more widespread activation within the left IPS when subjects listened to transitive sentences describing goal-directed actions executed with the arms/

hands. Furthermore, yet another recent fMRI study showed that the left IPS is strongly associated with not only verbs but also nouns that rank high on the semantic dimension of “manipulation” or “manipulability” (Saccuman et al., 2006; see also Arévalo et al., 2007)—a dimension that is closely related to a wide range of linguistic phenomena that fall under the rubric of transitivity (Dixon & Aikhenvald, 2000). It is difficult to explain the discrepancy between the results of the current study and those of the previous studies with regard to the left IPS. However, research on how this brain region contributes to language has only just begun, and further investigation may shed more light on the situation.

4.1.4. Component 4: CHANGE OF STATE

As predicted by Hypothesis 4, Cutting verbs and Change of State verbs engaged the left VTC, particularly several areas in the fusiform gyrus and the inferior temporal gyrus. Given that these cortical structures have been shown to contribute to both perceptual and conceptual processing of object properties like shape, color, and texture (for reviews see Martin, 2007; Kemmerer, in press), it is possible that the activations we observed reflect visual re-enactments of the idiosyncratic types of physical transformations that are designated by verbs in the Cutting and Change of State classes. For example, *slash* specifies that a long deep incision is made in an object, and *crumble* specifies that an object breaks into tiny bits. The task that our subjects performed required access to these sorts of semantic features, and according to the Simulation Framework, the features are stored in visual format. It is also noteworthy that our findings are compatible with a few neuropsychological (Lu et al., 2002; Wolk et al., 2005) and functional neuroimaging (Bedny & Thompson-Schill, 2006; Vigliocco et al., 2006) studies that have linked certain visual aspects of verb meanings with the left VTC. As in our earlier discussions of the ACTION and MOTION components, however, we must acknowledge that the interpretation based on the Simulation Framework should be treated with caution.

We also found that verbs of Speaking and Hitting did not significantly activate the left VTC. This is consistent with Hypothesis 4, because those verb classes do not incorporate the CHANGE OF STATE component and hence should not engage the left VTC. On the other hand, Running verbs did engage that brain region, even though they, like Speaking and Hitting verbs, do not incorporate the CHANGE OF STATE component. This result was surprising, and it is not easy to account for. One possible explanation, though, draws on a neurophysiologically plausible computational model of motion perception which posits two parallel, hierarchical, interactive processing streams, one called the “motion pathway” and the other called the “form pathway” (Giese & Poggio, 2003; for empirical support see Peuskens, Vanrie, Verfaillie, & Orban, 2005). Whereas the motion pathway includes the PLTC, the form pathway includes the VTC, and its func-

⁹ The region of interest was a 6 mm radius sphere, centered at MNI coordinates –40, 39, 42 based on previous literature (Tunik et al., 2007).

tional role is to recognize, by means of “snapshot neurons,” learned sequences of human postures. In the context of this model, the VTC activation elicited by Running verbs could be interpreted as reflecting the retrieval of stored visual knowledge about the sequences of body configurations that uniquely characterize various kinds of lexically specified locomotion patterns. Although such an account does not seem unreasonable, it raises the question of why Speaking verbs and Hitting verbs did not activate the form pathway as well. More research on this topic is clearly in order.

4.1.5. Component 5: TOOL USE

Consistent with Hypothesis 5, Cutting verbs, but none of the other verb classes, activated a widely distributed network of left-lateralized cortical areas that, according to a growing body of literature, constitute different nodes of an intricate neural system underlying tool knowledge (for reviews see Beauchamp & Martin, 2007; Johnson-Frey, 2004; Lewis, 2006). First, as noted in Section 4.1.3, Cutting verbs engaged a portion of the angular gyrus in the left IPL. This region is located near the parieto-temporo-occipital junction, and damage to it frequently engenders ideational apraxia—i.e., impaired conceptual knowledge of proper object use (e.g., Buxbaum, Kyle, & Menon, 2005, 2007; De Renzi & Lucchelli, 1988; Mahon et al., 2007). For example, patients may attempt to brush their teeth with a comb and eat with a toothbrush (e.g., Ochipa, Rothi, & Heilman, 1989). Our findings are in keeping with the neuropsychological profile of ideational apraxia, and they also fit nicely with a recent fMRI study that found activation in the left angular gyrus when a task requiring semantic decisions about the functional purposes of objects was contrasted with a task requiring semantic decisions about the visuospatial properties of objects; moreover, the activation was present regardless of whether the two tasks were performed with written object names or object drawings (Ebisch et al., 2007). Second, Cutting verbs engaged the left posterolateral temporo-occipital cortex, a few millimeters superior to a region that has been linked with the motion patterns of tools (see the reviews cited above). Finally, Cutting verbs engaged a large sector of the left posterior middle frontal gyrus, including the upper, hand-related portion of the ventral premotor cortex. This region has been implicated in both functional and manipulative aspects of tool knowledge (again, see the reviews cited above). Taken together, our results regarding Cutting verbs add to the existing literature on the neural substrates of tool knowledge by suggesting that many elements of the “tool circuit” may be incorporated directly into the meanings of verbs that denote actions involving the skilled use of certain types of sharp instruments. Our findings also correspond well with several studies which indicate that “instrumental verbs” are susceptible to distinctive kinds of impairment following brain damage (Jonkers & Bastiaanse, 2006, 2007; Kambanaros & van Steenbrugge, 2006; Kemmerer & Tranel, 2000).

4.1.6. Broca’s area

Finally, it should come as no surprise that all five verb classes activated left BA 45, and that almost all of them (the single exception being Change of State verbs) also activated left BA 47. Space limitations prevent us from attempting to integrate these findings with the rapidly evolving body of empirical and theoretical work on Broca’s area (e.g., Anwender, Tittgemeyer, von Cramon, Friederici, & Knösche, 2007; Grodzinsky & Amunts, 2006; Koehlin & Jubault, 2006; Novick, Trueswell, & Thompson-Schill, 2005; Schubotz & Fiebach, 2006). However, we will briefly mention two points of contact that we regard as especially noteworthy. First, BA 45 has been strongly associated not only with semantic and syntactic processing in general (Lindenberg et al., 2007), but also with verb processing in particular (e.g., Damasio et al., 2001; Hauk et al., 2004; Sahin, Pinker, & Halgren, 2006; Shapiro & Caramazza, 2003; Shapiro, Shelton, & Caramazza, 2000; Shapiro et al., 2006; Tranel et al., 2001, in press; Tsapkini, Jarema, & Kehayia, 2002). Second, BAs 47 and 45 have been linked with two mechanistically distinct types of computation that fall under the general rubric of semantic working memory (for a review see Badre & Wagner, 2007). In particular, BA 47 may control the retrieval of semantic content stored elsewhere in the brain (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Bunge, Wendelken, Badre, & Wagner, 2005; Sabb, Bilder, Chou, & Bookheimer, 2007; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001), and BA 45 may operate on the products of retrieval to select appropriate representations from among competitors (Badre et al., 2005; Chee, Hon, Caplan, Lee, & Goh, 2002; Fletcher, Shallice, & Dolan, 2000; Moss et al., 2005; Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997, 1999). Consistent with this view, a recent fMRI study found that BA 47 is involved in “strategic semantic facilitation,” whereas BA 45 is involved in “strategic semantic inhibition” (Gold et al., 2006). The notion that BAs 47 and 45 serve complementary semantic working memory functions can be applied to the results of the current study, because our subjects performed a demanding task that required them to discriminate between verbs that bear different degrees of semantic similarity to each other along multiple dimensions (e.g., determining that *tiptoe* is more like *creep* than *trudge*). In fact, our task was comparable in design to the ones used by Badre et al. (2005). From the perspective of the Simulation Framework, these considerations suggest that when people pay close attention to subtle semantic relationships among verbs, BAs 47 and 45 work together to generate and evaluate multimodal recapitulations of the types of actions encoded by those verbs.

4.2. Returning to the Two-Level Theory

In Section 1 we pointed out that, according to the Two-Level Theory, the composite meaning of a verb involves correspondences between two separate levels of semantic

structure: (1) the “event structure template,” which is (a) shared by all the verbs in a given class, (b) highly schematic in content, and (c) relevant to syntax; and (2) the “constant,” which is (a) unique to particular verbs, (b) highly concrete in content, and (c) grammatically irrelevant. As Pinker (2007, p. 82) put it, “basic conceptual distinctions assemble themselves into a scaffolding of meaning [at level 1], which has hooks here and there to hang images, sounds, emotions, mental movies, and the other contents of consciousness [at level 2].” For instance, Change of State verbs have in common a basic template that is very simple—[BECOME [y <STATE>]]—and the semantic constants of the individual verbs comprising this class elaborate the “state” variable of the template in idiosyncratic ways (e.g., *shatter*, *smash*, *chip*, etc.; see Table 1). Because the task we employed in our fMRI study required close attention to fine-grained, modality-specific semantic relations among verbs within certain classes, the results pertain mainly to the neural substrates of the second level of verb meaning; and because this is the level that the Simulation Framework attempts to capture, our discussion so far has focused on the implications of our findings for that theoretical model. We would be remiss, however, if we did not also address the question as to the neural substrates of the first, more abstract, level of verb meaning. A meticulous consideration of this complex topic is beyond the scope of the current paper, so we will simply mention a few studies that have begun to illuminate the issue.

If, as the Two-Level Theory maintains, a fundamental cognitive division exists between templates and constants, it is likely that these two semantic subsystems are mediated by at least partially separate brain regions. This in turn predicts that the two levels of verb meaning could be impaired independently of each other by focal lesions. In a series of studies with aphasic patients, Kemmerer and colleagues have obtained results that are consistent with this prediction (Kemmerer, 2000, 2003; Kemmerer & Wright, 2002; for a review see Kemmerer, 2006). For present purposes, what is most important about these studies is that they provide evidence in support of the following two points: first, knowledge and/or processing of templates can be disrupted while knowledge and/or processing of constants is preserved; and second, the patients who exhibit this type of dissociation tend to have left inferior frontoparietal lesions that include portions of Broca’s area (BAs 44 and 45), the supramarginal gyrus (roughly BA 40), and the underlying white matter.¹⁰ All of the studies were based on the assumption that, as described in detail in the technical literature on “constructionist” approaches to language, one of the major functions of event structure templates is to serve as the semantic interface between verb classes and syntactic frames (see especially Pinker, 1989; for related

perspectives see, e.g., Bornkessel, Schlesewsky, Comrie, & Friederici, 2006; Davis, 2001; Fried & Boas, 2005; Goldberg, 1995, 2006; Goldberg & Jackendoff, 2004; Iwata, 2005; Jackendoff, 2002; Kako, 2006; Kuno & Takami, 2004; Levin, 1993; Levin & Rappaport Hovav, 2005; Östman & Fried, 2005; Rappaport Hovav & Levin, 1998; Van Valin, 2005). To take a representative example, below we briefly summarize Kemmerer’s (2003) neuropsychological investigation of the so-called body part possessor ascension construction. This construction is particularly interesting in the current context because it involves three of the verb classes used in the fMRI study.

Consider the following sentences:

(3) Non-possessor ascension construction:

- | | |
|---------------|--|
| (a) Hitting | <i>Bill hit/bumped/tapped/whacked</i> |
| verbs | <i>Bob’s arm</i> |
| (b) Cutting | <i>Bill cut/scratched/scraped/nicked</i> |
| verbs | <i>Bob’s arm</i> |
| (c) Change of | <i>Bill broke/cracked/fractured/</i> |
| State verbs | <i>shattered Bob’s arm</i> |

(4) Possessor ascension construction:

- | | |
|---------------|--|
| (a) Hitting | <i>Bill hit/bumped/tapped/whacked</i> |
| verbs | <i>Bob on the arm</i> |
| (b) Cutting | <i>Bill cut/scratched/scraped/nicked</i> |
| verbs | <i>Bob on the arm</i> |
| (c) Change of | <i>*Bill broke/cracked/fractured/</i> |
| State verbs | <i>shattered Bob on the arm</i> |

In (3) the direct object is *arm*, which is modified by *Bob’s*, whereas in (4) the direct object is *Bob*, and *arm* is syntactically realized as the object of the locative preposition *on*. Although these syntactic differences appear to be superficial, in actuality they signify contrasting cognitive construals of the same action scenario. Basically, in (3) the action is portrayed as being directed at the body part to the exclusion of the person, whereas in (4)—the possessor ascension construction—the action is portrayed as being directed at, and as intimately affecting, the person, even though it takes effect through a body part. In Pinker’s (2007, p. 104), words, the contrast involves a gestalt shift “between construing a person as some kind of immaterial soul who *possesses* his body parts, and construing him as an incarnate hunk that *is* his body parts.” It is for this reason that the possessor ascension construction places semantic constraints on which verbs are acceptable. In short, verbs of Hitting and Cutting are permitted, whereas verbs of Change of State are not. Levin (1993, p. 8) argues that the relevant semantic component is CONTACT, which is incorporated by the event structure templates of the first two verb classes, but not by that of the third (for further justification see the references cited by Levin, 1993, p. 71; for similar phenomena in other languages, see Chappell & McGregor, 1996; Payne & Barshi, 1999; Velazquez-Cas-

¹⁰ The patient who fits this neuropsychological and neuroanatomical profile most accurately is 1962RR. He participated in all of the studies by Kemmerer cited above, and his lesion is depicted in a different paper by Kemmerer and Tranel (2003).

tillo, 1996).¹¹ Crucially, the possessor ascension construction is only sensitive to whether the meaning of a given verb includes the general notion of CONTACT at the template level; it is effectively blind to the idiosyncratic ways in which different verbs elaborate that notion at the level of constants. Thus, the subtle semantic distinctions between verbs within the Hitting class are irrelevant, as are the subtle semantic distinctions between verbs within the Cutting class.

In accord with the neuropsychological predictions of the Two-Level Theory, Kemmerer (2003) found that three patients with left inferior frontoparietal lesions exhibited the following type of dissociation. On the one hand, they performed normally on a verb–picture matching task that required discrimination between the idiosyncratic, modality-specific, grammatically irrelevant constants of not only Hitting verbs (e.g., *hit* vs. *poke* vs. *prod*) but also Change of State verbs (e.g., *break* vs. *crack* vs. *shatter*). On the other hand, they could no longer make accurate judgments about which of these verbs could occur in the possessor ascension construction (e.g., *She hit him on the arm* vs. **She broke him on the arm*). The patients' poor performances on the judgment test could not be attributed to purely syntactic disorders, because they had no difficulty with a different task that evaluated their knowledge of the clausal organization of the possessor ascension construction. Instead, the overall set of findings suggests that the patients have selectively impaired understanding of the fact that the possessor ascension construction only licenses verbs whose event structure templates incorporate the CONTACT component.

It is noteworthy that these results are consistent with our fMRI data, since the patients' lesions spared the cortical regions that we found to be associated with the constants of Hitting verbs (bilateral arm-related primary motor cortex and left PLTC) and Change of State verbs (left PLTC and left VTC). It is also intriguing, however, that Broca's area is implicated in the patients' lesion sites as well as in the fMRI data. The proper interpretation of this convergence is not clear. One possibility, however, is that besides contributing to many other types of linguistic operations, Broca's area may play an essential role in representing and/or processing the template level of verb meaning.¹² Further research is necessary to develop and explore this hypothesis, and the Two-Level Theory may provide the ideal framework to guide such research.

¹¹ “Carve” verbs, which constitute a subclass of verbs of Cutting (Levin, 1993), are somewhat problematic because although all of them denote CONTACT, some do not occur naturally in the possessor ascension construction (e.g., **The dentist drilled me in my tooth*). This issue is discussed by Kemmerer (2003).

¹² As indicated above, the task we used in the fMRI study emphasizes the level of constants. It is quite conceivable, however, that the task also taps into the level of templates.

4.3. Conclusions

We have reported a complex, hypothesis-driven fMRI experiment in which subjects made semantic judgments involving five classes of verbs (specifically, verbs of Running, Speaking, Hitting, Cutting, and Change of State) that differ with respect to the presence or absence of five semantic components (specifically, ACTION, MOTION, CONTACT, CHANGE OF STATE, and TOOL USE). Our results suggest that these semantic components are neurally subserved by a widely distributed network of predominantly left-hemisphere cortical structures that also contribute to the execution, observation, and imagination of actions. Overall, the findings support the Simulation Framework and are consistent with the broader Two-Level Theory of verb meaning. This line of research is still in its infancy, however, and further research is needed to assess the reliability of our findings and pursue additional questions.

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Appendix A

The matrix below shows the stimuli for the Semantic Similarity Judgment Task (SSJT), organized according to the design of the 5 blocks of verb trials in each of the 4 runs of the fMRI experiment.

The names of the verb classes are provided only for explanatory purposes; they were not included in the experimental paradigm itself, and the subjects were unable to predict which verb class would be represented in each consecutive block. The trial sequences are, however, exactly as they were in the actual experiment, with the left/right side of the correct verb in each item varying randomly.

Across the 4 runs there were a total of 24 items for each verb class (6 items in each block, and 1 block in each run). For 20 of those 24 items, the “pivot” verbs—i.e., the verbs at the top of the triangular arrays—were the same as the 20 verbs listed in Table 1. However, based on Levin's (1993) taxonomy, it was difficult to find 4 distinct new verbs in each class that we felt could be used appropriately as pivots for the remaining 4 items, so the following strategies were

adopted to circumvent this problem. For the Running class, 1 verb (*walk*) from the list of 20 was used twice as pivot, and 3 new verbs (*sashay*, *traipse*, and *plod*) were introduced to serve as pivots for the remaining 3 items. For the Speaking class, 4 verbs (*cry*, *shout*, *mutter*, and *holler*) from the list of 20 were each used twice as pivots. For the Hitting class, 4 verbs (*tap*, *spank*, *pummel*, and *hit*) from the list of 20 were each used twice as pivots. For the Cutting class, 3 verbs (*slice*, *nick*, and *scratch*) from the list of 20 were each used twice as pivots, and 1 new verb (*squish*) was introduced to serve as pivot for the remaining

item. Finally, for the Change of State class, 2 verbs (*break* and *sprout*) from the list of 20 were each used twice as pivots, and 2 new verbs (*splinter* and *twist*) were introduced to serve as pivots for the remaining items. When the same verb functioned as pivot for 2 items, those items were placed in separate runs. Furthermore, although for each class some verbs occurred in multiple items as target, distractor, or both, we attempted to keep those items as far apart as possible in order to minimize repetition suppression effects (for a review see Grill-Spector, Hensen, & Martin, 2006).

Run 1 Trial	Block 1 Running	Block 2 Speaking	Block 3 Hitting	Block 4 Cutting	Block 5 Change of State
1	walk	yell	spank	snip	break
2	stumble amble	shout whimper	tap slap	cut grate	snap bend
3	stagger	mumble	stroke	hack	tear
4	tiptoe limp	mutter bawl	caress hit	carve chop	crack rip
5	run	holler	prick	mash	crease
6	jog sneak	bellow whine	pat poke	gash squish	twist fold
7	stomp	chatter	pummel	shred	bloom
8	march saunter	stutter jabber	knock batter	slice gouge	blossom sprout
9	stumble	scream	clobber	slit	chip
10	walk trip	moan shriek	whack prick	nick mince	splinter smash
11	limp	cry	tap	grate	twist
12	stroll trudge	bawl sing	pound prod	pierce shred	bend rip
Run 2 Trial	Block 1 Hitting	Block 2 Running	Block 3 Change of State	Block 4 Speaking	Block 5 Cutting
1	whack	leap	split	mutter	chop
2	strike prick	jump strut	shatter crack	grumble chatter	dice scrape
3	poke	tiptoe	bend	shout	nick
4	whack jab	trudge creep	break twist	whimper yell	scratch hack
5	hit	march	wilt	cry	slice
6	tap knock	stomp amble	bloom wither	wail mumble	slash carve
7	caress	sprint	rip	chant	gouge
8	pat clobber	run walk	tear fold	scream sing	slit pierce
9	batter	skip	blossom	groan	clip
10	pound poke	limp dance	bloom sprout	bawl whine	cut squish
11	slap	jog	break	grumble	mince
12	jab smack	trudge skip	bend shatter	whimper holler	gash chop
Run 3 Trial	Block 1 Change of State	Block 2 Hitting	Block 3 Running	Block 4 Cutting	Block 5 Speaking
1	smash	jab	strut	scratch	whimper
2	shatter twist	hit poke	traipse limp	gouge clip	cry bellow
3	sprout	smack	amble	scrape	shout
4	wilt blossom	stroke spank	stroll skip	snip gash	murmur holler
5	crumble	pinch	plod	carve	shriek
6	break crease	prick pat	run trudge	crush cut	whisper yell
7	crack	pound	hop	dice	bellow
8	split rip	pummel prod	stumble jump	chop shred	shout cry

Run 3 Trial	Block 1 Change of State	Block 2 Hitting	Block 3 Running	Block 4 Cutting	Block 5 Speaking
5	shatter crumple	smash pound	pat tap	sashay strut	cut slice
6	wither bloom	wilt poke	strike hit	stroll saunter	gash scratch
Run 4 Trial	Block 1 Cutting	Block 2 Hitting	Block 3 Speaking	Block 4 Change of State	Block 5 Running
1	slice cut	prod tap	mutter chatter	snap break	saunter sprint
2	nick slit	tap clobber	bawl sing	crumple bend	trudge jog
3	scratch chop	spank poke	whisper murmur	sprout bloom	sneak tiptoe
4	gash squish	smack knock	whine sing	fracture crack	stagger jump
5	slice slash	whack pummel	prick holler	shatter splinter	march traipse
6	hack nick	caress batter	mutter shout	crumple chip	saunter run
	grind slice	hit pat	wail cry	fold crease	walk stroll

References

- Ackerman, F., & Moore, J. (2001). *Proto-properties and grammatical encoding: A correspondence theory of argument selection*. Stanford: CSLI Publications.
- Alford, J. L., van Donkelaar, P., Dassonville, P., & Marrocco, R. T. (2007). Transcranial magnetic stimulation over MT/MST fails to impair judgments of implied motion. *Cognitive, Affective, and Behavioral Neuroscience*, 7, 225–232.
- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, 4, 267–278.
- Arévalo, A., Perani, D., Cappa, S. F., Butler, A., Bates, E., & Dronkers, N. (2007). Action and object processing in aphasia: From nouns and verbs to the effect of manipulability. *Brain and Language*, 100, 79–94.
- Arzy, S., Thut, G., Mohr, C., Michel, C. M., & Blanke, O. (2006). Neural basis of embodiment: Distinct contributions of temporoparietal junction and extrastriate body area. *Journal of Neuroscience*, 26, 8074–8081.
- Anwander, A., Tittgemeyer, M., von Cramon, D. Y., Friederici, A. D., & Knösche, T. R. (2007). Connectivity-based parcellation of Broca's area. *Cerebral Cortex*, 17, 816–825.
- Assmus, A., Giessing, C., Weiss, P. H., & Fink, G. R. (2007). Functional interactions during the retrieval of conceptual action knowledge: An fMRI study. *Journal of Cognitive Neuroscience*, 19, 1004–1012.
- Astafiev, S. V., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience*, 7, 542–548.
- Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology*, 16, 1818–1823.
- Badre, D., Poldrack, R. A., Pare-Blagoev, J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, 47, 907–918.
- Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, 45, 2883–2901.
- Bak, T. H., & Hodges, J. R. (2003). “Kissing and Dancing”—A test to distinguish the lexical and conceptual contributions to noun/verb and action/object dissociation. Preliminary results in patients with frontotemporal dementia. *Journal of Neurolinguistics*, 16, 169–181.
- Bak, T. H., Yancopoulos, D., Nestor, P. J., Xuereb, J. H., Spillantini, M. G., Pulvermüller, F., et al. (2006). Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. *Brain*, 129, 321–332.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, 22, 577–660.
- Barsalou, L. W. (2005). Situated conceptualization. In: H. Cohen & C. Lefebvre (Eds.), *Handbook of categorization in cognitive science* (pp. 619–650). St Louis: Elsevier.
- Barsalou, L. W. (in press). Grounded cognition. *Annual Review of Psychology*.
- Beauchamp, M. S., & Martin, A. (2007). Grounding object concepts in perception and action. *Cortex*, 43, 461–468.
- Bedny, M., Aguirre, G. K., & Thompson-Schill, S. L. (2007). Item analysis in functional magnetic resonance imaging. *NeuroImage*, 35, 1093–1102.
- Bedny, M., & Thompson-Schill, S. L. (2006). Neuroanatomically separable effects of imageability and grammatical class during single-word comprehension. *Brain and Language*, 98, 127–139.
- Bergen, B. (2007). Experimental methods for simulation semantics. In: M. Gonzalez-Marquez, I. Mittelberg, S. Coulson, & M. J. Spivey (Eds.), *Methods in cognitive linguistics* (pp. 277–301). Amsterdam: John Benjamins.
- Bidet-Caulet, A., Voisin, J., Bertrand, O., & Fonlupt, P. (2005). Listening to a walking human activates the temporal biological motion area. *NeuroImage*, 28, 132–139.
- Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of Psychology*, 58, 47–73.
- Bornkessel, I., Schlesewsky, M., Comrie, B., & Friederici, A. D. (Eds.). (2006). *Semantic role universals and argument linking: Theoretical, typological, and psycholinguistic perspectives*. Berlin: Mouton de Gruyter.
- Borreggine, K. L., & Kaschak, M. P. (in press). The action-sentence compatibility effect: It's all in the timing. *Cognitive Science*.
- Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M., & Nazir, T. A. (2006). Cross-talk between language processes and overt motor behavior in the first 200 ms of processing. *Journal of Cognitive Neuroscience*, 18, 1607–1615.

- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.
- Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Cognitive Brain Research*, *24*, 355–363.
- Bunge, S. A., Wendelken, C., Badre, D., & Wagner, A. D. (2005). Analogical reasoning and prefrontal cortex: Evidence for separable retrieval and integration mechanisms. *Cerebral Cortex*, *15*, 239–249.
- Buxbaum, L. J., Kyle, K. M., Grossman, M., & Coslett, H. B. (2007). Left inferior parietal representations for skilled hand-object interactions: Evidence from stroke and corticobasal degeneration. *Cortex*, *43*, 411–423.
- Buxbaum, L. J., Kyle, K. M., & Menon, R. (2005). On beyond mirror neurons: Internal representations subserving imitation and recognition of skilled object-related actions in humans. *Cognitive Brain Research*, *25*, 226–239.
- Caetano, G., Jousmäki, V., & Hari, R. (2007). Actor's and observer's primary motor cortices stabilize similarly after seen or heard motor actions. *Proceedings of the National Academy of Sciences*, *104*, 9058–9062.
- Calvo-Merino, B., Grezes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, *16*, 1905–1910.
- Canessa, N., Borgo, F., Cappa, S. F., Perani, D., Falini, A., Buccino, G., et al. (2007). The different neural correlates of action and function knowledge in semantic memory: An fMRI study. *Cerebral Cortex*. doi:10.1093/cercor/bhm110.
- Cant, J. S., & Goodale, M. A. (2007). Attention to form or surface properties modulates different regions of human occipitotemporal cortex. *Cerebral Cortex*, *17*, 713–7131.
- Carroll, J. B., Davies, P., & Richman, B. (1971). *The American Heritage word frequency book*. New York: American Heritage Publishing Co.
- Chappell, H., & McGregor, W. (Eds.). (1996). *The grammar of inalienability: A typological perspective on body part terms and the part-whole relation*. Berlin: Mouton de Gruyter.
- Chee, M. W. L., Hon, N. H. H., Caplan, D., Lee, H. L., & Goh, J. (2002). Frequency of concrete words modulates prefrontal activation during semantic judgments. *NeuroImage*, *16*, 259–268.
- Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. *Current Opinion in Neurobiology*, *16*, 205–212.
- Damasio, A. R. (1989). Time-locked multiregional retroactivation: A systems level proposal for the neural substrates of recall and recognition. *Cognition*, *33*, 25–62.
- Damasio, H., Grabowski, T. J., Tranel, D., Ponto, L. L. B., Hichwa, R. D., & Damasio, A. R. (2001). Neural correlates of naming actions and of naming spatial relations. *NeuroImage*, *13*, 1053–1064.
- Damasio, H., Tranel, D., Grabowski, T. J., Adolphs, R., & Damasio, A. R. (2004). Neural systems behind word and concept retrieval. *Cognition*, *92*, 179–229.
- David, A. S., & Senior, C. (2000). Implicit motion and the brain. *Trends in Cognitive Sciences*, *4*, 293–295.
- Davis, A. R. (2001). *Linking by types in the hierarchical lexicon*. Stanford, CA: CSLI Publications.
- De Renzi, E., & Lucchelli, F. (1988). Ideational apraxia. *Brain*, *111*, 1173–1185.
- Dick, F., Saygin, A. P., Galati, G., Pitzalis, S., Bentrovato, S., D'Amico, S., et al. (2007). What is involved and what is necessary for complex linguistic and nonlinguistic auditory processing: Evidence from functional magnetic resonance imaging and lesion data. *Journal of Cognitive Neuroscience*, *19*, 799–816.
- Dixon, R. M. W. (2000). A typology of causatives: Form, syntax and meaning. In: R. M. W. Dixon & A. Y. Aikhenvald (Eds.), *Changing valency: Case studies in transitivity*. Cambridge, UK: Cambridge University Press.
- Dixon, R. M. W., & Aikhenvald, A. Y. (Eds.). (2000). *Changing valency: Case studies in transitivity*. Cambridge, UK: Cambridge University Press.
- Downing, P. E., Chan, A. W.-Y., Peelen, M. V., Dodds, C. M., & Kanwisher, N. (2006). Domain specificity in visual cortex. *Cerebral Cortex*, *16*, 1453–1461.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for the visual processing of the human body. *Science*, *293*, 2470–2473.
- Downing, P. E., Wiggett, A. J., & Peelen, M. V. (2007). Functional magnetic resonance imaging investigation of overlapping lateral occipitotemporal activations using multi-voxel pattern analysis. *Journal of Neuroscience*, *27*, 226–233.
- Dumoulin, S. O., Bittar, R. G., Kabani, N. J., Baker, C. L., Le Goualher, G., Pike, G. B., et al. (2000). A new anatomical landmark for reliable identification of human area V5/MT: A quantitative analysis of sulcal patterning. *Cerebral Cortex*, *10*, 454–463.
- Ebisch, S. J. H., Babiloni, C., Del Gratta, C., Ferretti, A., Perrucci, M. G., Caulo, M., et al. (2007). Human neural systems for conceptual knowledge of proper object use: A functional magnetic resonance imaging study. *Cerebral Cortex*. doi:10.1093/cercor/bhm001.
- Ehrsson, H. H., Geyer, S., & Naito, E. (2003). Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *Journal of Neurophysiology*, *90*, 3304–3316.
- Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinion in Neurobiology*, *15*, 213–218.
- Farné, A., Serino, A., & Ladavas, E. (2007). Dynamic size-change of peri-hand space following tool-use: Determinants and spatial characteristics revealed through cross-modal extinction. *Cortex*, *43*, 436–443.
- Filimon, F., Nelson, J. D., Hagler, D. J., & Sereno, M. I. (2007). Human cortical representations for reaching: Mirror neurons for execution, observation, and imagery. *NeuroImage*, *37*, 1315–1328.
- Fischer, M., & Zwaan, R. A. (in press). Embodied language: A review of the role of the motor system in language comprehension. *Quarterly Journal of Experimental Psychology*.
- Fletcher, P. C., Shallice, T., & Dolan, R. J. (2000). “Sculpting the response space”—An account of left prefrontal activation at encoding. *NeuroImage*, *12*, 404–417.
- Fried, M., & Boas, H. C. (Eds.). (2005). *Grammatical constructions: Back to the roots*. Amsterdam: John Benjamins.
- Gainotti, G. (2007). The anatomical locus of lesion in category-specific semantic disorders and the format of the underlying conceptual representations. In: J. Hart & M. A. Kraut (Eds.), *The neural basis of semantic memory* (pp. 28–64). Cambridge, UK: Cambridge University Press.
- Gallagher, S. (2005). *How the body shapes the mind*. Oxford, UK: Oxford University Press.
- Gallese, V., & Lakoff, G. (2005). The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology*, *22*, 455–479.
- Gazzola, V., Aziz-Zadeh, L., & Keysers, C. (2006). Empathy and the somatotopic auditory mirror neuron system in humans. *Current Biology*, *16*, 1824–1829.
- Gazzola, V., Rizzolatti, G., Wicker, B., & Keysers, C. (2007). The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. *NeuroImage*, *35*, 1674–1684.
- Gibbs, R. W. (2006). *Embodiment and cognitive science*. Cambridge, UK: University of Cambridge Press.
- Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, *4*, 179–192.
- Glenberg, A. M. (in press). Language and action: Creating sensible combinations of ideas. In G. Gaskell (Ed.), *The Oxford handbook of psycholinguistics*. Oxford, UK: Oxford University Press.

- Glenberg, A. M., de Vega, M., & Graesser, A. C. (Eds.). (in press-a). *The Garachico workshop on symbols and embodiment*. Oxford, UK: Oxford University Press.
- Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin & Reviews*, 9, 558–565.
- Glenberg, A. M., Sato, M., Cattaneo, L., Riggio, L., Palumbo, D., & Buccino, G. (in press-b). Processing abstract language modulates motor system activity. *Quarterly Journal of Experimental Psychology*.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*, 27, 1–78.
- Gold, B. T., Balota, D. A., Jones, S. J., Powell, D. K., Smith, C. D., & Andersen, A. H. (2006). Dissociation of automatic and strategic lexical-semantic: Functional magnetic resonance imaging evidence for differing roles of multiple frontotemporal regions. *Journal of Neuroscience*, 26, 6523–6532.
- Goldberg, A. E. (1995). *Constructions: A construction grammar approach to argument structure*. Chicago: University of Chicago Press.
- Goldberg, A. E. (2006). *Constructions at work: The nature of generalization in language*. Oxford, UK: Oxford University Press.
- Goldberg, A. E., & Jackendoff, R. (2004). The English resultative as a family of constructions. *Language*, 80, 532–568.
- Goldberg, R. F., Perfetti, C. A., & Schneider, W. (2006). Perceptual knowledge retrieval activates sensory brain regions. *Journal of Neuroscience*, 26, 4917–4921.
- Grandjean, D., Sander, D., Pourtois, G., Schwartz, S., Seghier, M. L., Scherer, K. R., et al. (2005). The voices of wrath: Brain responses to angry prosody in meaningless speech. *Nature Neuroscience*, 8, 145–146.
- Graziano, M. (2006). The organization of behavioral repertoire in motor cortex. *Annual Review of Neuroscience*, 29, 104–134.
- Grill-Spector, K., Hensen, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, 10, 14–23.
- Grodzinsky, Y., & Amunts, K. (Eds.). (2006). *Broca's region*. Oxford, UK: Oxford University Press.
- Hamilton, A. F., & Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. *Journal of Neuroscience*, 26, 1133–1137.
- Hampe, B. (Ed.). (2005). *From perception to meaning: Image schemas in cognitive linguistics*. Berlin: Mouton de Gruyter.
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41, 301–307.
- Hauk, O., & Pulvermüller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping*, 21, 191–201.
- Hopper, P., & Thompson, S. A. (1980). Transitivity in grammar and discourse. *Language*, 56, 251–299.
- Imazu, S., Sugio, T., Tanaka, S., & Inui, T. (2007). Differences between actual and imagined usage of chopsticks: An fMRI study. *Cortex*, 43, 301–308.
- Iwata, S. (2005). Locative alternation and two levels of verb meaning. *Cognitive Linguistics*, 16, 355–407.
- Jackendoff, R. (2002). *Foundations of language*. Oxford, UK: Oxford University Press.
- James, T. W., & Gauthier, I. (2003). Auditory and action semantic features activate sensory-specific perceptual brain regions. *Current Biology*, 13, 1792–1796.
- Jeannerod, M. (2006). *Motor cognition: What actions tell the self*. Oxford, UK: Oxford University Press.
- Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences*, 8, 71–78.
- Jonkers, R., & Bastiaanse, R. (2006). The influence of instrumentality and name relation to a noun on verb comprehension in Dutch aphasic speakers. *Aphasiology*, 20, 3–16.
- Jonkers, R., & Bastiaanse, R. (2007). Action naming in anomie aphasic speakers: Effects of instrumentality and name relation. *Brain and Language*, 102, 262–272.
- Kable, J. W., & Chatterjee, A. (2006). Specificity of action representations in the lateral occipitotemporal cortex. *Journal of Cognitive Neuroscience*, 18, 1498–1517.
- Kable, J. W., Lease-Spellmeyer, J., & Chatterjee, A. (2002). Neural substrates of action event knowledge. *Journal of Cognitive Neuroscience*, 14, 795–805.
- Kable, J. W., Kan, I. P., Wilson, A., Thompson-Schill, S. L., & Chatterjee, A. (2005). Conceptual representations of action in the lateral temporal cortex. *Journal of Cognitive Neuroscience*, 17, 1855–1870.
- Kako, E. (2006). The semantics of syntactic frames. *Language and Cognitive Processes*, 21, 562–575.
- Kambanaros, M., & van Steenbrugge, W. (2006). Noun and verb processing in Greek–English bilingual individuals with anomie aphasia and the effect of instrumentality and verb–noun name relation. *Brain and Language*, 97, 162–177.
- Kaschak, M. P., Madden, C. J., Theriault, D. J., Yaxley, R. H., Aveyard, M., Blanchard, A. A., et al. (2005). Perception of motion affects language processing. *Cognition*, 94, 879–889.
- Kemmerer, D. (2000). Grammatically relevant and grammatically irrelevant features of verb meaning can be independently impaired. *Aphasiology*, 14, 997–1020.
- Kemmerer, D. (2003). Why can you hit someone on the arm but not break someone on the arm? A neuropsychological investigation of the English body-part possessor ascension construction. *Journal of Neurolinguistics*, 16, 13–36.
- Kemmerer, D. (2006). Action verbs, argument structure constructions, and the mirror neuron system. In: M. Arbib (Ed.), *Action to language via the mirror neuron system* (pp. 347–373). Cambridge, UK: Cambridge University Press.
- Kemmerer, D. (in press). How words capture visual experience: The perspective from cognitive neuroscience. In B. Malt & P. Wolff (Eds.), *Words and the world: How words capture human experience*. Oxford, UK: Oxford University Press.
- Kemmerer, D., & Tranel, D. (2000). Verb retrieval in brain-damaged subjects: I. Analysis of stimulus, lexical, and conceptual factors. *Brain and Language*, 73, 347–392.
- Kemmerer, D., & Tranel, D. (2003). A double dissociation between the meanings of action verbs and locative prepositions. *Neurocase*, 9, 421–435.
- Kemmerer, D., & Tranel, D. (in press). Searching for the elusive neural substrates of body part terms: A neuropsychological study. *Cognitive Neuropsychology*.
- Kemmerer, D., & Wright, S. K. (2002). Selective impairment of knowledge underlying un-prefixation: Further evidence for the autonomy of grammatical semantics. *Journal of Neurolinguistics*, 15, 403–432.
- Keysers, C., & Gazzola, V. (2006). Towards a unifying neural theory of social cognition. *Progress in Brain Research*, 156, 383–406.
- Klatzky, R. L., Pellegrino, J. W., McClosky, B. P., & Doherty, S. (1989). Can you squeeze a tomato? The role of motor representations in semantic sensibility judgments. *Journal of Memory and Language*, 28, 56–77.
- Koechlin, E., & Jubault, T. (2006). Broca's area and the hierarchical organization of human behavior. *Neuron*, 50, 963–974.
- Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, 12, 48–55.
- Kuno, S., & Takami, K. (2004). *Functional constraints in grammar: On the unergative–unaccusative distinction*. Amsterdam: John Benjamins.
- Lakoff, G., & Johnson, M. (1999). *Philosophy in the flesh*. Chicago, IL: University of Chicago Press.
- Levin, B. (1993). *English verb classes and alternations: A preliminary investigation*. Chicago, IL: University of Chicago Press.
- Levin, B., & Rappaport Hovav, M. (1995). *Unaccusativity: At the syntax–semantics interface*. Cambridge, MA: MIT Press.
- Levin, B., & Rappaport Hovav, M. (2005). *Argument realization*. Cambridge, UK: Cambridge University Press.

- Levinson, S. C. (2007). 'Cut' and 'Break' verbs in Yeli Dnye, the Papuan language of Rossel Island. *Cognitive Linguistics*, 18, 207–218.
- Levinson, S. C., & Wilkins, D. (Eds.). (2006). *Grammars of space: Explorations in cognitive diversity*. Cambridge, UK: Cambridge University Press.
- Lewis, J. W. (2006). Cortical networks related to human use of tools. *The Neuroscientist*, 12, 211–231.
- Lewis, J. W., Phinney, R. E., Brefczynski, J. A., & DeYoe, E. A. (2006). Lefties get it "right" when hearing tool sounds. *Journal of Cognitive Neuroscience*, 18, 1314–1330.
- Lewis, J. W., Wightman, F., Brefczynski, J. A., Phinney, R. E., Binder, J. R., & DeYoe, E. A. (2004). Human brain regions involved in recognizing environmental sounds. *Cerebral Cortex*, 14, 1008–1021.
- Lindenbergh, R., Fangerau, H., & Seitz, R. J. (2007). "Broca's area" as a collective term. *Brain and Language*, 102, 22–29.
- Lu, L. H., Crosson, B., Nadeau, S. E., Heilman, K. M., Gonzalez-Rothi, L. J., Raymer, A., et al. (2002). Category-specific naming deficits for objects and actions: Semantic attribute and grammatical role hypotheses. *Neuropsychologia*, 40, 1608–1621.
- Mahon, B. Z., Milleville, S. C., Negri, G. A. L., Rumiati, R. I., Caramazza, A., & Martin, A. (2007). Action-related properties shape object representations in the ventral stream. *Neuron*, 55, 507–520.
- Majid, A., Bowerman, M., van Staden, M., & Boster, J. S. (2007). The semantics of "cutting and breaking" events: A crosslinguistic perspective. *Cognitive Linguistics*, 18, 133–152.
- Malikovic, A., Amunts, K., Schleicher, A., Mohlberg, H., Eickhoff, S. B., Wilms, M., et al. (2006). Cytoarchitectonic analysis of the human extrastriate cortex in the region of V5/MT+: A probabilistic, stereotaxic map of area hOc5. *Cerebral Cortex*, 17, 562–574.
- Malt, B. C., Gennari, S., Imai, M., Ameel, E., Tsuda, N., & Majid, A. (in press). Talking about walking: Biomechanics and the language of locomotion. *Psychological Science*.
- Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Sciences*, 8, 79–86.
- Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology*, 58, 25–45.
- Mayka, M. A., Corcos, D. M., Leurgans, S. E., & Vaillancourt, D. E. (2006). Three-dimensional locations and boundaries of motor and premotor cortices as defined by functional brain imaging: A meta-analysis. *NeuroImage*, 31, 1453–1474.
- McKoon, G., & MacFarland, T. (2000). Externally and internally caused change of state verbs. *Language*, 76, 833–858.
- Michelon, P., Vettel, J. M., & Zacks, J. M. (2006). Lateral somatotopic organization during imagined and prepared movements. *Journal of Neurophysiology*, 95, 811–822.
- Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action* (2nd ed.). Oxford, UK: Oxford University Press.
- Morris, J. S., Scott, S. K., & Dolan, R. J. (1999). Saying it with feeling: Neural responses to emotional vocalizations. *Neuropsychologia*, 37, 1155–1163.
- Moss, H. E., Abdallah, S., Fletcher, P. C., Bright, P., Pilgrim, L. K., Acres, K., et al. (2005). Selecting among competing alternatives: Selection and retrieval in the left inferior frontal gyrus. *Cerebral Cortex*, 15, 1723–1735.
- Nassi, J. J., & Callaway, E. M. (2006). Multiple circuits relaying primate parallel visual pathways to the middle temporal area. *Journal of Neuroscience*, 26, 12789–12798.
- Noppeney, U., Josephs, O., Kiebel, S., Friston, K. J., & Price, C. J. (2005). Action selectivity in parietal and temporal cortex. *Cognitive Brain Research*, 25, 641–649.
- Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: Re-examining the role of Broca's area in sentence comprehension. *Cognitive, Affective, and Behavioral Neuroscience*, 5, 263–281.
- Ochipa, C., Rothi, L. J., & Heilman, K. M. (1989). Ideational apraxia: A deficit in tool selection and use. *Annals of Neurology*, 25, 190–193.
- Olson, I. R., Gatenby, J. C., Leung, H.-C., Skudlarski, P., & Gore, J. C. (2003). Neuronal representation of occluded objects in the human brain. *Neuropsychologia*, 42, 95–104.
- Östman, J., & Fried, M. (Eds.). (2005). *Construction grammars: Cognitive grounding and theoretical extensions*. Amsterdam: John Benjamins.
- Payne, D. L., & Barshi, I. (Eds.). (1999). *External possession*. Amsterdam: John Benjamins.
- Pecher, D., & Zwaan, R. A. (Eds.). (2005). *Grounding cognition: The role of perception and action in memory, language, and thinking*. Cambridge, UK: Cambridge University Press.
- Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron*, 49, 815–822.
- Pelphrey, K. A., Mitchell, T. V., McKeown, M. J., Goldstein, J., Allison, T., & McCarthy, G. (2003). Brain activity evoked by the perception of human walking: Controlling for meaningful coherent motion. *Journal of Neuroscience*, 23, 6819–6825.
- Pelphrey, K. A., Morris, J. P., Michelich, C. R., Allison, T., & McCarthy, G. (2005). Functional anatomy of biological motion perception in posterior temporal cortex: An fMRI study of eye, mouth and hand movements. *Cerebral Cortex*, 15, 1866–1876.
- Peuskens, H., Vanrie, J., Verfaillie, K., & Orban, G. A. (2005). Specificity of regions processing biological motion. *European Journal of Neuroscience*, 21, 2864–2875.
- Phillips, M. L., Young, A. W., Scott, S. K., Calder, A. J., Andrew, C., Giampietro, V., et al. (1998). Neural responses to facial and vocal expressions of fear and disgust. *Proceedings of the Royal Society of London, B*, 265, 1809–1817.
- Pinker, S. (1989). *Learnability and cognition: The acquisition of argument structure*. Cambridge, MA: MIT Press.
- Pinker, S. (2007). *The stuff of thought: Language as a window onto human nature*. New York: Viking Press.
- Pirog, K. A., Aslin, R. N., & Tannenhaus, M. T. (submitted for publication). Gradient activation of human V5 by spoken words and phonological competitors that have newly acquired semantic properties.
- Pobric, G., & Hamilton, A. F. (2006). Action understanding requires the left inferior frontal cortex. *Current Biology*, 16, 524–529.
- Pourtois, G., Peelen, M. V., Spinelli, L., Seeck, M., & Vuilleumier, P. (2007). Direct intracranial recording of body-selective responses in human extrastriate visual cortex. *Neuropsychologia*, 45, 2621–2625.
- Prinz, J. J. (2002). *Furnishing the mind: Concepts and their perceptual basis*. Cambridge, MA: MIT Press.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6, 576–582.
- Pulvermüller, F., Härle, M., & Hummel, F. (2001). Walking or talking? Behavioral and neurophysiological correlates of action verb processing. *Brain and Language*, 78, 143–168.
- Pulvermüller, F., Hauk, O., Nikulin, V., & Ilmoniemi, R. (2005a). Functional links between motor and language systems. *European Journal of Neuroscience*, 21, 793–797.
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005b). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, 17, 884–892.
- Rappaport Hovav, M., & Levin, B. (1998). Building verb meanings. In: M. Butt & W. Geuder (Eds.), *The projection of arguments: Lexical and syntactic constraints* (pp. 97–134). Stanford, CA: CSLI Publications.
- Rüschemeyer, S.-A., Brass, M., & Friederici, A. D. (2007). Comprehending prehending: Neural correlates of processing verbs with motor stems. *Journal of Cognitive Neuroscience*, 19, 855–865.
- Rüschemeyer, S.-A., Glenberg, A. M., Kaschak, M. P., & Friederici, A. D. (submitted for publication). Listening to sentences describing motion activates MT/V5.
- Sabb, F. W., Bilder, R. M., Chou, M., & Bookheimer, S. Y. (2007). Working memory effects on semantic processing: Priming differences in pars orbitalis. *NeuroImage*, 37, 311–322.
- Saccuman, M. C., Cappa, S. F., Bates, E. A., Arevalo, A., Rosa, P. D., Danna, M., et al. (2006). The impact of semantic reference on word class: An fMRI study of action and object naming. *NeuroImage*, 32, 1865–1878.

- Sahin, N. T., Pinker, S., & Halgren, E. (2006). Abstract grammatical processing of nouns and verbs in Broca's area: Evidence from fMRI. *Cortex*, *42*, 540–562.
- Saxe, R., Jamal, N., & Powell, L. (2006). My body or yours? The effect of visual perspective on cortical body representations. *Cerebral Cortex*, *16*, 178–182.
- Saygin, A. P. (2007). Superior temporal and premotor brain areas necessary for biological motion perception. *Brain*, *130*, 2452–2461.
- Schirmer, A., & Kotz, S. A. (2006). Beyond the right hemisphere: Brain mechanisms mediating vocal emotional processing. *Trends in Cognitive Sciences*, *10*, 24–30.
- Schlesinger, I. (1995). *Cognitive space and linguistic case*. Cambridge: Cambridge University Press.
- Schubotz, R. I., & Fiebach, C. J. (Eds.). (2006). Integrative models of Broca's area and the ventral premotor cortex. *Cortex*, *42* (4), 461–463. (Special issue).
- Scorolli, C., & Borghi, A. M. (2007). Sentence comprehension and action: Effector specific modulation of the motor system. *Brain Research*, *1130*, 119–124.
- Senior, C., Barnes, J., Giampietro, V., Simmons, A., Bullmore, E. T., Brammer, M., et al. (2000). The functional neuroanatomy of implicit-motion perception or “representational momentum”. *Current Biology*, *10*, 16–22.
- Senior, C., Ward, J., & David, A. S. (2002). Representational momentum and the brain: An investigation into the functional necessity of V5/MT. *Visual Cognition*, *9*, 81–92.
- Shapiro, K., & Caramazza, A. (2003). Grammatical processing of nouns and verbs in left frontal cortex? *Neuropsychologia*, *41*, 1189–1198.
- Shapiro, K., Hillis, A. E., & Caramazza, A. (2007). The semantic representation of nouns and verbs. In: J. Hart & M. A. Kraut (Eds.), *The neural basis of semantic memory* (pp. 205–218). Cambridge, UK: Cambridge University Press.
- Shapiro, K., Moo, L. R., & Caramazza, A. (2006). Cortical signatures of noun and verb production. *Proceedings of the National Academy of Sciences*, *103*, 1644–1649.
- Shapiro, K., Shelton, J., & Caramazza, A. (2000). Grammatical class in lexical production and morphological processing: Evidence from a case of fluent aphasia. *Cognitive Neuropsychology*, *17*, 665–682.
- Shmuelof, L., & Zohary, E. (2005). Dissociation between ventral and dorsal fMRI activation during object and action recognition. *Neuron*, *47*, 457–470.
- Shmuelof, L., & Zohary, E. (2006). A mirror representation of others' actions in the human anterior parietal cortex. *Journal of Neuroscience*, *26*, 9736–9742.
- Silveri, M. C., & Ciccarelli, N. (2007). The deficit for the word-class “verb” in corticobasal degeneration: Linguistic expression of the movement disorder? *Neuropsychologia*, *45*, 2570–2579.
- Simmons, W. K., Ramjee, V., Beauchamp, M. S., McRae, K., Martin, A., & Barsalou, L. W. (2007). A common neural substrate for perceiving and knowing about color. *Neuropsychologia*, *45*, 2802–2810.
- Slobin, D. I. (2000). Verbalized events: A dynamic approach to linguistic relativity and determinism. In: S. Niemeier & R. Dirven (Eds.), *Evidence for linguistic relativity* (pp. 107–138). Amsterdam: John Benjamins.
- Slobin, D. I. (2004). The many ways to search for a frog: Linguistic typology and the expression of motion events. In: S. Strömquist & L. Verhoeven (Eds.), *Relating events in narrative: Typological and contextual perspectives* (pp. 219–258). Mahwah, NJ: Erlbaum.
- Smith, A. T., Greenlee, M. W., Singh, K. D., Kraemer, F. M., & Hening, J. (1998). The processing of first- and second-order motion in human visual cortex assessed by functional magnetic resonance imaging (fMRI). *Journal of Neuroscience*, *18*, 3816–3830.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, *17*, 273–281.
- 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 re-evaluation. *Proceedings of the National Academy of Sciences*, *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.
- Tomasino, B., Werner, C. J., Weiss, P. H., & Fink, G. R. (2007). Stimulus properties matter more than perspective: An fMRI study of mental imagery and silent reading of action phrases. *NeuroImage*, *36*, T128–T141.
- Tootell, R. B. H., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., et al. (1995). Functional analysis of human MT and related visual cortical areas using functional magnetic resonance imaging. *Journal of Neuroscience*, *15*, 3215–3230.
- Tranel, D., Adolphs, R., Damasio, H., & Damasio, A. R. (2001). A neural basis for the retrieval of words for actions. *Cognitive Neuropsychology*, *18*, 655–670.
- Tranel, D., Kemmerer, D., Adolphs, R., Damasio, H., & Damasio, A. (2003). Neural correlates of conceptual knowledge for actions. *Cognitive Neuropsychology*, *20*, 409–432.
- Tranel, D., Manzel, K., Asp, E., & Kemmerer, D. (in press). Naming static and dynamic actions: Neuropsychological evidence. *Journal of Physiology—Paris*.
- Tranel, D., Martin, C., Damasio, H., Grabowski, T. J., & Hichwa, R. (2005). Effects of noun–verb homonymy on the neural correlates of naming concrete entities and actions. *Brain and Language*, *92*, 288–299.
- Tsapkini, K., Jarema, G., & Kehayia, E. (2002). A morphological processing deficit in verbs but not in nouns: A case study in a highly inflected language. *Journal of Neurolinguistics*, *15*, 265–288.
- Tunik, E., Frey, S. H., & Grafton, S. T. (2005). Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. *Nature Neuroscience*, *8*, 505–511.
- Tunik, E., Rice, N. J., Hamilton, A., & Grafton, S. T. (2007). Beyond grasping: Representation of action in human anterior intraparietal sulcus. *NeuroImage*, *36*, T77–T86.
- Urgesi, C., Candidi, M., Ionta, S., & Aglioti, M. (2007). Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. *Nature Neuroscience*, *10*, 30–31.
- Vandenbulcke, M., Peeters, R., Fannes, K., & Vandenberghe, R. (2006). Knowledge of visual attributes in the right hemisphere. *Nature Neuroscience*, *9*, 964–970.
- Van Schie, H. T., Koolewijn, T., Jensen, O., Oostenveld, R., Maris, R., & Bekkering, H. (2007). Evidence for fast, low-level motor resonance to action observation: An MEG study. *Social Neuroscience*. doi:10.1080/17470910701414364.
- Van Valin, R. D. Jr., (2005). *Exploring the syntax–semantics interface*. Cambridge, UK: Cambridge University Press.
- Van Valin, R. D. Jr. (2006). Some universals of verb semantics. In: R. Mairal & J. Gil (Eds.), *Linguistic universals* (pp. 155–178). Cambridge: Cambridge University Press.
- Velazquez-Castillo, M. (1996). *The grammar of possession: Inalienability, incorporation and possessor ascension in Guarani*. Amsterdam: John Benjamins.
- Vigliocco, G., Warren, J., Siri, S., Arciuli, J., Scott, S., & Wise, R. (2006). The role of semantics and grammatical class in the neural representation of words. *Cerebral Cortex*, *16*, 1790–1796.
- Wagner, A. D., Pare-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. *Neuron*, *31*, 329–338.
- Wallentin, M., Lund, T. E., Ostergaard, S., Ostergaard, L., & Roepstorff, A. (2005). Motion verb sentences activate left posterior middle temporal cortex despite static context. *NeuroReport*, *16*, 649–652.
- Watson, J. D. G., Myers, R., Frackowiak, R. S. J., Hajnal, J. V., Woods, R. P., Mazziotta, J. C., et al. (1993). Area V5 of the human brain: Evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cerebral Cortex*, *3*, 79–94.
- Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin*, *131*, 460–473.

- Wolk, D. A., Coslett, H. B., & Glosser, G. (2005). The role of sensory-motor information in object recognition: Evidence from category-specific visual agnosia. *Brain and Language, 94*, 131–146.
- Wright, S. K. (2001). *Internally and externally caused change of state verbs*. PhD dissertation, Department of Linguistics, Northwestern University.
- Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. J. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience, 11*, 641–649.
- Zwaan, R. A., Madden, C. J., Yaxley, R. H., & Aveyard, M. E. (2004). Moving words: Dynamic representations in language comprehension. *Cognitive Science, 28*, 611–619.
- Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: Motor resonance in language comprehension. *Journal of Experimental Psychology: General, 135*, 1–11.