The Neural Career of Sensory-motor Metaphors

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Abstract

■ The role of sensory-motor systems in conceptual understanding has been controversial. It has been proposed that many abstract concepts are understood metaphorically through concrete sensory-motor domains such as actions. Using fMRI, we compared neural responses with literal action (Lit; *The daughter grasped the flowers*), metaphoric action (Met; *The public grasped the idea*), and abstract (Abs; *The public understood the idea*) sentences of varying familiarity. Both Lit and Met sentences activated the left anterior inferior parietal lobule, an area involved in action planning, with Met sentences also activating a homologous area in the right hemisphere, relative to Abs sentences. Both Met and Abs sentences activated the left superior temporal regions associated with abstract language. Importantly, activation in primary motor and biological motion perception regions was inversely correlated with Lit and Met familiarity. These results support the view that the understanding of metaphoric action retains a link to sensory-motor systems involved in action performance. However, the involvement of sensory-motor systems in metaphor understanding changes through a gradual abstraction process whereby relatively detailed simulations are used for understanding unfamiliar metaphors, and these simulations become less detailed and involve only secondary motor regions as familiarity increases. Consistent with these data, we propose that anterior inferior parietal lobule serves as an interface between sensory-motor and conceptual systems and plays an important role in both domains. The similarity of abstract and metaphoric sentences in the activation of left superior temporal regions suggests that action metaphor understanding is not completely based on sensory-motor simulations but relies also on abstract lexical-semantic codes. ■

INTRODUCTION

The relationship between sensory-motor and conceptual systems of the brain has been the focus of intense debate in recent years (Barsalou, 2008; Mahon & Caramazza, 2008; Pulvermuller, 2005). Neuroimaging, behavioral, and patient studies suggest a closer link between these systems than previously recognized (Kemmerer, in press; Aziz-Zadeh & Damasio, 2008; Fischer & Zwaan, 2008). The precise nature of the relationship between these systems, however, remains unclear. Weak embodiment views suggest engagement of sensory-motor systems only when concepts are transparently related to physical action. In contrast, strong embodiment assigns sensory-motor systems a pervasive role in comprehension, including more abstract concepts.

Action metaphors (e.g., *grab the chance* or *grasp an idea*), which convey abstract concepts via analogy to concrete concepts, provide an interesting opportunity to study the relationship between these two systems. Engagement of sensory-motor systems even when action language is clearly figurative would suggest a particularly close relationship between these systems, consistent with theories that many abstract concepts are understood through analogies to sensation and action (Bergen, 2007; Gibbs, 2006; Lakoff & Johnson, 1980, 1999).

The few imaging studies on figurative action language have yielded somewhat inconsistent results. Aziz-Zadeh, Wilson, Rizzolatti, and Iacoboni (2006) found somatotopic activation in the premotor cortex for literal action sentences, but not for idiomatic phrases ("biting off more than you can chew"). Boulenger, Hauk, and Pulvermuller (2009) found somatotopic activation for figurative and literal action sentences involving leg and arm verbs. Raposo, Moss, Stamatakis, and Tyler (2009) found activation in premotor/motor regions for isolated action verbs and to a lesser extent for literal action sentences, but not for figurative sentences using action verbs. Three studies have also shown activation in or near motion processing area MT+ for literal as well as figurative or fictive motion sentences ("The man fell under her spell"; "The bridge jumped over the brook") compared with nonmotive sentences (Saygin, McCullough, Alac, & Emmorey, 2010; Chen, Widick, & Chatterjee, 2008; Wallentin, Lund, Ostergaard, Ostergaard, & Roepstorff, 2005).

To elucidate the relationship between sensory-motor and conceptual systems and to adjudicate between weak and strong views of embodiment, we compared BOLD responses to metaphoric action sentences with two types of nonmetaphoric sentences—literal action and abstract. We varied the familiarity of each sentence type to investigate

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the modulation of activity in sensory-motor regions. In many studies of metaphors, processing difficulty has been a common confounding variable, in that metaphoric stimuli tend to be more difficult to process (as indexed by response latencies) than literal control stimuli. Additional activation resulting from processing more difficult stimuli can be mistaken as activation specific to metaphors (Schmidt & Seger, 2009; Yang, Edens, Simpson, & Krawczyk, 2009). We carefully controlled for processing difficulty and other confounding variables such as syntactic structure and sentence length, which can also lead to activation in sensory-motor regions. We hypothesized that relatively unfamiliar (literal and metaphoric) action language engages sensory-motor systems because comprehension of such expressions involves relatively detailed simulations of literal actions. As the expression becomes more familiar and conventionalized, the reliance on sensory-motor simulation diminishes. Alternative hypotheses are that sensory-motor systems are not engaged at all for metaphoric expressions or are engaged regardless of familiarity.

METHODS

Participants

Participants in the fMRI experiment were 22 healthy adults (11 women; average age = 24 years, range = 18–33 years; average years of education = 16 years, range = 12–23 years), with no history of neurological impairment. One additional participant was removed because of activations in the three main contrasts that were more than two standard deviations away from the group mean. Participants were native speakers of English and were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Informed consent was obtained from each participant before the experiment, in accordance with a protocol sanctioned by the Medical College of Wisconsin Institutional Review Board. Participants were paid for participation.

Stimuli

Stimuli were sentences divided into three main conditions: literal action (Lit), metaphoric action (Met), and abstract (Abs). The stimuli were constructed in triples consisting of one sentence from each condition, with the same syntactic form (examples in Table 1; complete listing provided in the Supplemental Material). The Lit sentence used a

Table 1. Example Stimuli

Literal	*The daughter grasped the flowers*	*The thief bashed the table*
Metaphor	*The jury grasped the concept*	*The council bashed the proposal*
Abstract	*The jury understood the concept*	*The council criticized the proposal*

hand/arm action verb to depict a physical action. The corresponding Met sentence used the same verb in a figurative manner, such that no physical action was described. The Abs sentence used an abstract verb to convey a meaning similar to that of the Met sentence. The agent in each sentence was chosen to imply either a literal or an abstract/metaphoric interpretation of the verb. Met and Abs sentences always used the same agent. This agent was an entity that makes literal physical actions unlikely (e.g., *the scandal*, *the crime*, *the government*). The Lit sentences, in contrast, always used a person (*the teacher, the doctor*) as an agent. For example, consider the fragments "The captain lifted…" and "The government lifted…." In the first example, when *lifted* is encountered, both physical action and figurative lifting (e.g., of a ban) are possible. In the second example, it is clear the physical action interpretation is infelicitous.

Twenty-seven action verbs were used three times each to create 81 Lit and Met sentences. In addition, there were 81 Abs sentences, 81 nonsense sentences (e.g., *The wedding strummed the introduction*, created by combining action and abstract verbs with inappropriate nouns), and 81 nonword sentences of the same form. Nonword sentences were composed of pronounceable nonwords created using the MCWord database (http://www.neuro.mcw.edu/mcword/) and the ARC nonword database (Rastle, Harrington, & Coltheart, 2002). Finally, there were 54 Filler sentences that used variable syntax (e.g., *All lawyers went on strike*). These were used to obscure the triplet construction of the stimuli and to provide syntactic variability in the stimulus set.

Stimulus Norming

One of our principal goals was to equate the three main conditions with respect to processing difficulty to remove the possible confound between figurativeness and difficulty. Numerous factors can affect the difficulty of processing sentences. In addition to word frequency, the frequency of the particular verb–noun combination (e.g., "grasp the idea" vs. "grasp the procedure") and the frequency and familiarity of the verb in a metaphoric versus literal sense can affect automaticity of comprehension. As described in the next section, stimuli were pretested using a meaningfulness judgment task, which reflects the combined effects of such factors.

A two-step procedure was used in developing the stimuli. First, a large set of sentences was prepared by combining action and abstract verbs with appropriate nouns to create Lit, Met, and Abs sentences for use in a preliminary experiment. Six participants made a meaningfulness judgment ("makes sense" or "does not make sense") for each sentence by pressing one of two buttons on a response pad. The sentences were presented in two parts, as shown in Figure 1. The first screen displayed a noun phrase (e.g., "The public") for 500 msec. This was replaced by the verb phrase (e.g., "grasped the idea") on the second

Figure 1. The presentation of the stimuli. The first noun phrase of the sentence was displayed for 500 msec, followed by the remaining sentence for 1300 msec. The sentences were separated by variable intervals.

screen, displayed for 1300 msec. This two-part presentation was used to ensure that the first noun phrase, which suggests the literal or metaphoric/abstract interpretation of the verb, was read first. Consistent with previous studies, Lit sentences yielded faster responses than Met and Abs sentences. Sentences were then modified to reduce these differences. (e.g., by using a more familiar noun–verb combination to reduce the difficulty of a metaphoric sentence or by using a less familiar noun–verb combination to replace literal sentences that were very easy). In modifying the sentences, we also reduced differences in word frequencies and in the number of phonemes, letters, and syllables. The revised set of stimuli was then tested in the meaningfulness judgment experiment to verify that the differences between conditions in RT were indeed minimized.

Meaningfulness Judgment

Participants in the meaningfulness judgment experiment were 24 adults (20 women; average age = 19 years, range = 18–21 years; average years of education = 12 years, range = 12–14 years). They were native speakers of English and did not participate in the fMRI experiment.

Participants made a meaningfulness judgment (meaningful/not meaningful) for each sentence, presented in two parts as in the preliminary experiment earlier. Participants were asked to judge the meaningfulness of the sentence as a whole by pressing one of two buttons.

As shown in Table 2, there were no significant differences between Met, Lit, and Abs conditions, whereas the nonsense condition had longer RTs than all of the other conditions (all p values < .0001).

Familiarity Rating

The familiarity of sentences can affect speed and accuracy of processing. Although familiarity differences would be expected to affect latencies in the meaningfulness judgment task mentioned earlier, we also collected familiarity ratings to enable a more direct assessment of familiarity effects in the imaging analysis.

Participants in the familiarity rating experiment were 28 adults (16 women; average age = 19 years, range = 18–21 years; average years of education = 13 years, range = 12–16 years). They were native speakers of English and did not participate in the fMRI experiment.

For each sentence, participants rated each sentence on a scale of 1 (*not at all familiar*) to 7 (*very familiar*). The results are shown in Table 2. Lit and Abs stimuli differed in familiarity (p < .02), with no other reliable differences between types.

As expected, the meaningfulness judgment RTs and the familiarity ratings were correlated (Pearson's $r = -0.52$, p < .0001).

Action Association Rating

We intentionally selected verbs that were clearly associated with actions in the Met/Lit conditions, whereas verbs used in the Abs condition were relatively abstract. It is possible, however, that some of these "abstract" verbs also have some association with actions. Action association ratings were collected to assess whether abstract verbs were in fact less associated with actions than Met/Lit verbs. Participants in this rating experiment were 14 adult, native speakers of English (7 women; average age = 20 years, range = 18–22 years; average years of education = 13 years, range = 12–15 years), who did not participate in the fMRI experiment. Participants rated each verb, preceded by *to* (e.g., *to understand*) on a scale of 1 (*not associated with action at all*) to 7 (*very much associated with action*). The mean for Met/Lit verbs was 6.17 (*SD* = 0.42) and for Abs verbs was 3.62 (*SD* = 0.70), a difference that was highly significant (p < .0001).

Table 2. The Mean (*SD*) RTs in the Meaningfulness Judgment Task and the Familiarity Ratings (on a Scale of 1 to 7) for Various Conditions

Condition	n	RT	Familiarity
Metaphor	81	1277 (165)	5.24 (0.77)
Literal	81	1241 (151)	4.97 (1.04)
Abstract	81	1265 (179)	5.37 (0.87)
Nonsense	81	1399 (167)	–
Pseudoword	81	723 (138)	–
Filler	54	1234 (232)	–

fMRI Tasks

The sentences in the imaging experiment were presented in two parts, as in the meaningfulness judgment experiment (Figure 1). Participants were instructed to read each sentence and to make a covert meaningfulness decision. A covert task was used to prevent strong activation of the motor cortex by a manual or vocal response. The order of sentences was pseudorandomized and the interval between the sentences was varied to allow optimal statistical separation of the hemodynamic response to each condition. The sentences were divided into nine runs lasting approximately 5 min each. To encourage attentiveness, participants were also tested on a recognition task after each run. Fourteen sentences were shown, and for each sentence, participants indicated by pressing one of two buttons whether they had seen the sentence in the preceding run. On average, half of the 14 sentences were taken from the previous run, whereas the others were not in the experiment. At the end of each run, participants were also asked to rate their attentiveness during the task on a scale of 1 (*not attentive at all*) to 10 (*very attentive*). Instructions and practice with all tasks were provided outside the scanner before the scan, and the participants were informed that the recognition test would be administered after each run.

Motor Localizer Task

After the sentence runs, a localizer task was used to locate hand motor regions of the brain, using a block design. Participants performed a repeating sequence of actions— make a fist, turn the palm up, touch thumb and fifth digit—with their left hand or right hand or rested. Before scanning, these actions were demonstrated by the experimenter outside the scanner, without using verbal labels, and the subjects were asked to repeat these actions, in the same sequence, for practice and verification of accuracy. In the scanner, the instructions "left," "right," or "rest" were displayed at the beginning of each block. Each block was 18 sec long, and three blocks of each condition were presented in a pseudorandomized order.

Image Acquisition and Analysis

A 3-T GE Excite scanner was used to acquire images. One volume of T2*-weighted, gradient-echo, echo-planar images (echo time = 25 msec, flip angle = 77°, NEX = 1) was acquired every 1.8 sec. Visual sentence presentation was time locked with the beginning of an acquisition. Volumes were composed of 30 axially oriented 3.5-mm slices with a 0.5-mm interslice gap, covering the whole brain, with field of view = 240 mm and matrix = 64 × 64, resulting in 3.75 × 3.75 × 4-mm voxel dimensions. Anatomical images of the entire brain were obtained using a three-dimensional spoiled gradient-echo sequence with 0.94 × 0.94 × 1-mm voxel dimensions.

The AFNI software package (Cox, 1996) was used for image analysis. Within-subject analysis involved spatial coregistration (Cox & Jesmanowicz, 1999) and registration of functional images to the anatomy (Saad et al., 2009). Runs were removed from the analysis if d' performance on the recognition test after a run was less then 1 or if the self-reported attentiveness rating was 5 or less; 11 runs (5.6%) were removed in this manner. Voxel-wise multiple linear regression was performed with reference functions representing each condition. In addition, familiarity ratings for each stimulus (see Stimulus Norming section) were used to create within-condition familiarity regressors for the Lit, Met, and Abs conditions. Mean-centered regressors for the number of syllables and phonemes in each sentence were used as additional item-wise regressors to account for differences because of these variables. A standard hemodynamic response function convolved with the reference functions and its temporal derivative were used. A correction for amplitude bias was applied using the method described by Calhoun, Stevens, Pearlson, and Kiehl (2004). Six motion parameters and the signal extracted from the ventricles, segmented using the FSL *fast* program (Zhang, Brady, & Smith, 2001), were included as noise covariates of no interest. General linear tests were conducted to obtain the Lit–Abs, Met–Lit, and Met–Abs contrasts and the Familiarity × Condition interactions.

The individual statistical maps and the anatomical scans were projected into standard stereotaxic space (Talairach & Tournoux, 1988) and smoothed with a Gaussian filter of 5-mm FWHM. In a random effects analysis, group maps were created by comparing activations against a constant value of 0. The group maps were thresholded at voxel-wise $p < .01$ and corrected for multiple comparisons by removing clusters smaller than 1000 µl to achieve a mapwise corrected two-tailed $p < .05$. The cluster threshold was determined through Monte Carlo simulations that estimate the chance probability of spatially contiguous voxels exceeding the voxel-wise p threshold. The analysis was restricted to a mask that excluded areas outside the brain as well as deep white matter areas and ventricles. The data from the motor localizer scan were analyzed as a block design in a similar way. To further examine motor areas, two ROIs were defined. One used the area activated by the motor localizer task as an ROI, and the other used primary motor and sensory cortex (M1 and S1) as defined by the HMAT atlas (Mayka, Corcos, Leurgans, & Vaillancourt, 2006). Small volume correction was applied in these ROIs to achieve corrected $p < .05$.

RESULTS

The mean d' in the postrun test was 2.56 ($SD = 0.74$), suggesting that the participants were attentive to the stimuli during the scans. We first describe the fMRI results for the contrasts between the three main conditions, Lit, Met, and Abs. The results are displayed on an inflated brain surface

using Caret (Van Essen et al., 2001). A complete listing of the activated areas with coordinates is provided in the Supplemental Material (Part I).

Literal–Abstract

The areas activated to a greater extent by the Lit condition relative to the Abs condition included the left anterior inferior parietal lobule (aIPL; including supramarginal gyrus and postcentral sulcus), the left parahippocampal and fusiform gyri, the left precuneus, the left posterior middle and inferior temporal gyrus and lateral occipital gyrus, the left superior frontal gyrus, the left orbitofrontal cortex [OFC], the bilateral cerebellum and thalamus, and the right hippocampus and fusiform gyrus (Figure 2A).

Abs sentences activated the left STS and the anterior superior temporal gyrus, the cuneus, and the right angular gyrus.

Metaphor–Abstract

The Met condition activated the left aIPL, the Rolandic operculum, the superior parietal gyrus, and the superior frontal gyrus. The cerebellum and the thalamus were activated bilaterally. The right aIPL, the parietal operculum, the insula, and the parahippocampal gyrus were also activated (Figure 2B). No areas were activated to a greater extent for the Abs sentences.

Metaphor–Literal

Compared with the Lit sentences, the Met sentences activated the left anterior and posterior cingulate gyrus, the cuneus, the STS, and the temporal pole. In the right hemisphere, the aIPL, the parietal operculum, and the superior parietal gyrus were activated (Figure 2C).

The Lit condition activated the left parahippocampal and the fusiform gyrus relative to the Met sentences.

Figure 2. Areas activated by condition contrasts. Yellow-orange scale shows positive activation (greater for the first condition in the contrast), and blue-cyan scale shows negative activation (greater for the second condition). L = left hemisphere; R = right hemisphere.
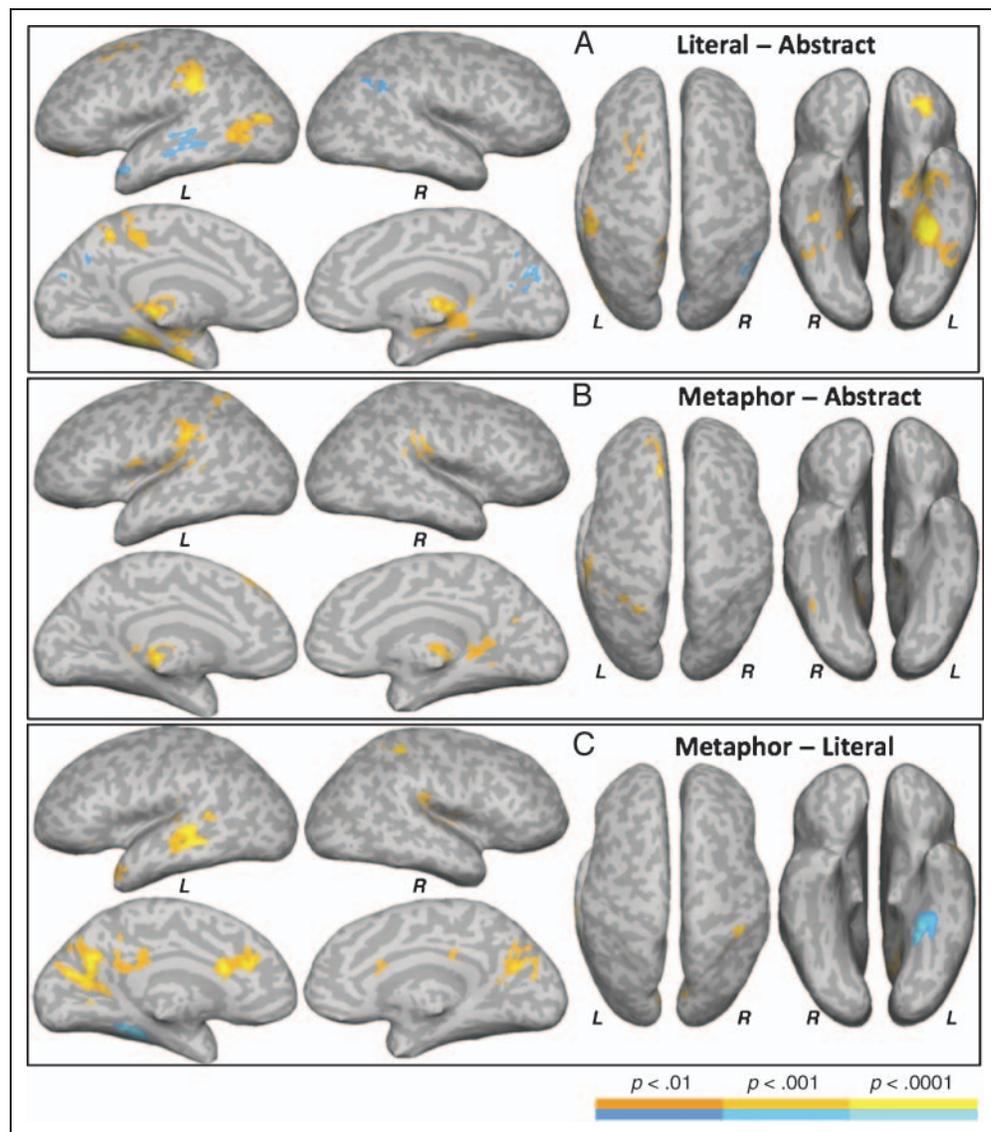
Correlations with Familiarity

To assess the effects of sentence familiarity on the activation, we used the familiarity rating as a condition-wise regressor in the analysis. Correlations with familiarity can pinpoint not only areas involved in semantic processing but also areas modulated because of general processing difficulty. To isolate, to the extent possible, activation modulation because of semantic factors, we computed the Familiarity × Condition interactions. The regions responding only to general difficulty and task load effects should be modulated similarly in all three conditions and therefore would not show interactions. Indeed, middle and inferior frontal lobe regions, commonly associated with task difficulty effects, were negatively correlated with familiarity in each condition (see Supplemental Material, Part II) and were absent from the interaction maps. In addition, because our hypotheses concern correlations with Lit or Met familiarity, we applied a mask to the interaction maps that included only voxels that showed a significant correlation with familiarity in Lit or Met conditions.

Literal–Abstract × Familiarity

All the regions in this interaction showed negative correlation with familiarity for Lit sentences and greater negative correlation for Lit than for Abs sentences (cyan and green in Figure 3A). They included the left anterior inferior

Figure 3. The overlap of condition contrasts, the Condition × Familiarity interactions, and the motor localizer. Interactions in panels A and B show significantly greater negative correlation to familiarity for Lit and Met conditions, respectively. Panel C shows greater positive correlation for the Met condition. Talairach *y* coordinates are indicated in the upper left corner of each slice. Stereotaxic *x* and *z* axes are shown in white.
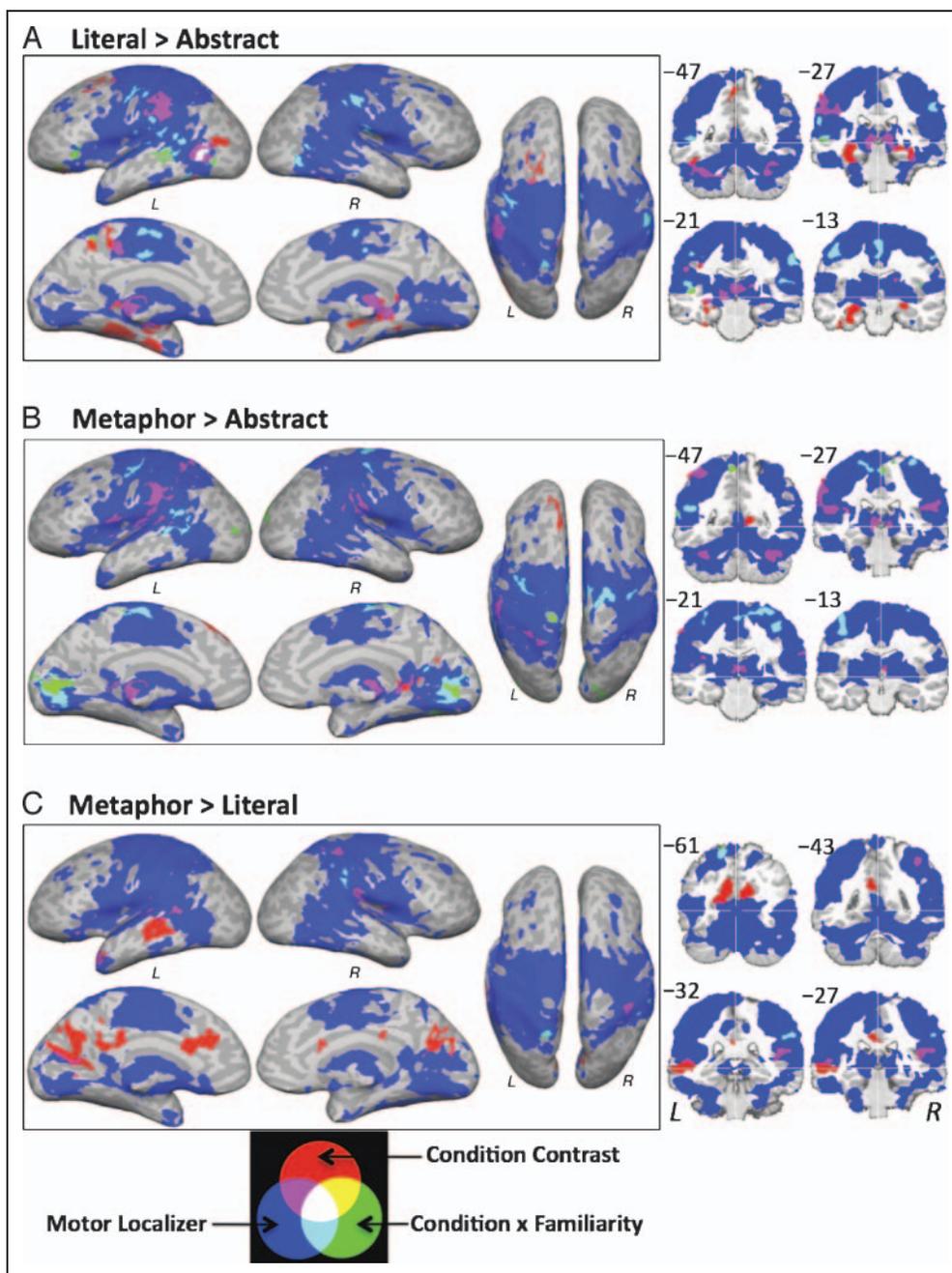
Table 3. A Summary of the Main Results

Area	Contrast				Overlap with Localizer
	Lit > Abs	Met > Abs	Lit–Abs × Fam	Met–Abs × Fam	
L dorsomedial prefrontal	x				
L parahippocampal/fusiform g	x				
L aIPL	x	x			x
Bilateral thalamus	x	x			x
Bilateral cerebellum	x	x			x
L posterior middle temporal gyrus	x		x		x
Bilateral parietal operculum		x	x		x
R aIPL		x	x		x
L superior parietal lobule		x	x		x
R posterior middle temporal gyrus			x		x
L central sulcus			x	x	x
L posterior superior temporal sulcus			x	x	x
Bilateral SMA			x	x	x
R central sulcus				x	x
Bilateral lingual gyrus				x	x

"x" indicates regions that are activated or correlated with familiarity or overlap with the localizer activation.

frontal gyrus, central sulcus, superior parietal gyrus, and posterior STS; the right aIPL; and the bilateral posterior middle and inferior temporal gyrus, parietal operculum, and SMA.

Metaphor–Abstract × Familiarity

Similar to the previous interaction, all areas here showed negative correlations for Met sentences and greater negative correlations for Met than for Abs sentences. These areas included the left posterior STS and the bilateral central sulcus, SMA, lingual gyrus, and cuneus (cyan and green in Figure 3B).

Metaphor–Literal × Familiarity

The right supramarginal gyrus and the left superior parietal gyrus showed a significant interaction. The right supramarginal gyrus showed a positive correlation with familiarity for Met, whereas the left superior parietal gyrus was negatively correlated in the Lit condition (cyan and green in Figure 3C).

Identical analyses were also carried out using RTs rather than familiarity ratings as regressors. No Condition × RT interactions in sensory-motor regions were found after identical application of corrections for multiple comparisons. This suggests that these interactions are unlikely to be due to differences only in the length of action simulations or some form of preresponse motor readiness

(although the latter is unexpected in any case because no responses were made during scanning).

Overlap with Localizer

Figure 3 also shows the overlap of the areas activated by the hand localizer task, the condition contrasts, and the Condition × Familiarity interactions. Activations in the central sulcus, aIPL, posterior STS, posterior middle and inferior temporal gyrus, opercular regions, SMA, thalamus, and cerebellum overlapped the localizer activation (magenta, cyan, and white colors). In contrast, activations in the dorsomedial prefrontal region, parahippocampal and fusiform gyrus, middle STS, and posterior cingulate did not overlap the localizer (red and green colors), and occipital regions partly overlapped. The left posterior middle/inferior temporal region was the only area to show an overlap between the condition contrasts and the familiarity interactions (white color).

A summary of the main results is presented in Table 3, where areas commonly and differentially activated between the contrasts and the familiarity interactions can be seen.

DISCUSSION

We presented participants with literal action, metaphoric action, and abstract sentences to examine the engagement of sensory-motor areas during their comprehension. We

asked whether sensory-motor areas are engaged even when processing metaphoric action sentences, and whether this engagement changes with sentence familiarity.

Literal Sentences

The Lit > Abs contrast produced results similar to a previous study (Desai, Binder, Conant, & Seidenberg, 2010). The aIPL region, overlapping the localizer activation, is a secondary sensory-motor area associated with action planning and complex hand–object interaction, as suggested by both imaging and lesion studies. It is structurally connected to posterior middle temporal and inferior frontal gyri, forming a tool-use network (Ramayya, Glasser, & Rilling, 2009), and is strongly linked to action performance, imitation, and semantics (Binder, Desai, Graves, & Conant, 2009; Buxbaum, Kyle, & Menon, 2005; Glover, 2004; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003; Haaland, Harrington, & Knight, 2000; for further discussion, see Desai et al., 2010). Peeters et al. (2009) compared human and trained as well as untrained monkeys as they observed actions performed using simple tools and found that aIPL was uniquely activated in humans. They proposed that this region has evolved only in humans to subserve complex actions. The present results suggest that this region may be unique to humans partly because it serves as an interface between language and action, playing a role in both domains.

Parahippocampal gyrus and surrounding cortex is most closely associated with episodic and spatial memory (Squire, Stark, & Clark, 2004). Several studies report activation in this region for processing actions, tools, or concrete objects, for example, for simulating rehearsed actions (Cross, Hamilton, & Grafton, 2006) and recognizing and naming actions (Tranel, Martin, Damasio, Grabowski, & Hichwa, 2005; Decety et al., 1997), for artifacts compared with living things (Martin, 2007), and for concrete compared with abstract words (Binder, 2007). These findings suggest that activation of this region for Lit sentences reflects the retrieval of contextual and spatial information related to actions and the concrete nouns in these sentences.

The posterior middle and inferior temporal gyri are associated with linguistic knowledge about tools and actions (Binder et al., 2009; Martin, 2007). This activation, overlapping with the localizer, was immediately anterior to the visual motion processing area MT/MST, suggesting a role in more abstract motion processing (Chen et al., 2008; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005).

The cerebellar and precuneus activation overlapped the localizer, whereas the dorsomedial prefrontal activation did not. This latter region is frequently activated during processing of concrete semantic concepts and is thought to play a role in their retrieval (Binder et al., 2009).

Thus, the pattern of activation for Lit sentences suggests a role for sensory-motor systems in their comprehension. This activation is consistent with the view that understanding such sentences involves action simulation, but this simulation is at a relatively abstract level, engaging higher level action planning and motion perception areas.

Metaphoric Sentences

Although the meaning conveyed by metaphoric sentences is abstract, an analogy with a concrete domain is used to convey the meaning. Some theorists have suggested that mental simulation is used to understand such action metaphors (Bergen, 2007; Gibbs, 2006), and thus the metaphoric meaning is "grounded" in the literal meaning.

The Met > Abs contrast activated regions associated with sensory-motor processing (the aIPL and the bilateral cerebellum), which were also activated by the Lit sentences and localizer task. Notably, Met and Lit sentences activated these regions to a similar extent and hence were absent from the Met–Lit comparison. The superior parietal lobule was activated additionally for metaphors, which is associated with control of action and computation of dynamic spatial information (Glover, 2004). If the activation of the left aIPL and bilateral cerebellum is taken as an index of sensory-motor processing during sentence comprehension, this suggests that the understanding of these metaphors is not abstracted away from their sensory-motor origins. As with literal action sentences, a (relatively abstract) motoric simulation is used in comprehension of action metaphors. *Grasping an idea* is understood much like *grasping a handle* is, using meanings that are based on sensory-motor representations.

An alternative interpretation of these activations is that verbs such as *grasp* are homonyms with two independent meanings, one related to the physical action and one meaning "to understand." Both meanings are initially activated during sentence processing, and the incongruent meaning is later suppressed. In this view, the activation of sensory-motor areas during Met simply represents the activation of the incongruous literal meaning, and the metaphoric meaning is abstract and unrelated to sensory-motor systems. However, a number of behavioral studies suggest that when processing homonymous or polysemous words in sentences, incongruous meanings are either not activated at all or suppressed within approximately 250–300 msec (Glucksberg, 2001; Pynte, Besson, Robichon, & Poli, 1996; Seidenberg, Tanenhaus, Leiman, & Bienkowski, 1982; Onifer & Swinney, 1981). The initial brief activation of an unrelated meaning should result in a signal that is weaker than the signal from sustained activation of the literal meaning for the Lit sentence, integrated over the sentence, whereas here the two signals were of similar magnitude. Furthermore, the initial noun phrases of the sentences were selected to prime an abstract or concrete meaning of the verb, and this property promotes rapid suppression of incongruous meanings.

Compared with both Lit and Abs conditions, the right aIPL was also activated for metaphors. The right hemisphere activation can be interpreted in terms of the fine-coarse coding theory of Beeman et al. (1994). It suggests that

the RH maintains a wider "semantic field," containing alternative meanings or distantly related features, whereas the left hemisphere processes the dominant meanings or features. The RH activation may therefore represent access to a wider variety of meanings to subserve metaphor interpretation.

The posterior cingulate activation in the Met > Lit contrast is found in many semantic studies (Binder et al., 2009). This region has been identified as a connectivity hub (Buckner et al., 2009; Sporns, Honey, & Kotter, 2007). Hubs contain disproportionally numerous connections and are hypothesized to integrate diverse informational sources. The involvement of posterior cingulate in metaphor comprehension may be related to integrating information from target and base domains.

Met sentences also activated the left middle STS, similar to the Abs sentences. This activation, which did not overlap with the localizer, could reflect the computation of abstract meaning conveyed by the Met sentences. This similarity between Abs and Met conditions suggests that sensory-motor metaphors are not represented entirely in a sensory-motor format. Although motoric simulations may be used to understand such metaphors, an abstract component is also present.

Abstract Sentences

The activation of the left middle and anterior STS for Abs sentences is consistent with a number of studies comparing abstract to concrete stimuli (for a review, see Binder, 2007). According to Paivio's (1986) dual coding theory, abstract information is represented mainly through verbal associations with other words. Andrews, Vigliocco, and Vinson (2009) distinguish between *distributional* and *experiential* statistics upon which representations are built. With limited experiential (sensory-motor) features, abstract concepts may rely heavily on distributional information (i.e., statistical information about word co-occurrences, also captured by computational models such as latent semantic analysis; Landauer & Dumais, 1997). For example, a representation of *justice* may be built gradually through associations with concepts such as *fair*, *law*, *good*, *court*, *right*, *truth*, and so forth. The left-dominant temporal activation is also consistent with this view, given the role of this area in lexical phonology. Further support for this view comes from aphasic patients with stroke in the left peri-sylvian region, who generally show greater processing deficits for abstract words (Franklin, Howard, & Patterson, 1995; Katz & Goodglass, 1990; Goodglass, Hyde, & Blumstein, 1969).

Correlations with Familiarity

Activation in a number of sensory-motor regions, overlapping with the localizer activation, was negatively correlated with familiarity for both Lit and Met sentences, even after accounting for the increased general difficulty of processing less familiar sentences. Notably, SMA and primary motor areas in the central sulcus—in the LH for Lit and

bilaterally for Met—were correlated with familiarity. The left posterior STS was also correlated with both Lit and Met familiarity and is implicated in biological motion (Saygin, 2007; Grossman & Blake, 2002). This suggests that to understand less familiar action-related language, a relatively detailed simulation is used that relies on primary motor areas, and this is true even for metaphoric language in which no literal action is implied. As familiarity increases, the abstractness of simulation also increases, involving only the secondary action-planning region (aIPL) that was activated regardless of familiarity. Moreover, it is possible that at the highest end on the familiarity scale that was not examined here, as in the case of idioms or the pervasive "time is space" metaphors, sensory-motor systems are engaged to a lesser extent or not at all (Kemmerer, 2005).

Notably, several areas that were *activated* consistently for Met—bilateral parietal operculum, left superior parietal gyrus, and right aIPL—were *correlated* with familiarity for Lit sentences. This suggests that metaphor processing is not fundamentally different from literal sentence processing but is similar to processing relatively unfamiliar sentences whose comprehension is more effortful.

Bowdle and Gentner (2005) proposed the "career of metaphor" hypothesis to explain the trajectory of metaphor processing as metaphors are conventionalized. According to this hypothesis, metaphors are initially understood by comparison or similarity matching between base and target domains. As the metaphor becomes more familiar, there is a switch to categorization mode in which abstract metaphoric meanings of the base concept are activated, and the appropriate meaning is assigned to the target. Our results suggest a different picture, at least for sensory-motor metaphors. The target is understood in terms of the base domain through motoric simulations, which gradually become less detailed while still maintaining their roots in the base domain. The negative correlation of primary motor areas with metaphor familiarity and the activation of secondary motor regions for metaphors regardless of familiarity suggest a gradual abstraction rather than a switch in the processing mode.

The right supramarginal gyrus was correlated positively with Met familiarity. For more familiar metaphors, this area may play a role in using the wider RH semantic field to efficiently combine words in phrases such as *grasp an idea*. For less familiar metaphors, such automatic combination is not possible, and more on-line simulation is necessary. This view is supported by a study in our laboratory in which this area was activated for meaningful two-word phrases such as *flower girl* relative to difficult-to-interpret combinations such as *girl flower* (Graves, Binder, Desai, Conant, & Seidenberg, 2010).

Although our aim was to investigate the effects of variations in familiarity, other factors, such as amount of personal experience with specific actions (Lyons et al., 2010), amount of physical effort (Moody & Gennari, 2010) and force (Frak, Nazir, Goyette, Cohen, & Jeannerod, 2010) required for an action, and semantic context (van Dam,

Rueschemeyer, Lindermann, & Bekkering, 2010), may also modulate sensory-motor areas. The effects of these variables and their interactions with familiarity await further research.

Conclusions

A comparison of literal action, metaphoric action, and abstract sentences revealed activation of secondary sensory-motor areas including the left aIPL, involved in action planning, for literal and metaphoric action sentences. The right aIPL was additionally involved for metaphors. This supports the view that the understanding of metaphoric action retains a link to sensory-motor systems involved in action performance. The aIPL may be an interface area that serves an important role in both conceptual and action domains. Activation of primary motor and biological motion perception areas was inversely correlated with metaphor familiarity, which is consistent with the view that a gradual abstraction process, whereby relatively detailed simulations are used for understanding unfamiliar metaphors, and that these simulations become less detailed and involve only secondary regions as the familiarity increases. The similarity of abstract and metaphoric sentences in the activation of the left temporal regions suggests that action metaphor understanding is not completely based on sensory-motor systems but contains an abstract element.

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