The Semantics of Syntax: The Grounding of Transitive and Intransitive Constructions

Wessel O. van Dam and Rutvik H. Desai

Abstract

■ Embodied theories of language maintain that brain areas associated with perception and action are also involved in the processing and representation of word meaning. A number of studies have shown that sentences with action verbs elicit activation within sensory–motor brain regions, arguing that sentence-induced mental simulations provide a means for grounding their lexical-semantic meaning. Constructionist theories argue, however, that form–meaning correspondence is present not only at the lexical level but also at the level of constructions. We investigated whether sentence-induced motor resonance is present for syntactic constructions. We measured the BOLD signal while participants read sentences with

(di)transitive (caused motion) or intransitive constructions that contained either action or abstract verbs. The results showed a distinct neuronal signature for caused motion and intransitive syntactic frames. Caused motion frames activated regions associated with reaching and grasping actions, including the left anterior intraparietal sulcus and the parietal reach region. Intransitive frames activated lateral temporal regions commonly associated with abstract word processing. The left pars orbitalis showed an interaction between the syntactic frame and verb class. These findings show that sensory–motor activation elicited by sentences entails both motor resonance evoked by single words as well as at the level of syntactic constructions. ■

INTRODUCTION

Traditionally, perceptual and motor brain systems were seen as categorically distinct from our representational systems subserving cognition. In this symbolic view, conceptual representations were taken to be of a symbolic and amodal nature and lexical-semantic meaning independent of sensory–motor systems of the brain (Kintsch, 2008; Pylyshyn, 1984; Fodor, 1983; Katz & Fodor, 1963). Opponents of such a symbolic account have raised the problem of how symbols can be mapped to their referents in the real world (Harnad, 1990) and its failure to provide an adequate description of the transduction process that maps perceptual states to amodal conceptual symbols (Barsalou, 1999). In contrast to such a symbolic account, embodied theories argue that experiential traces stored in sensory–motor brain areas can provide the means for grounding lexical-semantic meaning (Barsalou, 2008; Pulvermüller, 1999; Glenberg, 1997). In the past decade, a plethora of studies using various experimental techniques have directly contrasted predictions from symbolic and embodied accounts. Findings from behavioral experiments suggest that processes that play a role in perception and action are also involved in comprehending language about action (see Fisher & Zwaan, 2008; Zwaan & Kaschak, 2008, for reviews). In a similar vein, fMRI studies have shown that comprehension of action verbs, action sentences, and words denoting manipulable objects frequently activate sensory– motor brain areas (see Kiefer & Pulvermüller, 2012; Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012; Binder & Desai, 2011, for reviews).

This work has focused almost exclusively on meanings of nouns and verbs, either isolated or embedded in sentences. Several studies that use sentences compared action-related sentences with abstract sentences that have an identical or similar sentence structure (e.g., Desai, Conant, Binder, Park, & Seidenberg, 2013; Desai, Binder, Conant, Mano, & Seidenberg, 2011; Desai, Binder, Conant, & Seidenberg, 2009; Raposo, Moss, Stamatakis, & Tyler, 2009; Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Tettamanti et al., 2005). For example, Tettamanti et al. (2005) showed that listening to sentences that describe actions (e.g., "I bite an apple") as compared with similar transitive sentences with abstract content (e.g., "I appreciate sincerity") activated parts of the motor system. These findings have been taken to show that, to convey the meaning of a sentence as a whole, we rely on experiential traces of the referent action stored in sensory– motor brain areas. Furthermore, recent studies have suggested that conceptual features contribute to word and sentence level meaning in a flexible and contextdependent manner (Kemmerer, 2015; Van Dam, Van Dijk, Bekkering, & Rueschemeyer, 2012; Hoenig, Sim, Bochev, Herrnberger, & Kiefer, 2008). However, in most (if not all) of the studies in the conceptual representation literature, the effects of sentence structure are subtracted out by

University of South Carolina design.

Traditionally, it is assumed that argument structures convey their meaning by means of the main verb. For example, in "Pat gave Chris a cake," the meaning of transfer apparent in the overall expression is specified by the three-argument verb "give." That is, the three-argument verb "give" is expected to appear with phrases corresponding to the three characters required in the act of giving: a giver, a recipient, and something that is given. Therefore, it can be argued that the interpretation of this sentence pattern as a whole can be determined on the basis of its main verb. However, in many instances, the main verb does not reliably determine the interpretation of a sentence. For example, "Liza bought a book for Zach" can mean that Liza bought a book for a third person because Zach did not have time to buy it himself. However, "Liza bought Zack a book" can only mean that Liza intended to give the book to Zach (Goldberg, 2003). That is, although both sentences involve the same verb "to buy," the interpretation of these sentences is not reliably determined by its independent specification. The verb-centric view deals with such cases by proposing that verbs have multiple distinct senses because of the different linking patterns between syntax and semantics (Levin, 1995; Pinker, 1989). The main criticism of this view is that it leads to a proliferation of polysemous lexical entries (Goldberg, 1995).

An alternative is provided by a family of theories known as "contructionist" approaches (e.g., Bergen & Chang, 2003; Goldberg, 1995, 2003; Croft, 2001; Langacker, 1999; Fillmore, Kay, & O'Connor, 1988; Lakoff, 1987). Constructions are stored pairings of form and function, including words, idioms, or linguistic patterns that may be fully or partially filled. A central idea in these approaches is that constructions themselves have meaning. That is, form– meaning correspondences do not only exist at the level of verbs or single words but also at the level of constructions. Constructions are pairings of form and meaning, and therefore, a difference in syntactic form always spells a difference in meaning (Langacker, 1999; Wierzbicka, 1988; Haiman, 1985; Bolinger, 1968). This idea that argument structure constructions themselves carry meaning is often referred to as the "principle of no synonymy of grammatical forms" (Bolinger, 1968).

Given that embodiment theories reject the idea that language can convey meaning without it somehow being grounded in real-world sensory–motor experiences, this would suggest that semantics of constructions should be grounded in a similar fashion. In line with this idea, recent theorists have argued that sensory–motor activation elicited by sentences might be a complex phenomenon that entails both motor resonance evoked by single words and word combinations, but also more general motor resonance at the level of constructions (Kemmerer, 2006). Bergen and Chang (2003), in their Embodied Construction Grammar approach, argue that syntactic constructions can drive specific perceptual and motor simulations of a language user. For example, the directed motion construction may lead to the mental simulation of an event involving an animate mover moving along a path, even if the main verb in the construction does not explicitly specify motion (as in "The cat meowed down the street"). Experimental evidence for the principle of no synonymy of grammatical forms has been provided by, for example, work showing that comprehenders access different meanings for sentences using transitive versus ditransitive constructions (Kaschak & Glenberg, 2000). A ditransitive construction is a construction consisting of a verb, an agent argument, a recipient-like argument, and a theme argument (e.g., "He threw the ball to John"). It can be argued that, for example, the ditransitive (double-object) construction activates a transfer-of-possession schema (X causes Y to have Z), whereas a prepositional dative may activate a causedmotion schema (Goldberg, 1995).

These findings mesh with evidence from action observation, which suggests that the transitivity of an action is a crucial factor in determining the type of simulations. The finding that some mirror neurons of the macaque monkey were only responsive to object-directed actions suggests that activation of the parietal-frontal network depends on whether an action is goal directed (Tkach, Reimer, & Hatsopoulos, 2007; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996).

A number of fMRI studies also suggest a neural dissociation between these two types of actions. The inferior frontal gyrus (IFG), lateral precentral gyrus, inferior parietal lobule (IPL), posterior middle temporal gyrus (MTG), and the posterior part of the superior parietal lobule have been shown to play a role in the representation of transitive actions (Caspers, Zilles, Laird, & Eickhoff, 2010; Sakreida, Schubotz, Wolfensteller, & von Cramon, 2005; Buccino et al., 2001). Intransitive actions, on the other hand, seem to rely more on posterior regions in the parietal cortex, the angular gyrus (AG), and STS regions (Grosbras, Beaton, & Eickhoff, 2012; Lui et al., 2008). Recruitment of partially different brain regions might reflect the fact that transitive actions are object related and tend to be more complex (e.g., "throwing a ball"), whereas intransitive actions are not related to an object (e.g., "waving goodbye"). Additional evidence for a neural dissociation between transitive and intransitive actions comes from patient studies. For example, Watson, Fleet, Rothi, and Heilman (1986) observed an isolated disturbance of transitive but not intransitive movements in bilateral apraxia (see also Mozaz, Rothi, Anderson, Crucian, & Heilman, 2002; Foundas et al., 1999).

We hypothesized that mental simulations in service of language comprehension will be modulated by whether a construction (or syntactic frame) is of a transitive (caused motion) or intransitive nature. In the current study, we investigated whether distinct patterns of sensory–motor activation can be observed for different syntactic constructions, independent of the main verb. We also investigated if language-induced mental simulations differ as a function of the class of main verb used within the construction and whether the factors of construction and verb class interact with each other.

To this end, we measured changes in the hemodynamic response of participants while they read transitive and intransitive sentences that either contained a concrete or abstract main verb. We used a specific type of transitive sentences; transitives were defined here as a construction with the syntactic realization (NP V NP PP). Such a transitive construction is characterized by a transitive verb, an agent argument, a recipient-like argument, and a theme argument (Malchukov, Haspelmath, & Comrie, 2010). The schematic constructional meaning of this phrase is that of the causer argument directly causing the theme argument to move toward a recipient-like argument (X causes Y to move to Z), when used with a concrete verb. Note that the schematic constructional meaning is closely related to the transfer-of-possession schema (X causes Y to have Z), with the difference that the sentence "You threw the ball to her" does not actually entail that the recipient-like argument receives the ball (i.e., a change of possession), although that may typically be the case. Throughout the manuscript, we refer to our main constructions of interest as transitive (caused motion) and intransitive constructions. It needs to be noted that these terms are very broad in nature and actually embrace a whole family of constructions with more specific meanings. For example, a more specific label for the construction used in our transitive sentences would be the "caused motion construction." Therefore, to be more specific, we will adopt the term "caused motion construction" from here on.

We hypothesized a main effect of verb class, with sentences containing a concrete/action-related main verb eliciting stronger activation in the anterior IPL, primary motor cortex, premotor cortex, posterior MTG and inferior temporal gyrus (ITG), superior frontal gyrus (SFG), and IFG. On the other hand, for sentences containing an abstract main verb, we expect stronger activation within the anterior and middle STS (Desai et al., 2009, 2011, 2013). In addition, given that transitive sentences are strongly associated with a caused motion (X causes Y to move Z) schema (and take a direct object), we expect these sentences to elicit stronger activation in regions within the posterior middle/inferior temporal cortex that are involved in the processing of motion (Chen, Widick, & Chatterjee, 2008) and within the anterior IPL, a brain region that is involved in representing complex hand– object interactions and tool use. Stronger activation for intransitive sentences is hypothesized in the anterior and middle lateral temporal lobes, given that these regions are associated with more abstract semantics.

METHODS

Participants

Fourteen individuals participated in the study, all of whom were right-handed and between 19 and 22 years old $(M =$

20.64 years old, $SD = 0.93$ years old; six men). All participants had normal or corrected-to-normal vision and no history of neurological disorders. Before the experiment, participants were informed about the experimental procedures, signed informed consent forms, and were given practice trials according to a protocol sanctioned by the institutional review board of the University of South Carolina. Participants were paid for their participation. Every participant (except for one) underwent two scans on two different days within a 1-week period.

Stimuli

The four main experimental conditions contained 35 sentences each. They were (1) concrete caused motion (CCM; e.g., "You threw the ball to her"; "He gave the pizza to you"), (2) concrete intransitive (CI; e.g., "You waved at her whole family"; "He clapped after your big concert"), (3) abstract caused motion (ACM; e.g., "You delegated the task to her"; "He communicated the news to you"), and (4) abstract intransitive (AI; e.g., "You thought about her feelings"; "He cared about your new program"). The caused motion sentences used a ditransitive verb with a preposition. In addition, 30 filler sentences were also included (e.g., "You deduced the truth"; "He met the person"). The concrete conditions used an action-related verb, whereas the abstract conditions used verbs that did not have a strong association with actions. Verb concreteness ratings showed no difference between the CCM and CI conditions and the ACM and AI conditions (all $ps > .5$). Concreteness ratings for the main verb used in the concrete sentences $(M = 3.92)$ were significantly higher than for the main verb used in the abstract sentences ($M = 2.48$; $p < .001$). There were also pseudoword conditions in the experiment, but we do not discuss them here and focus on the interpretable conditions.

The sentences of all experimental conditions were matched on a number of psycholinguistic variables (see Table 1). Two-sample t tests ensured that all sentences were matched on number of words (all $ps > .10$), total number of phonemes (all $ps > .20$), total number of syllables (all $ps > .07$), total number of letters (all $ps > .10$), and the number of persons mentioned in a sentence (exact match). In addition, 11 participants performed a behavioral version of our experiment in which we collected RT data for the different sentences in a meaningfulness judgment task. Paired-sample t tests showed that our stimuli were not perfectly matched on RTs. Participants were faster to respond to ACM $(M = 1356$ msec) than to AI ($M = 1506$ msec) sentences ($p < .01$). Likewise, participants were faster to respond to CCM $(M = 1404 \text{ msec})$ than to CI ($M = 1532$ msec) sentences ($p = .001$). In addition, participants were faster to respond to ACM $(M =$ 1356 msec) than to CI ($M = 1532$ msec) sentences ($p < .001$). A regressor representing the mean-centered RT for each sentence from the behavioral experiment

was used as an additional item-wise regressor to account for variance due to time-on-task and difficulty.

In addition, we calculated the mean concreteness rating of the nouns of each of the four experimental conditions using the Brysbaert, Warriner, and Kuperman (2013) database. In the case in which the database did not have an entry for a compound word (e.g., "dining table"), we used the concreteness rating for the head noun (i.e., "table") of the compound word. Two-sample t tests revealed an overall difference in the mean noun concreteness ratings between the concrete sentences $(M = 4.61)$ and the abstract sentences $(M = 3.20; p <$.001). No difference was observed between transitive (caused motion) and intransitive frames, neither for constructions with a concrete verb or an abstract main verb (Table 1).

A number of studies show, using single-verb stimuli, that brain activations can be affected by other characteristics of verb classes, such as whether they allow causative alternation or number of obligatory arguments. The relevance of these results is not clear in the present case because we used sentences instead. Single verbs were used in these experiments as stimuli to examine the dominant or default response to the verb (e.g., those that require two arguments vs. three or those with and without causative alternation). When the argument structure is realized, the salience of these defaults (beyond general difficulty effects because of low familiarity of certain usage that is allowed but is uncommon) can be expected to reduce. We are not aware of any experiments that show similar differences between verb classes while using them in sentences. Nonetheless, we examined three such variables as a cautionary measure.

First, verbs with causative alternation (those that can be used both transitively and intransitively) and those without can potentially differ. A recent study by Meltzer-Asscher, Schuchard, den Ouden, and Thompson (2012) suggests that the pattern of neural activity elicited by a verb is different for verbs, which can alternate between transitive and intransitive frames and those that cannot. We used the VALEX database to obtain information on the relative frequency with which the main verb appears in a transitive versus intransitive construction (Korhonen, Krymolowski, & Briscoe, 2006; see Table 1). Two-sample t tests indicated that caused motion and intransitive sentences differed in the relative frequency with which its main verb was used in a caused motion versus intransitive construction ($p < .001$). That is, the main verbs in the caused motion condition occur relatively more often in caused motion constructions, whereas the main verbs in the intransitive condition occur relatively more often in intransitive constructions. Importantly, the concrete and abstract sentences did not differ in the relative frequency with which its main verb was used transitively versus intransitively ($p > .50$).

A second factor is whether verbs used in the transitive (caused motion) conditions obligatorily take two or three arguments. Some studies have indicated inferior parietal and posterior superior temporal regions to be involved in processing argument structure complexity, showing that verbs with more obligatory arguments show a stronger response than verbs with fewer obligatory arguments (Thompson, Bonakdarpour, & Fix, 2010; Thompson et al., 2007; Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003). We conducted an analysis on the number of arguments a verb obligatorily takes by using VerbNet (Kipper, Dang, & Palmer, 2000). This analysis indicated that there was no difference in the number of arguments a verb obligatorily takes between the CCM $(M =$ 2.11) and ACM ($M = 2.17$) conditions ($p = .50$).

Correspondingly, intransitive verbs have been subcategorized as unergatives and unaccusatives. Both verb types have the same number of arguments (i.e., a single argument) but differ syntactically. Unergatives and unaccusatives are often delineated in terms of whether the verb takes an internal versus external argument. Such a distinction is, however, associated with a syntactic movement analysis, which is only one of many approaches used in linguistic studies of unaccusativity (see Roehm, Sorace, & Bornkessel-Schlesewsky, 2012). Different approaches in this branch of linguistics tend to agree that, in an unaccusative construction, the participant is likely to be a patient or a nonvolitional causer of the event, whereas in the unergative construction, some property inherent in the argument of the verb is responsible for bringing about the event. Some studies with healthy participants and brain-damaged patients suggest that the neural structures that underlie the processing of these subtypes of intransitive verbs are dissociable (Agnew, van de Koot, McGettigan, & Scott, 2014; Shetreet & Friedmann, 2012; McAllister, Bachrach, Waters, Michaud, & Caplan, 2009; Luzzatti et al., 2002). Here, there was no difference in the number of unergative verbs between the CI $(n = 5)$ and AI $(n = 3)$ conditions $(p = .46)$. Several recent authors, however, have argued that the use of the terms "unergative" and "unaccusative" might be problematic, given that this distinction in intransitive verbs cannot account for the acceptability of the use of certain syntactic constructions (for an extensive discussion, see Kuno & Takami, 2004). In addition, it has been argued that the labels "unergative" and "unaccusative" are used to describe a wide variety of phenomena in different languages and therefore render them vague and imprecise (Dixon, 2010).

Procedure

The order of stimulus presentation was randomized individually for each participant. A single trial lasted 7.4 sec and constituted of the presentation of a single sentence. A variable jitter time of 0, 500, 1000, or 1500 msec was included at the beginning of each trial to enhance the temporal resolution of the acquired signal. After this, a fixation cross was presented in the center of the screen. A 400-msec blank screen followed the fixation cross; thereafter, the sentence appeared on screen for 3000 msec. The time between offset of the sentence and onset of the next trial was filled with a blank screen, to ensure that each trial lasted exactly 7.4 sec. Participants were instructed to read all sentences carefully to be able to answer a surprise yes/no question after some of the sentences (responses were made by performing a right-hand button click with their thumb). Thirty comprehension questions (e.g., "Did he clap after your big concert?") were used. This catch trial design was used to encourage participants to read all sentences for comprehension while avoiding motor execution after every trial.

fMRI Data Acquisition

Functional images were acquired on a Siemens TRIO 3.0-T MRI system (Siemens, Erlangen, Germany) equipped with a 12-channel head coil. BOLD-sensitive functional

images were acquired using a single-shot gradient EPI sequence (echo time/repetition time $= 34/1850$ msec, 34 axial slices in ascending order, slice gap $= 0.60$ mm, field of view = 208 mm, flip angle = 90° , voxel size = $3.25 \times$ 3.25×3.60 mm³). High-resolution anatomical images were acquired using a magnetization prepared rapid gradientecho sequence (echo time $= 4.15$ msec, voxel size $=$ $1 \times 1 \times 1$ mm³, 192 sagittal slices, field of view = 256 mm).

fMRI Data Analysis

Functional data were preprocessed and analyzed with the AFNI software package (Cox, 1996). A standardized preprocessing pipeline involved registration of functional images to the anatomy (Saad et al., 2009). Subsequently, functional images were co-registered (Cox & Jesmanowicz, 1999) and projected into standard stereotaxic space (Talairach & Tournoux, 1988). The normalized images were smoothed with an isotropic 5-mm FWHM Gaussian kernel, and the run mean of each voxel was scaled to 100. The ensuing preprocessed fMRI time series were analyzed on a participant-by-participant basis using an eventrelated approach in the context of voxelwise multiple linear regression with regressors for each condition (ACM, AI, CCM, CI,) as well as the filler items and question trials convolved with a canonical hemodynamic response function. Six motion parameters and the signal extracted from the ventricles were included as noise covariates of no interest. General linear tests were conducted to obtain the main effect of Transitivity and Concreteness and the Transitivity \times Condition interactions.

In a random effects analysis, group maps were created by comparing activations against a constant value of 0. The group maps were thresholded at voxelwise $p < .01$ and corrected for multiple comparisons by removing clusters smaller than 800 μl to achieve a map-wise corrected two-tailed $p < .05$.¹ Using the 3dClustSim program with 10,000 iterations, the cluster threshold was determined through Monte Carlo simulations that estimate the chance probability of spatially contiguous voxels exceeding the voxelwise p threshold. The analysis was restricted to a mask that excluded areas outside the brain as well as deep white matter areas and the ventricles. This mask is based on the probabilistic Desikan–Killiany atlas that contains 35 cortical areas in each hemisphere (Desikan et al., 2006) and the subcortical parcellation provided by FreeSurfer. In addition to this whole-brain analysis, two other (bilateral) ROIs were defined for a more sensitive analysis. One used the primary motor and sensory cortex (M1 and S1) as defined by the HMAT atlas (Mayka, Corcos, Leurgans, & Vaillancourt, 2006). Given its association with transitive actions and action sentence processing, we also defined a bilateral supramarginal gyrus (SMG) ROI. This ROI was defined on the basis of the maximum probability map provided with AFNI, which is based on the Destrieux atlas (Destrieux, Fischl, Dale, & Halgren, 2010). Small volume correction was applied in these ROIs to achieve a corrected $p < .05$, determined in the same manner as above.

RESULTS

Concrete–Abstract

Areas activated to a greater extent by the Concrete condition relative to the Abstract condition included the left MTG and ITG, superior frontal sulcus, inferior frontal sulcus (IFS), and IFG (pars triangularis). The ROI analyses revealed an additional cluster in the left SMG. The Abstract condition relative to the Concrete condition led to stronger activation in the left superior temporal gyrus (STG), STS, fusiform gyrus, right precuneus, MTG, and AG (Figure 1, Table 2).

Caused Motion (Transitive)–Intransitive

Caused Motion sentences elicited greater levels of activation than Intransitive sentences within the bilateral middle frontal gyrus (MFG), SMG, and left AG as well as precuneus. Structures more strongly activated by the Intransitive condition relative to the Caused Motion condition included bilateral STS and rectal gyrus, left occipital pole, SFG, and precentral gyrus as well as the right MTG and precuneus (Figure 2, Table 2).

Overlap

Some similarities as well as differences were found between the Concrete > Abstract and the Caused Motion > Intransitive contrasts (Figure 3). Both contrasts activated the left IFG and IFS (pars triangularis), with the former extending ventrally and the latter extending dorsally into MFG. A similar dorsal–ventral pattern was found in the left IPL. Both contrasts activated the SMG, with the Concrete > Abstract contrast extending ventrally into the parietal operculum, whereas the Caused Motion > Intransitive contrast extending dorsally into the anterior intraparietal sulcus (IPS).

The Abstract > Concrete and Intransitive > Caused Motion comparisons also showed some similarities (Figure 4),

Figure 1. Areas activated by the Concrete–Abstract contrast. Red-orange colors show greater activation for the Concrete condition; blue-cyan colors show greater activation for the Abstract condition. Mean percent signal change relative to rest is shown for the CCM, CI, ACM, and AI conditions, in a sphere of 5-mm radius around the peak voxel. L = left hemisphere; $R =$ right hemisphere.

Table 2. Activations in the Main Contrasts of Interest

Volume Max $x \quad y \quad z$			<i>Structure</i>
Concrete > Abstract			
3078			$3.61 -52 -58$ 0 LMTG
2268			$3.79 - 40$ 34 14 L IFG, IFS (pars triangularis)
918			3.15 -22 1 44 L sup frontal s
675			$2.95 -49 -34$ 32 L SMG

Abstract > Concrete

Caused Motion > Intransitive

Intransitive > Caused Motion

The volume of the cluster (μl) , peak z score, Talairach coordinates, and the anatomical structures that the clusters overlap are shown. $L =$ left hemisphere; $R =$ right hemisphere; $g =$ gyrus; $s =$ sulcus; sup = superior.

where the left middle and anterior STS were activated by both contrasts.

CCM–ACM

The CCM condition relative to the ACM condition led to stronger activation in the left IFG (pars opercularis), MTG, SMG, and paracentral gyrus. Areas activated to a greater extent by the ACM condition relative to the CCM condition included the left fusiform gyrus, precuneus, posterior dorsal cingulum, right AG, and MTG (Figure 5A, Table 3).

CI–AI

Areas activated to a greater extent by the CI condition relative to the AI condition included the left middle occipital gyrus (MOG), MTG, and SMG. Stronger activation was observed for the AI condition relative to the CI condition in the left MTG, STS, right MFG, and SFG (Figure 5B, Table 3).

CCM–CI

Stronger activation was observed for the CCM condition relative to the CI condition in the bilateral MFG, left IPS, frontomarginal gyrus and sulcus, and right SMG. Areas activated to a greater extent by the CI condition relative to the CCM condition included the bilateral MTG, left MOG, right rectus, and posterior ventral cingulum (Figure 5C, Table 3).

ACM–AI

The ACM condition elicited stronger activation relative to the AI condition in the left MFG, AG, and right occipitotemporal lingual gyrus. The ROI analyses revealed an additional cluster in the left SMG. Areas activated to a greater extent by the AI condition relative to ACM condition included the left IFG (pars opercularis), STS, MTG, SFG, occipital pole, and right MOG (Figure 5D, Table 3).

CA × TI Interaction

The left IFG (mostly in pars orbitalis, approximately BA 47) showed an interaction between Concreteness (Concrete vs. Abstract) and Transitivity (Transitive [Caused Motion] vs. Intransitive; Figure 6, Table 3). This interaction arose from a small difference between CCM and CI conditions and a bigger difference between the abstract conditions $(AI > ACM)$.

DISCUSSION

The current experiment explored if distinct patterns of sensory–motor activation can be observed for different

Figure 2. Areas activated by the Caused Motion–Intransitive contrast. Red-orange colors show greater activation for the Transitive/Caused Motion condition; blue-cyan colors show greater activation for the Intransitive condition. Mean percent signal change relative to rest is shown for the CCM, CI, ACM, and AI conditions, in a sphere of 5-mm radius around the peak voxel. L = left hemisphere; $R = right$ hemisphere.

Figure 3. Areas activated by the Transitive/Caused Motion > Intransitive (red) and Concrete > Abstract (blue) contrasts. Yellow indicates the overlap between the two.

syntactic constructions and how these patterns relate to those induced by verbs.

Main Effect of Verb Concreteness

In the current study, constructions that contained a concrete verb elicited greater levels of activation in the anterior part of the left IPL (aIPL) and the left inferior MTG (ITG) and inferior temporal sulcus. The IPL has shown to be critical for the representation of action plans and goals and tool use (Lewis, 2006; Rumiati et al., 2004) and the performance of complex hand–object interactions (Ramayya, Glasser, & Rilling, 2010; Hamilton & Grafton, 2006). It has also been shown to be part of a tool use network encompassing the middle/inferior temporal and inferior frontal regions (Ramayya et al., 2010). Damage to the aIPL/IPL is associated with ideomotor apraxia, which results in impairments in skilled performance of motor acts, difficulty imitating gestures, impairments in Figure 4. Areas activated by the Intransitive > Transitive/Caused Motion (red) and Abstract > Concrete (blue) contrasts. Yellow indicates the overlap between the two.

performing appropriate actions in response to a visually presented object, and carrying out the appropriate action for a certain object (Jax, Buxbaum, & Moll, 2006; Haaland, Harrington, & Knight, 2000; Heilman & Rothi, 1993; Heilman, Rothi, & Valenstein, 1982). In addition, sentences with action verbs elicited greater activation within the left posterior temporal gyrus, in proximity to the human motion area (MT+; Rees, Friston, & Koch, 2000). This brain region is implicated in accessing conceptual information about motion attributes and is also associated with tool use (Gallivan & Culham, 2015; Brandi, Wohlschläger, Sorg, & Hermsdörfer, 2014; Ramayya et al., 2010; Saygin, McCullough, Alac, & Emmory, 2010; Kable, Kann, Wilson, Thompson-Schill, & Chatterjee, 2005). Several studies have obtained similar effects of concreteness within premotor and primary motor cortices (Raposo et al., 2009; Aziz-Zadeh et al., 2006; Tettamanti et al., 2005; Pulvermüller, Härle, & Hummel, 2000). In our study, concrete sentences showed a higher BOLD signal

than abstract sentences within the left precentral gyrus, at a reduced statistical threshold (corrected $p < .09$). Similarly, concrete transitive sentences showed a higher BOLD signal than abstract transitive sentences within the left precentral gyrus, at a slightly reduced statistical threshold (corrected $p < .07$). Activations were exclusively observed within the left premotor cortex. This result is in line with previous findings that, during lexical decisions on manual action verbs, right-handers preferentially activate the left premotor cortex, whereas lefthanders predominantly activate the right premotor cortex (Willems, Hagoort, & Casasanto, 2010). In addition, our activation clusters both fell within the premotor cortex, anterior to primary motor areas. Such an anterior shift of activation away from primary sensory and motor cortices has been observed across a number of studies investigating the neural correlates of action understanding (Chatterjee, 2010; Willems et al., 2010; Willems, Hagoort, Toni, Hagoort, & Casasanto, 2009; Wallentin,

Figure 5. Areas activated by the CCM–CI, CI-AI, and ACM–AI contrasts. Red-orange colors show greater activation for the CI, CCM and ACM conditions; blue-cyan colors show greater activation for the ACM, AI, CI, and AI conditions. $L = \text{left hemisphere}$; $R = \text{right hemisphere}$.

 $CI > CCM$

1782			-3.98 7 -49 8 R post ventral cingul
1323			-3.93 58 -4 -9 RMTG
999			-3.95 -55 -1 -9 LMTG
945			-3.42 -31 -82 -6 LMOG
918			-4.38 4 49 -6 R rectus g

837 3.67 −28 43 2 L frontomarginal g, s

Table 3. (continued)

The volume of the cluster (μl) , peak z score, Talairach coordinates, and the anatomical structures that the clusters overlap are shown. post = posterior; oc-temp = occipito-temporal; cingul = cingulate. $L = left$ hemisphere; $R =$ right hemisphere; $g =$ gyrus; $s =$ sulcus; ant $=$ anterior.

Ellegaard, Ostergaard, Ostergaard, & Roepstorff, 2005). Several authors have proposed that such anterior activations might reflect representations that are abstracted away from perceptually based representations and schematized over the course of learning, which are nevertheless shared between language and perception (see, e.g., Humphreys, Newling, Jennings, & Gennari, 2013).

Constructions that contained an abstract verb elicited greater levels of activation within lateral temporal regions, most notably the left middle and anterior STS and STG, as well as in the posterior cingulate. These results corroborate earlier findings showing that portions of the left STS and STG play a role in processing abstract concepts (Wilson-Mendenhall, Simmons, Martin, & Barsalou, 2013; Desai et al., 2009, 2011; Wang, Conder, Blitzer, & Shinkareva, 2010; Binder, Westbury, McKiernan, Possing, & Medler, 2005; Wise et al., 2000). In summary, the current results of verb concreteness effects are consistent with a number of previous studies, showing activation of higher level sensory–motor regions for action verb processing. These findings provide evidence for the embodied framework insofar as they confirm that the meaning of sentences that refer to action is represented in a cortical network including areas that play a role in perception and action.

Main Effect of Transitivity

Of central interest was the question of whether constructions themselves are associated with meaning, when controlling for verb meaning. In the Caused Motion– Intransitive contrast, the effects of verbs were eliminated, as both constructions contained similar action and abstract verbs. The results show that sentences with caused motion frames elicited greater levels of activation in the left aIPL, which overlapped with the activation found because of action verbs (Figure 3). As discussed above, this region is associated with action planning and control. Although the same general region of the left aIPL was activated by both action verbs and caused motion constructions, some differences were also observed. Verbs activated a more ventral aspect of SMG, extending into the parietal operculum. Parietal operculum is associated with secondary somatosensory cortex. Caused Motion constructions, on the other hand, activated a somewhat more dorsal section of the SMG, extending into the anterior IPS (aIPS). The aIPS is thought to be the human analog of monkey area AIP (Culham & Valyear, 2006). Both of these dorsal and ventral regions are commonly coactivated in grasping and tool use tasks, and it is somewhat difficult to distinguish their role in relation to control of actions. However, the dorsal region, and especially AIP/aIPS, is associated more strongly with hand–object interactions, visually guided grasping, and on-line dynamic control of movements (Reichenbach, Thielscher, Peer, Bülthoff, & Bresciani, 2014; Rice, Tunik, & Grafton, 2006; Tunik, Frey, & Grafton, 2005; Culham et al., 2003; see Tunik, Rice, Hamilton, & Grafton, 2007, for a review).

Figure 6. Areas showing an interaction between Concreteness (Concrete vs. Abstract) and Transitivity (Transitive/Caused Motion vs. Intransitive). Mean percent signal change relative to rest is shown for the CCM, CI, ACM, and AI conditions, in a sphere of 5-mm radius around the peak voxel.

The left dorsal AG was also activated for caused motion constructions relative to intransitive constructions. The entire AG has been shown to play a role in semantic processing (Bonner, Peelle, Cook, & Grossman, 2013; Binder & Desai, 2011; Binder, Desai, Graves, & Conant, 2009). Likewise, TMS and patient studies have substantiated the idea that the AG is involved in controlled semantic processing (Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011, 2012; Corbett, Jefferies, & Lambon Ralph, 2009; Jefferies & Lambon Ralph, 2006). More specifically, the dorsal AG has shown to play a role in action planning and execution, especially reach-to-grasp actions. In a bifocal TMS study, Koch et al. (2010) examined connectivity between dorsal AG and the primary motor cortex (M1) as well as between dorsal SMG and M1. They found that, during early (∼50 msec) preparation of reaching and grasping movements, AG–M1 connectivity was sensitive to both type of grasp (whole-hand grasp) and location of the object in space, whereas SMG–M1 connectivity was sensitive only to the type of grasp (precision grasp). Structurally, both dorsal SMG and dorsal AG were connected to M1 and to ventral premotor cortex, through different bundles within the superior longitudinal fasciculus.

In addition, caused motion constructions also activated the posterior medial aspect of the parietal lobe. This region, dorsal to the parieto-occipital sulcus and near the posterior edge of the hemisphere, is termed the "parietal reach region" (PRR) and is found in both monkeys and humans (Yttri, Wang, Liu, & Snyder, 2014; Chang, Papadimitriou, & Snyder, 2009; Filimon, Nelson, Huang, & Sereno, 2009; Connolly, Andersen, & Goodale, 2003). PRR plays a role in planning visually guided reaching movements, possibly by computing the initial response by taking into account the difference between the initial hand position and gaze location.

The left MFG and IFS were also activated by both caused motion constructions and action verbs. A dorsal– ventral pattern, similar to the one seen in the aIPL, was also seen in the frontal lobe, whereby the caused motion constructions activated more dorsal MFG regions, whereas activation because of action verbs extended more ventrally to the IFS. These frontal regions have a wide-ranging role in executive function (e.g., Duncan & Owen, 2000) and can be interpreted here as reflecting executive aspects of action processing.

In summary, the activation of areas responsible for action planning, reaching, and grasping, namely, aIPS/aIPL, dorsal AG, and PRR, suggests that caused motion constructions, regardless of the verb used, are associated with action semantics, and this conceptual content is grounded in regions used in action planning and control. This is consistent with the idea that caused motion constructions activate a caused motion schema, which is grounded through areas controlling reaching and grasping actions. We did not obtain an effect of transitivity within the premotor, primary motor, or supplementary motor cortex. A potential explanation is that motor resonance elicited by these constructions represents relatively abstract action plans and does not contain detailed or specific parameters related to selection and execution of the actions. In a study of patients with stroke, Desai, Herter, Riccardi, Rorden, and Fridriksson (2015) showed that comprehension accuracy of action-related words was selectively predicted by detailed parameters (e.g., initial direction error or number speed maxima) of reaching actions performed by the patients. This suggests that such details are part of simulations at least at a single-word level. Constructions, by their very nature, are general, contain slots that can be filled by a variety of words, and are unlikely to be grounded in specific action parameters. Rather, they are grounded in more general, higher-order action plans.

Sentences with an intransitive frame elicited activations that are similar to those seen for abstract relative to concrete language, both at the word and sentence levels. The left STS plays a role in processing abstract concepts (Wilson-Mendenhall et al., 2013; Wang et al., 2010; Desai et al., 2009; Sabsevitz, Medler, Seidenberg, & Binder, 2005; Noppeney & Price, 2004; Mellet, Tzourio, Denis, & Mazoyer, 1998). The OFC has shown to play a role in emotion and decision-making and has been argued to play a role in processing the affective significance of concepts (Rolls & Grabenhorst, 2008; Binder et al., 2005; Kringelbach, 2005; Bechera, Damasio, & Damasio, 2000). The IFG was activated by intransitives, mostly involving pars orbitalis. An examination of the CCM–CI and ACM–AI contrasts reveals that this activation was mostly driven by AIs. This was also the case for most of the activation in the left STS/STG. Given that these regions are commonly activated for abstract relative to concrete concepts, this suggests that AIs were the most abstract of the conditions. Abstract words occur in more diverse semantic contexts (Hoffman, Rogers, & Lambon Ralph, 2011), and their meaning is more dependent on distributional information and integration with context (Andrews, Vigliocco, & Vinson, 2009). The left IFG activation can be interpreted as contributing to deriving meaning through integration with context. The current results suggest that this applies to intransitive constructions as well, and their meaning is more abstract and constructed through integration.

Interaction between Verb and Construction Types

To investigate if the degree to which the main verb elicits perceptual and motor simulations is modulated by syntactic structure, we calculated an interaction between the class of the main verb (concrete vs. abstract) and transitivity (transitive/caused motion vs. intransitive). Our results show an interaction between these two factors in the left anterior IFG, involving the pars orbitalis (spreading slightly into pars triangularis). An examination

of the four conditions indicates that the syntactic frame modulates activation within the pars orbitalis of the IFG to a greater extent for sentences with an abstract as compared with a concrete main verb. Although both Abstract conditions activated this region relatively more than the Concrete conditions, the difference between AI and ACM was greater, giving rise to this interaction.

As the meaning of a concrete noun like "rose" is less dependent on context, a concrete verb ("throw") would strongly guide a specific perceptual/motor simulation that can be expected to show a weaker modulation by context. The syntactic frame is therefore expected to have a smaller influence on these verbs. In contrast, abstract verbs ("consider") rely more on the surrounding frame for their interpretation and should be modulated more. This is precisely what our results show: A stronger effect of syntactic frame for sentences with an abstract main verb as compared with a concrete main verb, within pars orbitalis (BA 47), which is thought to play a role in controlled semantic retrieval (Wagner, Koutstaal, Maril, Schacter, & Buckner, 2000; Gabrieli, Poldrack, & Desmond, 1998). In a large-scale meta-analysis (Binder et al., 2009), BA 47 was found to be sensitive to semantics, when overall difficulty is controlled (i.e., cases where conditions with greater executive demands are compared with relatively easier conditions are eliminated). Our results suggest that the syntactic frame can guide the ease with which certain semantic representations are selected, especially when selection of semantic information is not easily achieved on the basis of the main verb alone. As mentioned above, these findings are consistent with the proposal by Andrews and colleagues (2009) suggesting that concrete and abstract representations are learned from different types of statistical data. Concrete representations are based on a set of perceived physical properties of an object and the experiential information we acquired while interacting with them. Abstract representations, on the other hand, rely more strongly on information of how words are distributed across different linguistic environments. The results suggest that the left pars orbitalis is especially relevant to integrating verb and construction-level meaning.

The two-level theory of verb meaning suggests that such an interface would be provided by the template level of the verb. This theoretical framework argues for two separate levels of verb meaning. The composite meaning of a verb constitutes an association of the root and template level of a particular verb (for an overview, see Levin & Rappaport Hovav, 2005). The uniqueness of every verb is constituted by the root level of meaning, which is not visible to grammar and provides subtle distinctions between each verb in a given class. In contrast to the root level of verb meaning, the template level is visible to grammar and provides a schematic representation that is common to all verbs in a given class (Kemmerer, 2012; Kemmerer & Gonzalez-Castillo, 2010). Several neuropsychological studies have provided evidence that these two levels of verb meaning are segregated in the mind. For example, studies with brain-damaged participants have shown a double dissociation in the impairment in the discrimination of features of verb meaning that are relevant to grammar versus features that are irrelevant to grammar (Kemmerer, 2000, 2003; Kemmerer & Wright, 2002). There is some evidence for the association of the left IFG with the schematic motor component of template-level verb meanings. For example, Tettamanti and colleagues (2005) compared prototypical caused motion constructions with and without motor components, such as "I bite an apple" and "I appreciate sincerity" (in Italian), and found activation in the left pars opercularis for motor sentences. However, both verbs and nouns differed in these sentences, and it is not clear whether the differences were due only to verb concreteness. On the other hand, Desai et al. (2011) performed a similar comparison (using simple caused motion sentences such as "The thief bashed the table" and "The jury criticized the proposal") and did not find activation in the left IFG. In another study, Desai et al. (2009) compared prototypical transitive sentences ("I throw the ball") with abstract sentences ("I consider the risk") and again did not find activation in the left IFG. In addition, to control for the effect of noun manipulability, they compared action sentences with sentences with visual verbs ("I see the ball"), and no IFG activation was found in that comparison either. Thus, the evidence associating left IFG with simple or prototypical transitive constructions is mixed. A potentially relevant factor is that the posterior region of the left IFG (pars opercularis/BA 44) is also involved in overt or covert speech production and perception. If the action sentences have longer syllable or phoneme length than the control sentences, activation of posterior IFG can be expected. Both Desai et al. (2009) and Desai et al. (2011) ensured that action sentences were not longer (in terms of words, letters, phonemes, or syllables) than the control abstract or visual sentences. Tettamanti and colleagues (2005) do not report syllable or phoneme length of their sentences, and it is not clear if they were matched. Studies that compare pronounceable stimuli (e.g., words or sentences) with nonpronounceable materials (e.g., false fonts or hash marks) and report activation of posterior IFG can therefore be questioned on these grounds. In our study, we did not observe activation of the pars opercularis. It is possible that this region was activated equally by all verbs because it is always involved in processing the argument structure and is not seen in any contrasts. An alternative possibility is that template-level meaning is not necessarily attached to specific verbs, but templates or constructions themselves have semantics over and above those of the verb that is filled in. Several psycholinguistic studies have provided evidence that syntactic constructions carry meanings (Kako, 2006; Kaschak & Glenberg, 2000; Fisher, 1994, 1996). Furthermore, a recent study by Allen, Pereira, Botvinick, and Goldberg (2012) showed different neural activations for the dative (e.g., "Sally gave the book to

Joe") and the ditransitive construction (e.g., "Sally gave Joe a book"), which share the same content words. These results provide evidence that different grammatical constructions are associated with distinct patterns of neural activation.

Finally, we note that several areas in various comparisons, such as the left STS and MFG, showed negative activations, relative to the baseline of gaps between the stimuli, for all conditions. Here, only the differences between conditions are relevant, and not the sign, for two reasons. First, the sentences were separated only by 7.4 sec, which is not long enough for the hemodynamic response to return to baseline or even to become weak. A "resting" state never occurs during the experiment; there is only modulation due to reading various sentences. Thus, activations are not against rest but against a baseline where general processes involved in processing sentences are still active. Second, resting is not an "off" or "neutral" state with respect to semantic processing but is instead a very active period of rich semantic processing. It has been suggested that engagement in effortful tasks reliably suppresses such task-unrelated semantic processing (Binder et al., 2009). Applying this logic leads to the prediction that, if the AG plays a role in semantic processing than it's expected to be deactivated during nonsemantic tasks, no deactivation is expected during semantic tasks. The finding that deactivation of the left IPL (particularly the AG), which is part of the Default Mode Network, is modulated by the semantic nature of the task, shows that resting state and semantic networks greatly overlap (Seghier & Price, 2012; Seghier, Fagan, & Price, 2010; but see Humphreys, Hoffman, Visser, Binney, & Lambon Ralph, 2015).

Conclusion

Our results show that the transitive/caused motion and intransitive constructions are associated with distinct patterns of neural activation. The caused motion constructions, across both action and abstract verbs, elicited activation in areas associated with reaching and grasping. The intransitive constructions were processed similarly to abstract sentences, activating lateral temporal areas. These results provide evidence that the transitive construction, by virtue of being associated with a caused motion schema, elicits activations within sensory–motor brain regions. That is, the syntactic construction itself may drive the mental simulation of an event involving the movement of an object (along a designated path). Pars orbitalis has an important role in construction and verb-level meaning, showing an interaction between verb and construction type. These findings provide evidence for constructionist approaches that claim that form–meaning correspondences do not exclusively exist at the level of verbs or lexical items but also at the level of constructions.

Acknowledgment

We thank David Kemmerer and an anonymous reviewer for their helpful suggestions. All mistakes are ours. This research was supported by NIH/NIDCD grant R01 DC010783 (R. H. D.).

Reprint requests should be sent to Rutvik H. Desai, 220 Discovery Building, 915 Greene St., University of South Carolina, Columbia, SC 29208, or via e-mail: rutvik@sc.edu.

Note

1. On the basis of the data from an experiment that involved physical application of painful heat at different levels of intensity, Woo, Krishnan, and Wagner (2014) suggested using a voxelwise threshold of $p < .001$ or lower. The recommendation of such a stringent threshold is appropriate given that sensory tasks typically lead to activations that are large in extent. On the other hand, studies of higher cognitive functions often involve a comparison of conditions that are closely matched in their sensory properties and differ in more subtle ways. In our experience, such contrasts show activations that are lower in magnitude and are much more variable between participants. To balance false positives and false negatives in group maps, thresholds in the range of $p < .025$ to $p < .005$ are more appropriate in these cases. This is why a large number of cognitive experiments use voxelwise thresholds in the neighborhood of $p < .01$, and similar values are used as defaults in some packages. Although Woo et al.'s (2014) recommendation remains valuable in many cases, our choice of threshold is based on these considerations.

REFERENCES

- Agnew, Z. K., van de Koot, H., McGettigan, C., & Scott, S. K. (2014). Do sentences with unaccusative verbs involve syntactic movement? Evidence from neuroimaging. Language, Cognition, and Neuroscience, 29, 1035–1045.
- Allen, K., Pereira, F., Botvinick, M., & Goldberg, A. E. (2012). Distinguishing grammatical constructions with fMRI pattern analysis. Brain and Language, 123, 174–182.
- Andrews, M., Vigliocco, G., & Vinson, D. (2009). Integrating experiential and distributional data to learn semantic representations. Psychological Review, 116, 463–498.
- 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.
- Barsalou, L. W. (1999). Perceptual symbol systems. Behavioral and Brain Sciences, 22, 577–660.
- Barsalou, L. W. (2008). Grounded cognition. Annual Review of Psychology, 59, 617–645.
- Bechera, A., Damasio, H., & Damasio, A. R. (2000). Emotion, decision making and the orbitofrontal cortex. Cerebral Cortex, 10, 295–307.
- Ben-Shachar, M., Hendler, T., Kahn, I., Ben-Bashat, D., & Grodzinsky, Y. (2003). The neural reality of syntactic transformations: Evidence from functional magnetic resonance imaging. Psychological Science, 14, 433–440.
- Bergen, B. K., & Chang, N. C. (2003). Embodied construction grammar in simulation-based language understanding. In J. O. Ostman & M. Fried (Eds.), Construction grammar(s): Cognitive and cross-language dimensions. Amsterdam: John Benjamin Publishing Company.

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. Trends in Cognitive Sciences, 15, 527–536.

- Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and metaanalysis of 120 functional neuroimaging studies. Cerebral Cortex, 19, 2767–2796.
- Binder, J. R., Westbury, C. F., McKiernan, K. A., Possing, E. T., & Medler, D. A. (2005). Distinct brain systems for processing concrete and abstract words. Journal of Cognitive Neuroscience, 17, 905–917.
- Bolinger, D. (1968). Entailment and the meaning of structures. Glossa, 2, 199–127.
- Bonner, M. F., Peelle, J. E., Cook, P. A., & Grossman, M. (2013). Heteromodal conceptual processing in the angular gyrus. Neuroimage, 71, 175–186.
- Brandi, M.-L., Wohlschläger, A., Sorg, C., & Hermsdörfer, J. (2014). The neural correlates of planning and executing actual tool use. Journal of Neuroscience, 34, 13183–13194.
- Brysbaert, M., Warriner, A. B., & Kuperman, V. (2013). Concreteness ratings for 40 thousand generally known English word lemmas. Behavior Research Methods, 46, 904–911.
- 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.
- Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. Neuroimage, 50, 1148–1167.
- Chang, S. W. C., Papadimitriou, C., & Snyder, L. H. (2009). Using a compound gain field to compute a reach plan. Neuron, 64, 744–755.
- Chatterjee, A. (2010). Disembodying cognition. Language and Cognition, 2, 79–116.
- Chen, E., Widick, P., & Chatterjee, A. (2008). Functionalanatomical organization of predicate metaphor processing. Brain and Language, 119, 149–157.
- Connolly, J. D., Andersen, R. A., & Goodale, M. A. (2003). fMRI evidence for a "parietal reach region" in the human brain. Experimental Brain Research, 153, 140–145.
- Corbett, F., Jefferies, E., & Lambon Ralph, M. A. (2009). Different impairments of semantic cognition in semantic dementia and semantic aphasia: Evidence from the non-verbal domain. Brain, 132, 2593–2608.
- Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. Computers and Biomedical Research, 29, 162–173.
- Cox, R. W., & Jesmanowicz, A. (1999). Real-time 3D image registration of functional MRI. Magnetic Resonance in Medicine, 42, 1014–1018.
- Croft, W. A. (2001). Radical construction grammar: Syntactic theory in typological perspective. Oxford: Oxford University Press.
- Culham, J. C., Danckert, S. L., DeSouza, J. F. X., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. Experimental Brain Research, 153, 180–189.
- Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. Current Opinion in Neurobiology, 16, 205–212.
- Desai, R. H., Binder, J. R., Conant, L. L., Mano, Q. R., & Seidenberg, M. S. (2011). The neural career of sensory–motor metaphors. Journal of Cognitive Neuroscience, 23, 2376–2386.
- Desai, R. H., Binder, J. R., Conant, L. L., & Seidenberg, M. S. (2009). Activation of sensory–motor areas in sentence comprehension. Cerebral Cortex, 20, 468–478.
- Desai, R. H., Conant, L. L., Binder, J. R., Park, H., & Seidenberg, M. S. (2013). A piece of the action: Modulation of sensory– motor regions by action idioms and metaphors. Neuroimage, 83, 862–869.
- Desai, R. H., Herter, T., Riccardi, N., Rorden, C., & Fridriksson, J. (2015). Concepts within reach: Action performance predicts action language processing in stroke. Neuropsychologia, 71, 217–224.
- Desikan, R. S., Ségonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., et al. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. Neuroimage, 31, 968–980.
- Destrieux, C., Fischl, B., Dale, A., & Halgren, E. (2010). Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. Neuroimage, 53, 1–15.
- Dixon, R. M. W. (2010). Basic linguistic theory. In Grammatical topics (Vol. 2). Oxford: Oxford University Press.
- Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. Trends in Neurosciences, 23, 475–483.
- Filimon, F., Nelson, J. D., Huang, R. S., & Sereno, M. I. (2009). Multiple parietal reach regions in humans: Cortical representations for visual and proprioceptive feedback during online reaching. Journal of Neuroscience, 29, 2961–2971.
- Fillmore, C., Kay, P., & O'Connor, C. (1988). Regularity and idiomaticity in grammatical constructions: The case of let alone. Language, 64, 501–538.
- Fisher, C. (1994). Structure and meaning in the verb lexicon: Input for a syntax-aided verb learning procedure. Language and Cognitive Processes, 9, 473–517.
- Fisher, C. (1996). Structural limits on verb mapping: The role of analogy in children's interpretations of sentences. Cognitive Psychology, 23, 331–392.
- Fisher, M., & Zwaan, R. (2008). Embodied language: A review of the role of the motor system in language comprehension. Quarterly Journal of Experimental Psychology, 61, 825–850.
- Fodor, J. (1983). The modularity of mind. Cambridge, MA: MIT Press.
- Foundas, A. L., Macauley, B. L., Raymer, A. M., Maher, L. M., Rothi, L. J., & Heilman, K. M. (1999). Ideomotor apraxia in Alzheimer disease and left hemisphere stroke: Limb transitive and intransitive movements. Neuropsychiatry,
- Neuropsychology, and Behavioral Neurology, 12, 161–166. Gabrieli, J. D., Poldrack, R. A., & Desmond, J. E. (1998). The role of left prefrontal cortex in language and memory. Proceedings of the National Academy of Sciences, U.S.A., 95, 906–913.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. Brain, 119, 593–603.
- Gallivan, J. P., & Culham, J. C. (2015). Neural coding within human brain areas involved in actions. Current Opinion in Neurobiology, 33, 141–149.
- Glenberg, A. M. (1997). What memory is for. Behavioral and Brain Sciences, 20, 1–55.
- Goldberg, A. E. (1995). Constructions: A construction grammar approach to argument structure. Chicago: University of Chicago Press.
- Goldberg, A. E. (2003). Constructions: A new theoretical approach to language. Trends in Cognitive Sciences, 7, 219–224.
- Grosbras, M.-H., Beaton, S., & Eickhoff, S. B. (2012). Brain regions involved in human movement perception: A quantitative voxel-based meta-analysis. Human Brain Mapping, 33, 431–454.
- Haaland, K. Y., Harrington, D. I., & Knight, R. T. (2000). Neural representations of skilled movement. Brain, 123, 2306–2313.
- Haiman, J. (1985). Natural syntax: Iconicity and erosion. Cambridge: Cambridge University Press.
- Hamilton, A. F. C., & Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. Journal of Neuroscience, 26, 1133–1137.
- Harnad, S. (1990). The symbol grounding problem. *Physica D*, 42, 335–346.
- Heilman, K. M., & Rothi, L. J. (1993). Apraxia. In K. M. Heilman & E. Valenstein (Eds.), Clinical neuropsychology (3rd ed., pp. 141–163). New York: Oxford University Press.
- Heilman, K. M., Rothi, L. J. G., & Valenstein, E. (1982). Two forms of ideomotor apraxia. Neurology, 32, 342–346.
- Hoenig, K., Sim, E.-J., Bochev, V., Herrnberger, B., & Kiefer, M. (2008). Conceptual flexibility in the human brain: Dynamic recruitment of semantic maps from visual, motor, and motion-related areas. Journal of Cognitive Neuroscience, 20, 1799–1814.
- Hoffman, P., Rogers, T. T., & Lambon Ralph, M. A. (2011). Semantic diversity accounts for the "missing" word frequency effect in stroke aphasia: Insights using a novel method to quantify contextual variability in meaning. Journal of Cognitive Neuroscience, 23, 2432–2446.
- Humphreys, G., Hoffman, P., Visser, M., Binney, R. J., & Lambon Ralph, M. A. (2015). Establishing task- and modalitydependent dissociations between the semantic and default mode networks. Proceedings of the National Academy of Sciences, U.S.A., 112, 7857–7862.
- Humphreys, G., Newling, K., Jennings, C., & Gennari, S. P. (2013). Motion and actions in language: Semantic representations in occipito-temporal cortex. Brain and Language, 125, 94–105.
- Jax, S. A., Buxbaum, L. J., & Moll, A. D. (2006). Deficits in movement planning and intrinsic coordinate control in ideomotor apraxia. Journal of Cognitive Neuroscience, 18, 2063–2076.
- Jefferies, E., & Lambon Ralph, M. A. (2006). Semantic impairment in stroke aphasia versus semantic dementia: A case-series comparison. Brain, 129, 2131–2147.
- Kable, J. W., Kann, 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.
- Kaschak, M. P., & Glenberg, A. M. (2000). Constructing meaning: The role of affordances and grammatical constructions in sentence comprehension. Journal of Memory and Language, 43, 508-529.
- Katz, J. J., & Fodor, J. A. (1963). The structure of a semantic theory. Language, 39, 170–210.
- 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. Cambridge: Cambridge University Press.
- Kemmerer, D. (2012). The crosslinguistic prevalence of SOV and SVO word orders reflects the sequential and hierarchical representation of action in Broca's area. Language and Linguistics Compass, 6, 50–66.
- Kemmerer, D. (2015). Are the motor features of verb meanings represented in the precentral motor cortices? Yes, but

within the context of a flexible, multilevel architecture for conceptual knowledge. Psychonomic Bulletin and Review, 22, 1068–1075.

Kemmerer, D., & Gonzalez-Castillo, J. (2010). The two-level theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system. Brain and Language, 112, 54–76.

Kemmerer, D., & Wright, S. (2002). Selective impairment of knowledge underlying un-prefixation: Further evidence for the autonomy of grammatical semantics. Journal of Neurolinguistics, 15, 403–432.

Kiefer, M., & Pulvermüller, F. (2012). Conceptual representations in mind and brain: Theoretical developments, current evidence and future directions. Cortex, 48, 805–825.

Kintsch, W. (2008). Symbol systems and perceptual representations. In M. De Vega, A. Glenberg, & A. Graesser (Eds.), Symbols and embodiment (pp. 145–164). Oxford: Oxford University Press.

Kipper, K., Dang, H. T., & Palmer, M. (2000). Class-based construction of a verb lexicon. In Proceedings of the Seventh National Conference on Artificial Intelligence (AAAI-2000), pp. 691–696.

Koch, G., Cercignani, M., Pecchioli, C., Versace, V., Oliveri, M., Caltagirone, C., et al. (2010). In vivo definition of parieto-motor connections involved in planning of grasping movements. Neuroimage, 51, 300–312.

Korhonen, A., Krymolowski, Y., & Briscoe, T. (2006). A large subcategorization lexicon for natural language processing applications. In Proceedings of LREC, pp. 1326–1331.

Kringelbach, M. L. (2005). The human orbitofrontal cortex: Linking reward to hedonic experience. Nature Reviews Neuroscience, 6, 691–702.

Kuno, S., & Takami, K. (2004). Functional constraints in grammar: On the unergative-unaccusative distinction. Philadelphia: John Benjamins Publishing Co.

Lakoff, G. (1987). Women, fire, and dangerous things: What categories reveal about the mind. Chicago: University of Chicago Press.

Langacker, R. W. (1999). Grammar and conceptualizations. Berlin & New York: Mouton de Gruyter.

Levin, B. (1995). Approaches to lexical semantic representation. In D. E. Walker, A. Zampolli, & N. Calzolari (Eds.), Automating the lexicon: Research and practice in a multilingual environment (pp. 53–91). Oxford: Oxford University Press.

Levin, B., & Rappaport Hovav, M. (2005). Argument realization. Cambridge: Cambridge University Press.

Lewis, J. (2006). Cortical networks related to human use of tools. The Neuroscientist, 12, 211–231.

Lui, F., Buccino, G., Duzzi, D., Benuzzi, F., Crisi, G., Baraldi, P., et al. (2008). Neural substrates for observing and imagining non-object-directed actions. Social Neuroscience, 3, 261–275.

Luzzatti, C., Raggi, R., Zonca, G., Pistarini, C., Contardi, A., & Pinna, G. D. (2002). Verb-noun double dissociation in aphasic lexical impairments: The role of word frequency and imageability. Brain and Language, 81, 432–444.

Malchukov, A., Haspelmath, M., & Comrie, B. (Eds.) (2010). Studies in ditransitive constructions: A comparative handbook. Berlin: De Gruyter.

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.

McAllister, T., Bachrach, A., Waters, G., Michaud, J., & Caplan, D. (2009). Production and comprehension of unaccusatives in aphasia. Aphasiology, 23, 989–1004.

- Mellet, E., Tzourio, N., Denis, M., & Mazoyer, B. (1998). Cortical anatomy of mental imagery of concrete nouns based on their dictionary definition. NeuroReport, 9, 803–808.
- Meltzer-Asscher, A., Schuchard, J., den Ouden, D.-B., & Thompson, C. K. (2012). The neural substrates of complex argument structure representations: Processing "alternating transitivity" verbs. Language and Cognitive Processes, 28, 1154–1168.
- Meteyard, L., Cuadrado, S. R., Bahrami, B., & Vigliocco, G. (2012). Coming of age: A review of embodiment and neuroscience of semantics. Cortex, 48, 788–804.
- Mozaz, M., Rothi, L. J., Anderson, J. M., Crucian, G. P., & Heilman, K. M. (2002). Postural knowledge of transitive pantomimes and intransitive gestures. Journal of the International Neuropsychological Society, 8, 958–962.
- Noppeney, U., & Price, C. J. (2004). Retrieval of abstract semantics. Neuroimage, 22, 164-170.
- Pinker, S. (1989). Learnability and cognition: The acquisition of argument structure. Cambridge, MA: MIT Press.

Pulvermüller, F. (1999). Words in the brain's language. Behavioral and Brain Sciences, 22, 253–336. Pulvermüller, F., Härle, M., & Hummel, F. (2000).

Neurophysiological distinction of verb categories. NeuroReport, 11, 2789–2793.

Pylyshyn, Z. W. (1984). Computation and cognition: Towards a foundation for cognitive science. Cambridge, MA: MIT Press.

- Ramayya, A. G., Glasser, M. F., & Rilling, J. K. (2010). A DTI investigation of neural substrates supporting tool use. Cerebral Cortex, 20, 507–516.
- Raposo, A., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2009). Modulation of motor and premotor cortices by actions, action words and action sentences. Neuropsychologia, 47, 388–396.
- Rees, G., Friston, K., & Koch, C. (2000). A direct quantitative relationship between functional properties of human and macaque V5. Nature Neuroscience, 3, 716–723.
- Reichenbach, A., Thielscher, A., Peer, A., Bülthoff, H. H., & Bresciani, J. P. (2014). A key region in the human parietal cortex for processing proprioceptive hand feedback during reaching movements. Neuroimage, 84, 615–625.

Rice, N. J., Tunik, E., & Grafton, S. T. (2006). The anterior intraparietal sulcus mediates grasp execution independent of requirement to update: New insights from transcranial magnetic stimulation. Journal of Neuroscience, 26, 8176–8182.

- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. Cognitive Brain Research, 3, 131–141.
- Roehm, D., Sorace, A., & Bornkessel-Schlesewsky, I. (2012). Processing flexible form-to-meaning mappings: Evidence for enriched composition as opposed to indeterminacy. Language and Cognitive Processes, 28, 1244–1274.
- Rolls, E. T., & Grabenhorst, F. (2008). The orbitofrontal cortex and beyond: From affect to decision-making. Progress in Neurobiology, 86, 216–244.
- Rumiati, R. I., Weiss, P. H., Shallice, T., Ottoboni, G., North, J., Zilles, K., et al. (2004). Neural basis of pantomiming the use of visually presented objects. Neuroimage, 21, 1224–1231.
- Saad, Z. S., Glen, D. R., Chen, G., Beauchamp, M. S., Desai, R., & Cox, R. W. (2009). A new method for improving functional-to-structural MRI alignment using local Pearson correlation. Neuroimage, 44, 839–848.
- Sabsevitz, D. S., Medler, D. A., Seidenberg, M., & Binder, J. R. (2005). Modulation of the semantic system by word imageability. Neuroimage, 27, 188–200.
- Sakreida, K., Schubotz, R. I., Wolfensteller, U., & von Cramon, D. Y. (2005). Motion class dependency in observers' motor

areas revealed by functional magnetic resonance imaging. Journal of Neuroscience, 25, 1335–1342.

Saygin, A. P., McCullough, S., Alac, M., & Emmory, K. (2010). Modulation of bold response in motion-sensitive lateral temporal cortex by real and fictive motion sentences. Journal of Cognitive Neuroscience, 22, 2480–2490.

Seghier, M. L., Fagan, E., & Price, C. J. (2010). Functional subdivisions in the left angular gyrus where the semantic system meets and diverges from the default network. Journal of Neuroscience, 30, 16809–16817.

Seghier, M. L., & Price, C. J. (2012). Functional heterogeneity within the default network during semantic processing and speech production. Frontiers in Psychology, 3, 281. doi:10.3389/fpsyg.2012.00281.

Shetreet, E., & Friedmann, N. (2012). Stretched, jumped, and fell: An fMRI investigation of reflexive verbs and other intransitives. Neuroimage, 60, 1800–1806.

Talairach, J., & Tournoux, P. (1988). Co-planar stereotaxic atlas of the human brain. New York: Thieme.

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, C. K., Bonakdarpour, B., & Fix, S. F. (2010). Neural mechanisms of verb argument structure processing in agrammatic aphasic and healthy age-matched listeners. Journal of Cognitive Neuroscience, 22, 1–35.

Thompson, C. K., Bonakdarpour, B., Fix, S. F., Blumenfeld, H. K., Parrish, T. B., Gitelman, D. R., et al. (2007). Neural correlates of verb argument structure processing. Journal of Cognitive Neuroscience, 19, 1753–1767.

Tkach, D., Reimer, J., & Hatsopoulos, N. G. (2007). Congruent activity during action and action observation in motor cortex. Journal of Neuroscience, 27, 13241–13250.

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(Suppl. 2), T77–T86.

Van Dam, W. O., Van Dijk, M., Bekkering, H., & Rueschemeyer, S.-A. (2012). Flexibility in embodied lexical-semantic representations. Human Brain Mapping, 33, 2322–2333.

Wagner, A. D., Koutstaal, W., Maril, A., Schacter, D. L., & Buckner, R. L. (2000). Task-specific repetition priming in left inferior prefrontal cortex. Cerebral Cortex, 10, 1176–1184.

Wallentin, M., Ellegaard, T., Ostergaard, S., Ostergaard, L., & Roepstorff, A. (2005). Motion verb sentences activate left posterior middle temporal cortex despite static context. NeuroReport, 16, 649–652.

Wang, J., Conder, J. A., Blitzer, D. N., & Shinkareva, S. (2010). Neural representation of abstract and concrete concepts: A meta-analysis of neuroimaging studies. Human Brain Mapping, 31, 1459–1468.

Watson, R. T., Fleet, W. S., Rothi, L. J. G., & Heilman, K. M. (1986). Apraxia and the supplementary motor area. Archives of Neurology, 43, 787–792.

Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M. A., & Jefferies, E. (2011). The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus. Cerebral Cortex, 21, 1066–1075.

Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M. A., & Jefferies, E. (2012). Executive semantic processing is underpinned by a large-scale neural network: Revealing the contribution of let prefrontal, posterior temporal, and parietal cortex to controlled retrieval and selection using TMS. Journal of Cognitive Neuroscience, 24, 133–147.

Wierzbicka, A. (1988). The semantics of grammar. The semantics of English causative constructions, in a universal-typological perspective. In M. Tomasello (Ed.), The new psychology of language (Vol. 1, pp. 113-153). Mahwah, NJ: Lawrence Erlbaum.

Willems, R. M., Hagoort, P., & Casasanto, D. (2010). Body-specific representations of action verbs: Neural evidence from right- and left-handers. Psychological Science, 21, 67–74.

Willems, R. M., Hagoort, P., Toni, I., Hagoort, P., & Casasanto, D. (2009). Neural dissociations between action verb understanding and motor imagery. Journal of Cognitive Neuroscience, 22, 2387–2400.

Wilson-Mendenhall, C. D., Simmons, W. K., Martin, A., & Barsalou, L. W. (2013). Contextual processing of abstract concepts reveals neural representations of nonlinguistic semantic content. Journal of Cognitive Neuroscience, 25, 920–935.

Wise, R., Howard, D., Mummery, C. J., Fletcher, P., Leff, A., Buchel, C., et al. (2000). Noun imageability and the temporal lobes. Neuropsychologia, 38, 985–994.

Woo, C.-W., Krishnan, A., & Wagner, T. D. (2014). Cluster-extent based thresholding in fMRI analyses: Pitfalls and recommendations. Neuroimage, 91, 412–419.

Yttri, E. A., Wang, C., Liu, Y., & Snyder, L. H. (2014). The parietal reach region is limb specific and not involved in eye-hand coordination. Journal of Neurophysiology, 111, 520–532.

Zwaan, R. A., & Kaschak, M. P. (2008). Language in the brain, body, and world. In M. Robbins & M. Aydede (Eds.), Cambridge handbook of situated cognition (pp. 368–381). Cambridge: Cambridge University Press.