

Comprehending Prehending: Neural Correlates of Processing Verbs with Motor Stems

Shirley-Ann Rüschemeyer¹, Marcel Brass^{1,2}, and Angela D. Friederici¹

Abstract

■ The interaction between language and action systems has become an increasingly interesting topic of discussion in cognitive neuroscience. Several recent studies have shown that processing of action verbs elicits activation in the cerebral motor system in a somatotopic manner. The current study extends these findings to show that the brain responses for processing of verbs with specific motor meanings differ not only from that of other motor verbs, but, crucially, that the comprehension of verbs with motor meanings (i.e., *greifen*, to grasp) differs fundamentally from the processing of verbs with abstract meanings (i.e., *denken*, to think). Second, the current study investigated the neural correlates of processing morphologically complex verbs with abstract mean-

ings built on stems with motor versus abstract meanings (i.e., *begreifen*, to comprehend vs. *bedenken*, to consider). Although residual effects of motor stem meaning might have been expected, we see no evidence for this in our data. Processing of morphologically complex verbs built on motor stems showed no differences in involvement of the motor system when compared with processing complex verbs with abstract stems. Complex verbs built on motor stems did show increased activation compared with complex verbs built on abstract stems in the right posterior temporal cortex. This result is discussed in light of the involvement of the right temporal cortex in comprehension of metaphoric or figurative language. ■

INTRODUCTION

The neural organization of language in the brain remains elusive in many respects. Neuroanatomical models of language processing have progressed in identifying specific cerebral networks to specifically underlie the processing of different types of linguistic information (i.e., syntax, semantics; Friederici, 2002). It remains unclear, however, what factors within various domains might be further represented at the brain level. Research with aphasic patients provides good evidence that the neural representation of verbs is unique from that of other word categories (i.e., nouns) in that focal lesions of frontal areas, in particular, can lead to a disproportionate impairment in processing of verbs (Hillis, Tuffiash, & Caramazza, 2002; Damasio & Tranel, 1993).

One current topic of interest within the domain of semantics addresses the question of whether/how motor versus abstract verbs might be represented differently from one another on the brain level. This discussion has been fueled by the discovery of the mirror neuron system in monkeys. Mirror neurons, specific neurons initially described in the premotor cortex of the monkey, discharge (1) when the monkey makes a specific, goal-oriented grasping movement and also (2) when

the monkey observes a human or conspecific making the same specific gesture (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Mirror neurons with properties similar to those observed in the prefrontal cortex have additionally been identified in the posterior parietal lobule (PF mirror neurons) (Gallese, Fadiga, Fogassi, & Rizzolatti, 2002; Rizzolatti, Fogassi, & Gallese, 2001). PF mirror neurons, like prefrontal mirror neurons, are responsive for both action observation and action execution. However, PF mirror neurons appear to be less selective in the actions they encode, some neurons firing for more than one action.

Mirror neurons have been postulated to be a crucial component in understanding others' actions and so allowing the observer to respond appropriately to the actions of others. The fact that these neurons are located in the monkey premotor cortex, in an area analogous to the human ventrolateral prefrontal cortex (or Broca's area), has led researchers to suggest that the human language system may have made early use of the mirror neuron system (Rizzolatti & Craighero, 2004; Rizzolatti & Arbib, 1998). Specifically, Rizzolatti and Arbib (1998) propose that "the development of the human lateral speech circuit is a consequence of the fact that the precursor of Broca's areas was endowed, before speech appearance, with a mechanism for recognizing actions made by others" (p. 190). This system is hypothesized to have evolved to support a gestural

¹Max-Planck-Institute for Human Cognitive and Brain Sciences, Germany, ²Ghent University, Belgium

protolanguage, which may have resembled pantomime and which ultimately progressed from a motor (gestural) to an auditory (speech) language system (Arbib, 2005).

For methodological reasons, the existence of mirror neurons as seen in the monkey (via single cell recordings) has not been demonstrated in humans. However, good evidence exists in favor of the idea that execution and observation of motor acts rely on overlapping cortical resources. Behaviorally, Brass et al. (2000) showed that cuing motor activity with a perceptually identical cue (i.e., cuing finger movement with finger movement) facilitated response significantly compared to when the action was cued by an irrelevant symbolic or spatial cue. This demonstrates that action observation can influence movement execution in holding with an ideomotor account of action perception/execution. Furthermore, neuroimaging studies have shown that action observation activates motor areas (putative mirror neuron areas) in humans in a somatotopically organized manner (Buccino et al., 2001). Specifically, Buccino et al. (2001) showed that observation of hand, mouth, and foot movements elicits increased activation in the brain of the observer in effector-specific lateral premotor cortex. If a manipulated object was included in the presented stimuli, somatotopically organized activation was additionally observed in the parietal cortex.

Several recent neuroimaging studies have provided evidence for the idea that the comprehension of language describing a motor act also draws on the resources of motor circuits in the brain (Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005; Tettamanti et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004). Specifically, Pulvermüller et al. (2005) have collected evidence in a series of experiments with various methodologies supporting the idea that processing verbs with motor meanings elicits activation in primary motor and premotor cortices in a somatotopically organized manner. In particular, verbs denoting hand actions, such as *pick*, elicit increased levels of activation in premotor and motor hand areas, whereas verbs denoting foot actions, such as *kick*, elicit increased levels of activation in premotor and motor foot areas. It has been proposed that the meaning of an action word is thus represented in a cortical network incorporating areas that typically play a role in the actual execution of the action described.

The current experiment endeavored to further explore the interaction between action and language. Specifically, we were interested in seeing whether verbs describing motor actions (e.g., *greifen*, to grasp) would elicit greater levels of activation in motor cortices than verbs describing abstract actions (e.g., *denken*, to think). Although Pulvermüller et al. (2005) report effector-relevant differences for action verb stimuli, there is no discussion of how abstract verbs might be processed differently than concrete verbs. Tettamanti et al. (2005) included sentences with abstract meanings in their

design and observed differences between motor and abstract sentences in the premotor (but not primary motor) cortex. Crucially, the sentences differed not only in the semantic content of the verbs used (motor vs. abstract), but also used different sentential objects that had either concrete or abstract meanings in correspondence with the verb used. Thus, in this study, abstractness of the verb and its object argument varied at the same time, leaving open the question of whether the difference found was due to the meaning of the verb, the object noun, or both. We wanted to explore whether dissociation between abstract and motor meaning was evident for verbs alone. We hypothesized, based on the results of these previous studies, that dissociation between motor and abstract verbs should indeed be observed in motor cortices.

Second, we were interested in seeing whether such a dissociation would carry over to morphologically complex abstract verbs when built either on motor or on abstract verb stems. German is a morphologically rich language with many derived words based on a single word root. Many motor verb stems can be prefixed to form morphologically complex words with abstract, rather than motor, meanings. For example the verb *begreifen* (to comprehend) is a prefixed form of the simple motor verb *greifen* (to grasp), and *bedenken* (to consider) a prefixed form of *denken* (to think) (Table 1). Assuming a difference could be detected between the processing of motor and abstract verb stems in motor cortices, we were interested to see how the brain would deal with morphologically complex derivations of these single verb stems. If the action-based approach of language not only holds for concrete verbs, but also more generally serves as a basis for language at a more abstract level, we should observe a residual motor component in the brain's response to the word *begreifen* (to comprehend) based on the fact that it is a morphologically complex derivative of the motor verb *greifen* (to grasp).

METHODS

Participants

Twenty native German-speaking men, age 22–33 years ($M = 27$, $SD = 3$), participated in this experiment after giving informed written consent.

Table 1. Examples of Visually Presented Verbs in German with English Translation

	<i>Motor</i>	<i>Abstract</i>
Simple	<i>Greifen</i> (to grasp)	<i>Denken</i> (to think)
Complex	<i>Begreifen</i> (to comprehend)	<i>Bedenken</i> (to consider)

Participants read morphologically simple verbs (Simple) with both motor meanings (Motor) and abstract meanings (Abstract), as well as morphologically complex forms (Complex) of the same verb stems.

Materials

A 2×2 factorial design was used with the factors Morphological Complexity (Morph: simple [S], complex [C]) and Verb Stem Meaning (Stem: motor [M], abstract [A]).

The critical stimuli consisted of 92 verbs in the infinitive form. Forty-six of these items were morphologically simple (stem + infinitive ending) and 46 were morphologically complex (prefix + stem + infinitive ending). The morphologically simple items had either a clearly motor meaning (i.e., *greifen*, to grasp; $n = 23$) or a clearly abstract meaning (i.e., *denken*, to think; $n = 23$). Morphologically complex items were built on the simple stems and were always abstract in meaning (i.e., *begreifen*, to comprehend; *bedenken*, to consider).

In addition to the 92 critical stimuli, 42 filler verbs were included to distract participants from the actual task. These consisted of 28 real verbs (14 morphologically simple and 14 morphologically complex) as well as 14 pseudowords, which were orthographically possible words in German (i.e., *mopfen*). Half of the morphologically simple real verbs had motor meanings that did not denote hand movements (i.e., *laufen*, to run); the other half were abstract verbs. Morphologically complex verbs were built on the simple stems paralleling the critical experimental stimuli (see list of materials, Table 2).

Stimulus Presentation

Participants, lying on their backs in the scanner, were given 3-D glasses through which they saw a computer monitor on which the stimuli were presented. In their right hand, participants held a response box on which they were instructed to press one of the keys only in response to pseudowords. No response was required for real words. Participants were told that the goal of the study was to investigate interference in the detection of pseudowords in the noisy scanner environment. Participants did not report being aware of the manipulation of verb meaning.

A single trial constituted presentation of a single verb. Each trial lasted 8 sec. To enhance the temporal resolution of the acquired signal, a variable jitter time of 0, 500, 1000, or 1500 msec was included at the beginning of each trial. Following this, the actual stimulus was introduced by a fixation cross in the center of the screen, which remained visible for 300 msec. Directly following the fixation cross, the stimulus (verb) appeared in the center of the screen for 700 msec. The interstimulus interval was approximately 6 sec.

The 92 critical words plus 42 filler trials and 30 null events (low-level baseline) were presented in pseudorandomized order to participants in two blocks of just under 10 min with a 1-min pause in the middle. Each block was introduced by two dummy trials that were not included in any further analysis. Trial conditions were balanced across the two blocks. Half of the participants saw the experimental stimuli in reversed order.

fMRI Data Acquisition

Twenty axial slices (4 mm thick, 1-mm interslice distance, FOV 19.2 cm, data matrix of 64×64 voxels, in-plane resolution of 3×3 mm) were acquired every 2 sec during functional measurements (BOLD sensitive gradient EPI sequence, TR = 2 sec, TE = 30 msec, flip angle = 90° , acquisition bandwidth = 100 Hz) with a 3-T Bruker (Ettlingen, Germany) Medspec 30/100 system. Prior to functional imaging, T1-weighted modified driven equilibrium Fourier transform (MDEFT) images (data matrix 256×256 , TR = 1.3 sec, TE = 10 msec) were obtained with a non-slice-selective inversion pulse followed by a single excitation of each slice (Norris, 2000). These images were used to coregister functional scans with previously obtained high-resolution whole-head 3-D brain scans: 128 sagittal slices, 1.5-mm thickness, FOV $25.0 \times 25.0 \times 19.2$ cm, data matrix of 256×156 voxels.

fMRI Data Analysis

The functional imaging data were processed using the software package LIPSIA (Lohmann et al., 2001). Functional data were corrected first for motion artifacts by using a matching metric based on linear correlation. Data were subsequently corrected for the temporal offset between slices acquired in one scan using a cubic spline interpolation based on the Nyquist–Shannon theorem. Low-frequency signal changes and baseline drifts were removed by applying a temporal high-pass filter to remove frequencies lower than 1/80 Hz and a spatial Gaussian filter with 5.65 mm full width at half maximum (FWHM) was applied.

To align the functional data slices with a 3-D stereotactic coordinate reference system, a rigid linear registration with six degrees of freedom (three rotational, three translational) was performed. The rotational and translational parameters were acquired on the basis of the MDEFT (Norris, 2000) and EPI T1 slices to achieve an optimal match between these slices and the individual 3-D reference data set, which was acquired during a previous scanning session. The MDEFT volume data set with 160 slices and 1-mm slice thickness was standardized to the Talairach stereotactic space. The rotational and translational parameters were subsequently transformed by linear scaling to a standard size. The resulting parameters were then used to transform the functional slices using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system. This linear normalization process was improved by a subsequent processing step that performed an additional nonlinear normalization (Thiron, 1998). The transformation parameters obtained from both normalization steps were subsequently applied to the functional data. Voxel size was interpolated during coregistration from $3 \times 3 \times 4$ to $3 \times 3 \times 3$ mm.

Table 2. Complete List of Materials

<i>Critical Items</i>		<i>Filler Items</i>
<p>Simple Motor Verbs</p> <p><i>bauen</i> (to build) <i>binden</i> (to tie) <i>brechen</i> (to break) <i>dreben</i> (to turn over, roll) <i>drücken</i> (to press) <i>fechten</i> (to fence) <i>greifen</i> (to grasp) <i>halten</i> (to hold) <i>heben</i> (to lift) <i>kehren</i> (to sweep) <i>legen</i> (to lay) <i>mischen</i> (to mix) <i>nehmen</i> (to take) <i>schlagen</i> (to beat) <i>schreiben</i> (to write) <i>stechen</i> (to stab) <i>stellen</i> (to place) <i>stricken</i> (to knit) <i>tragen</i> (to carry) <i>werfen</i> (to throw) <i>wischen</i> (to mop) <i>zeichnen</i> (to draw) <i>ziehen</i> (to pull)</p> <p>Complex Verbs with Motor Stems</p> <p><i>aufbauen</i> (to encourage) <i>unterbinden</i> (to prevent) <i>unterbrechen</i> (to interrupt) <i>verdreben</i> (to distort) <i>unterdrücken</i> (to suppress) <i>anfechten</i> (to appeal) <i>begreifen</i> (to comprehend) <i>einhalten</i> (to maintain) <i>entheben</i> (to depose) <i>bekehren</i> (to proselytize) <i>überlegen</i> (to contemplate) <i>vermischen</i> (to confuse) <i>übernehmen</i> (to take over)</p>	<p>Simple Abstract Verbs</p> <p><i>achten</i> (to regard) <i>denken</i> (to think) <i>ehren</i> (to honor) <i>fordern</i> (to demand) <i>glauben</i> (to believe) <i>gleichben</i> (to resemble) <i>heißen</i> (to be called) <i>helfen</i> (to help) <i>hoffen</i> (to hope) <i>kennen</i> (to know) <i>leben</i> (to live) <i>lernen</i> (to learn) <i>loben</i> (to commend) <i>lügen</i> (to lie, as in tell a lie) <i>meiden</i> (to avoid) <i>merken</i> (to note, as in remember) <i>raten</i> (to guess) <i>rechnen</i> (to calculate) <i>trauen</i> (to trust) <i>wundern</i> (to wonder) <i>wünschen</i> (to wish) <i>zaubern</i> (to conjure) <i>zweifeln</i> (to doubt)</p> <p>Complex Verbs with Abstract Stems</p> <p><i>beachten</i> (to attend, consider) <i>bedenken</i> (to consider) <i>verehren</i> (to admire) <i>erfordern</i> (to necessitate) <i>beglaubigen</i> (to accredit) <i>vergleichen</i> (to compare) <i>verbeißen</i> (to auger) <i>verbelfen</i> (to support) <i>erhoffen</i> (to wish, expect) <i>erkennen</i> (to recognize) <i>beleben</i> (to animate) <i>verlernen</i> (to forget, unlearn) <i>belobigen</i> (to praise, honor)</p>	<p>Simple Filler Items</p> <p><i>bören</i> (to hear) <i>laufen</i> (to run) <i>reden</i> (to talk) <i>sprechen</i> (to speak) <i>springen</i> (to jump) <i>suchen</i> (to search) <i>treten</i> (to kick) <i>fluchen</i> (to curse) <i>klagen</i> (to complain) <i>lieben</i> (to love) <i>schaffen</i> (to accomplish) <i>schwören</i> (to swear) <i>steuern</i> (to steer) <i>zwingen</i> (to force)</p> <p>Complex Filler Items</p> <p><i>verbören</i> (to interrogate) <i>unterlaufen</i> (to overflow) <i>überreden</i> (to convince) <i>versprechen</i> (to promise) <i>einspringen</i> (to stand in, as in replace) <i>versuchen</i> (to attempt) <i>vertreten</i> (to represent) <i>verfluchen</i> (to hex) <i>verklagen</i> (to sue) <i>verlieben</i> (to fall in love) <i>abschaffen</i> (to abolish) <i>beschwören</i> (to attest) <i>versteuern</i> (to tax) <i>erzwingen</i> (to enforce)</p> <p>Pseudowords</p> <p><i>mopfen</i> <i>trampfen</i> <i>wienen</i> <i>trimpfen</i> <i>gieblen</i> <i>kallen</i></p>

Downloaded from <http://direct.mit.edu/jocn/article-pdf/13/9/858/19963274/jocn.2007.13.9.858.pdf> on 18 May 2021

Table 2. (continued)

Critical Items		Filler Items
Complex Verbs with Motor Stems	Complex Verbs with Abstract Stems	Pseudowords
<i>verschlagen</i> (to suggest)	<i>belügen</i> (to lie)	<i>balfen</i>
<i>ausschreiben</i> (to announce/post)	<i>vermeiden</i> (to avoid)	<i>beklatten</i>
<i>bestechen</i> (to bribe)	<i>bemerkten</i> (to comment)	<i>abfergen</i>
<i>unterstellen</i> (to imply)	<i>verraten</i> (to betray)	<i>verklüren</i>
<i>verstricken</i> (to enmesh)	<i>abrechnen</i> (to balance accounts)	<i>einziehen</i>
<i>vertragen</i> (to tolerate/get along with)	<i>vertrauen</i> (to rely, trust)	<i>verkidnen</i>
<i>entwerfen</i> (to design)	<i>bewundern</i> (to admire)	<i>ausseppen</i>
<i>erwischen</i> (to see someone doing something)	<i>verwünschen</i> (to imprecate)	<i>beplapfen</i>
<i>verzeichnen</i> (to denote)	<i>bezaubern</i> (to charm)	
<i>erziehen</i> (to educate/parent)	<i>bezweifeln</i> (to doubt, disbelieve)	

The statistical evaluation was based on a least squares estimation using the general linear model for serially autocorrelated observations (Worsley & Friston, 1995). The design matrix was generated with a synthetic hemodynamic response function and its first derivative (Friston et al., 1998; Josephs & Henson, 1999). The model equation, made up of the observed data, the design matrix, and the error term, was convolved with a Gaussian kernel of dispersion of 4 sec FWHM.

The experimental design was a 2 × 2 factorial design with the factors Morphological Complexity (Morph: Simple [S], Complex [C]) and Verb Stem Meaning (Stem: Motor [M], Abstract [A]). The main hypotheses were related to (1) the interaction between Morph × Stem and (2) the effect of Stem within each level of Morphological Complexity. Therefore, for each participant four contrast images were generated. These represented (1) the interaction between Morph × Stem ($[S_M - S_A] - [C_M - C_A]$), (2) the main effect of processing Stem meaning for simple verbs ($S_M - S_A$), (3) the main effect of processing Stem meaning for complex verbs ($C_M - C_A$), and (4) the main effect of motor responses to the pseudoword stimuli (Task baseline). Because individual functional data sets had been aligned to the standard stereotactic reference space, a group analysis based on the contrast images could be performed. Single-participant contrast images were entered into a second-level random effects analysis for each of the contrasts. The group analysis consisted of a one-sample *t* test across the contrast images of all subjects that indicated whether observed differences between conditions were significantly distinct from zero. Subsequently, *t* values were transformed into *Z* scores. To protect against false-positive activation a double threshold was applied, by which only regions with a *Z* score exceeding 3.09 (*p* < .001, uncorrected) and a volume exceeding five voxels (135 mm³) were considered (Forman et al., 1995). At

the second level we also performed a conjunction analysis, showing the common activated network for motor response to button presses and motor verbs ([Task baseline] ∩ $[S_M - S_A]$).

RESULTS

Direct Contrasts

A list of significant activations can be seen in Table 3 and in Figure 1.

The whole-brain analysis of the interaction between Morph × Stem ($[S_M - S_A] - [C_M - C_A]$) showed reliably greater differences between the simple verb forms (motor stem > abstract stem) than between complex verb forms (motor verb stem > abstract verb stem) in several regions within the motor circuit. Specifically, an interaction was seen in the left dorsal postcentral gyrus, the left parietal operculum (secondary somatosensory cortex), and the left posterior medial temporal lobe (see Figure 1).

The direct contrast between simple verb stems with motor versus abstract meanings ($S_M - S_A$) showed reliably greater levels of activation for motor stems in primary motor and somatosensory cortices. Activation differences (motor > abstract) were observed in the bilateral postcentral gyri, directly opposite the central sulcus from the primary hand motor area in the precentral knob (Yousry et al., 1997), as well as the left parietal operculum (secondary somatosensory cortex). The postcentral gyrus activation extended from its local maximum in the postcentral gyrus (−47, −18, 44) into the central sulcus (−44, −15, 59) and further into the posterior portion of the precentral gyrus (−47, −9, 57). Because this activation encompasses regions within both primary somatosensory and motor areas, we refer from here on to the sensorimotor cortex (SM). In

Table 3. Results of fMRI Experiment (Mean Z Value > 3.09, Cluster > 135 mm³)

	<i>Contrast</i>	<i>Region</i>	<i>Z_{max}</i>	<i>Extent (mm³)</i>	<i>x</i>	<i>y</i>	<i>z</i>
Interaction	[S _M - S _A] - [C _M - C _A]	Left postcentral gyrus (SM)	3.53	189	-38	-21	56
		Left parietal operculum (S2)	3.36	135	-47	-15	14
		Left medial temporal lobe	3.58	216	-23	-54	11
Simple verbs	S _M > S _A	Left sensorimotor cortex (SM)					
		Postcentral gyrus	3.35	162	-47	-18	44
		Central sulcus	3.42	135	-44	-15	59
		Precentral gyrus	3.41		-47	-9	57
		Right postcentral gyrus	3.37	135	37	-15	38
		Left parietal operculum (S2)	3.58	783	-59	-15	14
			3.31	135	-53	-30	17
		Left medial temporal lobe (calcarine sulcus)	3.37	405	-26	-63	8
		Left medial temporal lobe	3.13	189	-14	-54	5
		Right medial temporal lobe	3.28	162	13	-45	5
	S _A > S _M	No significantly activated regions					
Complex verbs	C _M > C _A	Right posterior middle temporal gyrus	4.05	513	46	-69	23
		Left cerebellum	3.22	135	-8	-66	-13
		C _A > C _M	No significantly activated regions				
Conjunction analysis	[Task-base] ∩ [S _M - S _A]	Left sensorimotor cortex (SM)					
		Postcentral gyrus	3.35	162	-47	-18	44
		Central Sulcus	3.42	135	-44	-15	59
		Left parietal operculum (S2)	3.58	756	-59	-15	14
			3.31	135	-53	-30	17
		Left medial temporal lobe	3.37	405	-26	-63	8

Activations are listed for the interaction between the factors Morphological Complexity (simple, complex) and Verb Stem Meaning (motor, abstract), as well as for the main effect of verb stem meaning within each verb type. Contrasts, region, maximum Z values, extent, and Talairach coordinates are presented.

addition, greater activation was observed for motor verbs in the bilateral medial temporal lobes, extending into the calcarine sulcus.

No regions were observed with greater activation for verb stems with abstract meanings (S_A - S_M).

Comparison of morphologically complex verbs with motor versus abstract stems (C_M - C_A) showed increased levels of activation for verbs with motor stems in the right posterior middle temporal gyrus and left cerebellum.

No regions of greater activation were observed for morphologically complex verbs with abstract stems versus complex verbs with motor stems (C_A - C_M).

A conjunction analysis was conducted in order to identify those areas of brain that were involved both in performing a hand movement (button press) and in the processing of simple verbs with motor meanings ([Task baseline] ∩ [S_M - S_A]). We do not report the entire set of areas activated by button presses, as this contrast was

built only for conducting the conjunction analysis. Areas commonly activated by both button presses and motor verbs included the left sensorimotor area (postcentral gyrus extending to central sulcus and posterior portion of precentral gyrus), the left posterior operculum, and the left medial temporal cortex.

Analysis of Percent Signal Change

The whole-brain analysis revealed a significant interaction between Morph × Stem in two brain regions relevant to motor function (see above). We performed an analysis of percent signal change within the voxels surrounding the peak activation in the group average within these two regions in order to examine the nature of the Morph × Stem interaction. This analysis differs conceptually from the use of functional localizers (see Friston, Rotshtein, Geng, Sterzer, & Henson, 2006; Saxe,

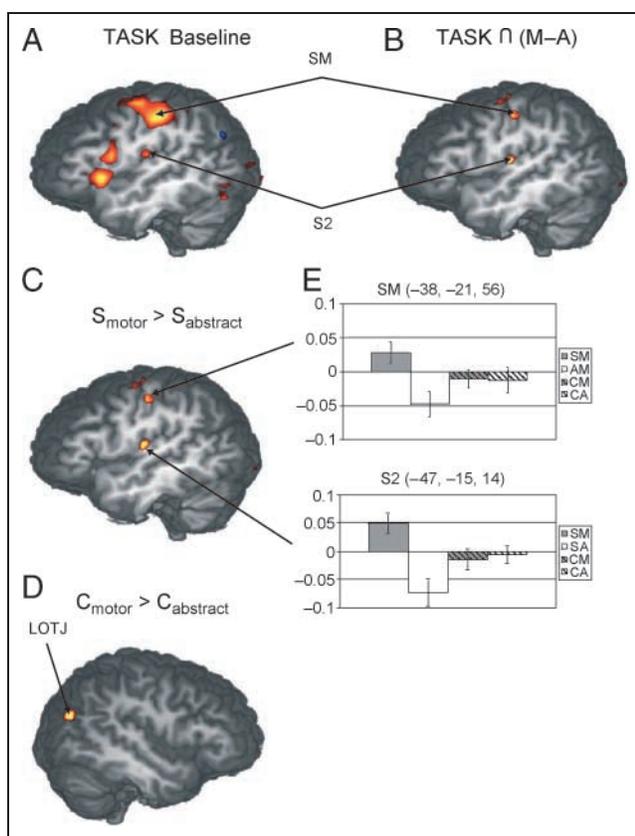


Figure 1. Areas showing a (A) reliable activation for button presses versus baseline, (B) common activation for button presses and simple motor verbs, (C) greater activation for simple motor verbs than simple abstract verbs, and (D) greater activation for complex verbs with motor stems versus complex verbs with abstract stems. In addition, the significant interaction between morphological complexity and verb stem meaning is shown in terms of percent signal change (E).

Brett, & Kanwisher, 2006) in that regions were selected from the whole-brain analysis showing significant areas of interaction and not from whole-brain analysis for main effects of any one single factor.

Mean percent signal change, reflecting values for each participant in the spherical 26 voxels (702 mm^3) adjacent to the peak voxel of activation observed in the group interaction, were entered into a 2×2 analysis of variance (ANOVA). As our hypothesis and discussion focus on activations within motor-related areas, we restricted the number of regions included in this analysis to (1) the SM ($-38, -21, 56$) and (2) the secondary somatosensory cortex (S2: $-47, -15, 14$). The results of this analysis can be seen in Figure 1E.

Mean activation per participant was calculated between 4 and 8 sec after stimulus onset. The means were entered into a two-factor ANOVA with the factors (1) Morphological Complexity (Morph) and (2) Stem Meaning (Stem). The factor Morph was characterized by two levels: simple and complex. The factor Stem likewise consisted of two levels: Motor and Abstract.

In the left SM, no main effect of Morph or Stem was observed; however, the interaction between Morph \times Stem was significant, $F(1,19) = 6.15, p < .05$. This reflected significantly more activation for simple motor verbs than for simple abstract verbs but no significant difference between verb stem types for complex verbs.

The same pattern of activation was seen in the left secondary somatosensory cortex (S2). Here an interaction between Morph \times Stem was observed, $F(1,19) = 10.21, p < .005$, with no main effect of either Morph or Stem. The interaction resulted from significantly enhanced activation for simple motor verbs as compared to simple abstract verbs, with no significant difference between verb stem types for complex verbs.

DISCUSSION

The current experiment was designed to explore the influence of word meaning on the cerebral representation of word processing. We had two specific hypotheses in mind in designing this experiment: First, motor areas would be more involved in the processing of verbs denoting motor actions (i.e., *greifen*, to grasp) than in processing verbs denoting nonmotor actions (i.e., *denken*, to think). Second, morphologically complex verbs with abstract meanings built on motor stems (i.e., *begreifen*) might also show more involvement of motor cortices than morphologically complex verbs built on abstract stems (i.e., *bedenken*), due to a residual effect of processing the verb stem. However, we showed a reliable interaction between differences in activation in the two verb types. Although the SM was seen to be reliably more activated by simple motor verbs than by simple abstract verbs, no difference could be detected in SM between the morphologically complex verb forms. We discuss the implications of this interaction with regard to the main effects detected within each verb type (resolution of the interaction).

Morphologically Simple Verbs

The results of the current study showed reliable differences between the processing of simple motor verbs describing actions conducted with the hand (i.e., *greifen*, to grasp) versus simple abstract verbs (i.e., *denken*, to think). These differences were reflected in greater signal changes for motor verbs than for abstract verbs in several regions within the posterior premotor, primary motor (M1), and somatosensory (S1) cortex (together: SM) as well as secondary somatosensory (S2) cortex. Enhanced activation for motor verbs was observed bilaterally in sensorimotor areas, but to a greater extent in the left hemisphere. Somatosensory cortex activation was observed primarily in the left hemisphere; however, when the activation threshold is reduced minimally ($Z > 2.58, p < .005$) it immediately becomes apparent that

differences were also present in the right hemisphere. The peak of activation within SM lay somewhat inferior to the classical hand motor area in humans (Yousry et al., 1997). However, in comparing the pattern of activation with that observed for participants actually performing a button press task, a large degree of overlap is seen (see Figure 1). Although the peak activation does not overlap between the motor verb and motor task conditions, the activation observed in conjunction with the processing of motor verbs lies entirely within the greater activation elicited by the motor task. For this reason, we feel confident in drawing a parallel between the activation increase observed for motor verbs and general motor performance.

A functional link between motor and language systems based on meaning has been postulated previously (Pulvermüller et al., 2005; Tettamanti et al., 2005; Hauk et al., 2004). Specifically, Pulvermüller et al. (2005) have collected evidence in a series of experiments with various methodologies in favor of the idea that processing verbs denoting motor meanings draws on resources in primary motor and premotor cortices in a somatotopically organized manner. In other words, verbs denoting hand actions elicit increased levels of activation in premotor and motor hand areas, whereas verbs denoting foot actions elicit increased levels of activation in premotor and motor foot areas. It has been proposed that the meaning of action words is thus represented in a cortical network including areas that typically play a role in the actual execution of the action described. The findings of the current study appear to support this assumption. The current study, however, cannot determine whether motor system involvement is a fundamental necessity or a consequence of verb comprehension.

Several recent studies have suggested that a somatotopically organized pattern of activation can be observed in the premotor cortex for the perception of (1) actions performed by others (Buccino et al., 2001) and (2) action-related sentences (Tettamanti et al., 2005). These results have been discussed directly with respect to involvement of the putative human mirror neuron system in understanding the actions of others. We do not observe a differential involvement of frontal mirror neuron areas for comprehension of single action verbs versus abstract verbs. This may be due to several factors: First, the frontal mirror neuron system in monkeys is located within the ventral premotor cortex in area F5. In the monkey, this area is thought to support observation and execution of goal-directed hand–mouth movements. The precise human homologue of monkey area F5 remains unclear; however, Broca's area within the ventral prefrontal cortex is often named a likely candidate (Binkofski & Buccino, 2006). Broca's area in humans is known to be central not only to speech production, but also to many aspects of language comprehension (i.e., Price, 2000). For this reason, Rizzolatti and Arbib (1998) have suggested that language systems

may have evolved atop the mirror neuron system in humans, and thus, language stimuli per se will elicit activation within the system. In the current study, it is therefore possible that both motor and abstract verbs (both natural language stimuli) elicited activation within the ventral premotor cortex and that the direct comparison of these two language conditions yielded no differences. This explanation is possible; however, it relates most directly to Broca's area in the inferior frontal gyrus, and not so directly to activation with the premotor cortex (Brodmann's area 6)—a region in which differential activation has been reported in other language studies (Tettamanti et al., 2005; Hauk et al., 2004).

Second, although involvement of the premotor cortex in action observation is well recognized, the idea of an intransitive, effector-specific organization of the premotor cortex is more controversial. To be more precise, it has been suggested that the premotor cortex may be subdivided along functional rather than effector-specific lines (Koski et al., 2002). This account holds that although hand, mouth, and foot effectors have no distinct representation in the premotor cortex, complex goal-directed action schema involving hand and mouth (i.e., moving hand to mouth) are represented in the premotor cortex. If this is the case, it is perhaps not surprising that our single effector verbs did not elicit activation in the premotor cortex in the manner seen in previous studies (in the Tettamanti et al., 2005, study, sentences describing transitive actions were used as stimuli). In other words, comprehension of a single hand motion verb without a specified target (grasp vs. grasp the cup) may not draw on the target-oriented mirror neuron system in the manner described in previous studies.

A further difference between our results and the results of those studies arguing for involvement of the mirror neuron system in action language comprehension is the lack of any observable difference in parietal lobule for the processing of motor versus abstract verbs. The inferior parietal lobule has been suggested to house PF mirror neurons, which respond to action observation in a manner similar to that seen in the frontal cortex, but which functionally have been suggested to feed the ventral premotor cortex with visual information about perceived transitive actions (Gallese et al., 2002). Therefore, although the inferior parietal lobe may be a fundamental part of the mirror neuron system for understanding goal-directed actions that are visually perceived, their specific role in the understanding of non-visually perceived actions is not documented. In the previously described language study in which action sentences were used (Tettamanti et al., 2005), participants were presented with transitive sentences containing a concrete object. Both the increased visual content of the sentences used in this study (due to the inclusion of an imageable direct object) and the explicit goal-directedness of the sentence materials may have contributed to greater involvement of the parietal cortex.

It is interesting to note that the activation increase observed for motor verbs in the current study is seen bilaterally, whereas that elicited by actual hand motions was strongly left lateralized. The difference between percent signal change observed in the left and right motor cortex in conjunction with verb processing compared with the difference in percent signal change with regard to task performance is highly significant ($p < .001$; see Figure 2), indicating that processing verbs was less lateralized than an actual button press. In the case of the motor task, participants were instructed to press a button on a task box with the pointer finger of the right hand. For this reason, the strong left lateralization of the activation is entirely plausible. In the case of motor verbs, on the other hand, no specific effector is designated. It is perhaps more likely that a right-handed individual will grasp with his or her right hand; however, it is possible for the individual to perform the same action with the left hand. For this reason, the bilateral distribution of the motor cortex activation for language stimuli is quite intriguing. An alternative explanation for the difference in lateralization may be found in the verb stimuli themselves. Although all motor verbs denoted hand actions, many of these actions are generally performed bimanually (i.e., *stricken*, to knit). Clearly, this may alternatively have led to increased involvement of the SM in both hemispheres. Also worthy of notice is the fact that the motor task elicited a very large activation in M1 and only a small activation in S2. S2 activation in this region has been described in other studies in response to stimulation of finger and hand (Ruben et al., 2001). Action word stimuli, on the other hand, elicited a comparatively reduced activation of M1 and comparatively greater activation of S2. We interpret this to reflect less importance of the actual motor programs associated with carrying out described actions, and a greater relevance of understanding the effect, or perception, of theoretically carrying out the described action.

Differences between simple motor and abstract verbs were also observed in cortical areas related to visual imagery, in particular the bilateral medial temporal cortex, extending into the calcarine sulcus. Previous neuroimag-

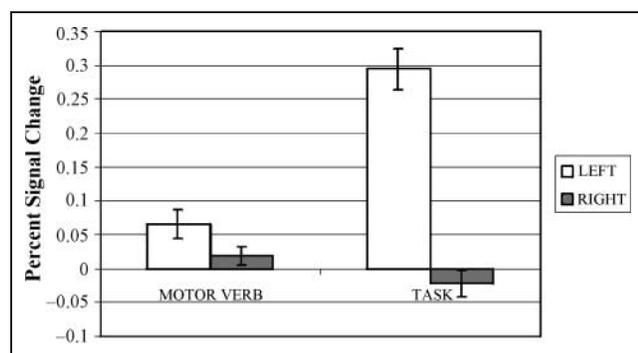


Figure 2. Laterality differences between task performance and motor verb processing.

ing studies have shown increased involvement of the medial temporal cortex for the processing of concrete versus abstract nouns (Fiebach & Friederici, 2003; Wise et al., 2000). In these studies, it is suggested that the left medial temporal lobe in particular supports the representation of concrete word meanings by calling forth aspects of visual imagery. The more imageable concrete items in both studies elicited greater levels of activation in the left medial temporal lobe. In the current study, motor actions, which can also be visualized, elicited greater levels of activation in the medial temporal lobe than abstract actions, which are more difficult to visualize distinctly. We suggest that differences in medial temporal lobe activation may, as in the case of nouns, reflect differences in the imageability of motor versus abstract actions.

No reliable activation increases were observed for simple abstract verbs compared with simple motor verbs. Some authors have postulated that abstract words should rely more heavily on cortical structures in the right hemisphere (Perani et al., 1999). This has been postulated in part based on the higher emotional content of abstract words (i.e., to love, to hate) and the observed dominance of the right hemisphere in emotive processing. Although we see no indication of this in our data, this may be the result of too little overlap in the meaning or emotional content of abstract words in our study. Abstract words were selected that matched motor verbs in frequency and length, and which had a plausible morphologically complex counterpart. These were our critical factors in choosing abstract verb stimuli rather than controlling for overlap in meaning between abstract verbs.

Morphologically Complex Verbs

Given that simple motor verbs showed greater levels of activation than abstract verbs in primary motor areas, we were interested to see whether morphologically complex verbs built on these same stems would show a comparable dissociation. The morphologically complex words in our study all had abstract meanings; however, half of them were built on motor stems. For example, *begreifen* (to comprehend) does not denote a motor act, but is a prefixed form of the simple motor verb *greifen* (to grasp), which clearly denotes a hand movement.

Morphologically complex verbs built on motor stems showed no residual effects of motor verb comprehension. Neither the direct contrast between activation elicited by complex verbs built on motor versus abstract stems nor the analysis of percent signal change provided any evidence for differential activation within the motor system. Crucially, the interaction between the factors stem meaning and complexity was significant, showing that the manipulation of simple verbs alone was sufficient to detect activation differences, whereas the manipulation of complex verb stems had no effect. Our results therefore indicate that the processing of morphologically complex verbs does not proceed along the

same lines as processing of individual components within the words. The overall meaning of the word (in this case the abstract meaning of *begreifen*, to comprehend) appears to be more important in determining how a word is processed than the meaning of its morphological components (i.e., the motor verb *greifen*).

Although differences in motor systems were not detected, one fairly large region of increased activation for complex verbs with motor stems was observed in the right lateral occipitotemporal junction area (see Figure 1). The right lateral occipitotemporal cortex has been discussed to house a brain region known to respond selectively to presentation of body parts, the extrastriate body area (EBA) (Downing, Jiang, Shuman, & Kanwisher, 2001). However, the coordinates presented in these studies are somewhat ventral to those seen in our study. At a slightly reduced threshold ($p < .005$), it is evident that the posterior occipitotemporal activation in our study extends ventrally toward EBA (second peak: 37, -69, 12); however, an interpretation with regard to our experimental manipulation remains difficult. EBA activation for complex verbs with motor stems might be argued to reflect some residual body representation in conjunction with the original motor movement. Indeed, although EBA was traditionally described to be selectively involved in the visual processing of human body parts other than faces, it has recently been shown to respond to goal-directed movements of specific body parts even in the absence of visual input (Astafiev, Stanley, Shulman, & Corbetta, 2004). However, this argument in the context of the current study is rather weak, as simple motor verbs were not seen to elicit greater activation in EBA than simple abstract verbs. Furthermore, an analysis of percent signal change in this area shows no main effect of motor meaning.

Neuroimaging studies on language processing have reported increased involvement of the right posterior temporal cortex in tasks involving comprehension of figurative language and metaphor (St. George, Kutas, Martinez, & Sereno, 1999; Bottini et al., 1994), cohesion and repair (Meyer, Friederici, & von Cramon, 2000), and prosodic processing (Buchanan et al., 2000; for a review, see Bookheimer, 2002). In our study, complex words built on motor verb stems were abstractions of the underlying motor meaning. For example, although *begreifen* (to comprehend) retains no motor meaning itself, it can be figuratively understood as the grasping (*greifen*) of an idea. In the case of complex verbs built on abstract stems, the meaning of complex and simple verbs was often more related than in the case of motor stems. For example, *bedenken* (to consider) is based on the abstract stem *denken* (to think). This abstraction of the stem's literal meaning in the case of verbs built on motor stems may have caused greater activation in the right posterior temporal cortex as compared with comprehension of verbs based on abstract stems.

The driving force behind posterior temporal activation in the current study remains speculative. The result

was certainly not predicted, and no post hoc explanation is entirely satisfactory. Further research will be needed to investigate the true origins of this right temporal activation for complex verbs.

Conclusion

It has been postulated that, phylogenetically, the language system is based on the motor system (Rizzolatti & Arbib, 1998). In the current study, we found a greater involvement of the sensorimotor and secondary somatosensory cortex in processing of simple motor verbs compared with processing of simple abstract verbs. This finding supports a simulation account of action–language understanding focused on motor pathways, but not necessarily involvement of the putative mirror neuron system. Moreover, increased levels of activation were observed for motor verbs in medial temporal lobes. This may reflect the higher imageability of motor actions, such as “to grasp,” compared with abstract actions, such as “to think.” On the other hand, no differences in the motor circuitry could be detected when the processing of complex verbs with motor and abstract stems conveying a figurative meaning were compared. This indicates that the meaning of a complex verb is not necessarily grounded in a full representation of its component parts. Unexpectedly, more activation was seen for the processing of complex verbs with motor stems in the right lateral temporooccipital junction area. Although we can reach no conclusive comment on the basis of these results alone, we suggest that involvement of this brain region may reflect either an increased awareness of body representation for verbs that have some motor component, or use of figurative language in transferring the motor meaning of a verb such as *greifen* (to grasp) to an abstract concept such as *begreifen* (to comprehend). The different activation patterns found for simple and complex verbs suggest that the relation between the language system and motor system is less direct for abstract verbs derived from motor verbs than for motor verbs themselves.

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Reprint requests should be sent to Shirley-Ann Rüschemeyer, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1a, 04103 Leipzig, Germany, or via e-mail: ruesch@cbs.mpg.de.

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