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 than many abstract concepts are understood metaphorically through concrete sensory-motor domains such as actions. Using fMRI, we compared neural responses to 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 partial lobule (aIPL), 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 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 aIPL 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 (Pulvermuller, 2005; Barsalou, 2008; Mahon and Caramazza, 2008). Neuroimaging, behavioral, and patient studies suggest a closer link between these systems than previously recognized (Aziz-Zadeh and Damasio, 2008; Fischer and Zwaan, 2008; Kemmerer, in press). 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 (Lakoff and Johnson, 1980, 1999; Gibbs, 2006; Bergen, 2007).

The few imaging studies on figurative action language have yielded somewhat inconsistent results. Aziz-Zadeh et al. (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 et al. (2009) found somatotopic activation for figurative and literal action sentences involving leg and arm verbs. Raposo et al. (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 to non-motive sentences (Wallentin et al., 2005; Chen et al., 2008; Saygin et al., 2010).

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 non-metaphoric sentences – literal action and abstract. We varied the familiarity of each sentence type to investigate 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 and Seger, 2009; Yang et al., 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; average years of education 16, range 12–23), with no history of neurological impairment. One additional participant was removed due to activations in the three main contrasts that were more than two s.d. 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 prior to 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 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 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 a physical action as well as 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. Additionally, 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 et al., 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 vs. literal sense can affect automaticity of comprehension. As described below, stimuli were pre-tested 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 Fig. 1.

The first screen displayed a noun phrase (e.g., "The public") for 500 ms. This was replaced by the verb phrase (e.g., "grasped the idea") on the second screen, displayed for 1300 ms. 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 below, to verify that the differences between conditions in response time (RT) were indeed minimized.

Meaningfulness Judgment—Participants in the meaningfulness judgment experiment were 24 adults (20 women; average age 19 years, range 18–21; average years of education 12, range 12–14). 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 above. 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, while the Nonsense condition had longer RTs than all of the other conditions (all $p < 0.0001$).

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 above, 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; average years of education 13, range 12–16). 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 ($p < 0.02$), with no other reliable differences between types.

As expected, the Meaningfulness Judgment RTs and the familiarity ratings were correlated (Pearson's $r = -0.52$, $p < 0.0001$).

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 adults (7 women; average age 20 years, range 18–22; average years of education 13, range 12–15), native speakers of English 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 (s.d.) for Met/Lit verbs was 6.17 (0.42) and for Abs verbs was 3.62 (0.70), a difference that was highly significant ($p < 0.0001$).

FMRI Tasks

The sentences in the imaging experiment were presented in two parts, as in the Meaningfulness judgment experiment (Fig 1). Participants were instructed to read each sentence and 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 pseudo-randomized, 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 9 runs lasting approximately 5 minutes 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. Prior to 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 seconds long, and three blocks of each condition were presented in a pseudo-randomized order.

Image Acquisition and Analysis

A 3T GE Excite scanner was used to acquire images. One volume of T2*-weighted, gradient echo, echo-planar images (TE = 25 ms, flip angle = 77°, NEX = 1) was acquired every 1.8 s. 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 FOV = 240 mm and 64×64 matrix, resulting in $3.75 \times 3.75 \times 4$ mm voxel dimensions. Anatomical images of the entire brain were obtained using a 3D spoiled gradient echo sequence (SPGR) with $0.94 \times 0.94 \times 1$ mm voxel dimensions.

The AFNI software package (Cox, 1996) was used for image analysis. Within-subject analysis involved spatial co-registration (Cox and 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. Additionally, familiarity ratings for each stimulus (see *Stimulus Norming*, above) 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 due to 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 et al. (2004). Six motion parameters and the signal extracted from the ventricles, segmented using the FSL *fast* program (Zhang et al., 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 Familiarity $\times$ Condition interactions.

The individual statistical maps and the anatomical scans were projected into standard stereotaxic space (Talairach and 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 voxelwise $p < 0.01$ and corrected for multiple comparisons by removing clusters smaller than 1000 μl to achieve a mapwise corrected two-tailed $p < 0.05$. 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. The

data from the motor localizer scan were analyzed as a block design in a similar way. To further examine motor areas, two regions of interest (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 et al., 2006). Small volume correction was applied in these ROIs to achieve corrected $p < 0.05$.

RESULTS

The mean (s.d.) d' in the post-run test was 2.56 (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), left parahippocampal and fusiform gyrus, left precuneus, left posterior middle and inferior temporal gyrus and lateral occipital gyrus, left superior frontal gyrus, left orbitofrontal cortex, bilateral cerebellum and thalamus, as well as the right hippocampus and fusiform gyrus (Fig 2a).

Abs sentences activated the left superior temporal sulcus and the anterior superior temporal gyrus, cuneus, as well as the right angular gyrus.

Metaphor - Abstract

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

Metaphor - Literal

Compared to Lit sentences, the Met sentences activated the left anterior and posterior cingulate gyrus, cuneus, superior temporal sulcus, and the temporal pole. In the right hemisphere, the aIPL, parietal operculum and the superior parietal gyrus were activated (Fig 2c).

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

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 areas involved in the semantic processing, but also areas modulated due to general processing difficulty. To isolate, to the extent possible, activation modulation due to semantic factors, we computed 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-Abs × 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 Fig 3a). They included the left anterior inferior frontal gyrus, central sulcus, superior parietal gyrus, and posterior superior temporal sulcus; the right aIPL; and 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 superior temporal sulcus and bilateral central sulcus, SMA, lingual gyrus, and cuneus (cyan and green in Fig 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, while the left superior parietal gyrus was negatively correlated in the Lit condition (cyan and green in Fig 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 pre-response 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 superior temporal sulcus, 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 superior temporal sulcus, 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 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 et al., 2009). 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 et al., 2009), and is strongly linked to action performance, imitation, and semantics (Haaland et al., 2000; Tranel et al., 2003; Glover, 2004; Buxbaum et al., 2005; Binder et al., 2009; for further discussion, see Desai et al., 2009). 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 et al., 2004). Several studies report activation in this region for processing actions, tools, or concrete objects, e.g., for simulating rehearsed actions (Cross et al., 2006), recognizing and naming actions (Decety et al., 1997; Tranel et al., 2005), for artifacts compared to living things (Martin, 2007), and for concrete compared to 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 (Martin, 2007; Binder et al., 2009). 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 (Kable et al., 2005; Chen et al., 2008).

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 (Gibbs, 2006; Bergen, 2007), 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 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 sensory-motor 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 are suppressed within approximately 250–300 ms (Onifer and Swinney, 1981; Seidenberg et al., 1982; Pynte et al., 1996; Glucksberg, 2001). 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 Lit sentence, integrated over the sentence, whereas here the two signals were of similar magnitude. Futhermore, 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 to both Lit and Abs conditions, the right aIPL was also activated for metaphors. The RH activation can be interpreted in terms of Beeman's (1994) fine-coarse coding theory. It suggests that the RH maintains a wider "semantic field," containing alternative meanings or distantly related features, while the LH 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 (Sporns et al., 2007; Buckner et al., 2009). 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 superior temporal sulcus, 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 superior temporal sulcus for Abs sentences is consistent with a number of studies comparing abstract to concrete stimuli (for a review, see Binder, 2007). According to Pavio's (1986) dual coding theory, abstract information is represented mainly through verbal associations with other words. Andrews et al. (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 and Dumais, 1997). For example, a representation of justice may be built gradually through associations with concepts such as fair, law, good, court, right, truth, etc. 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 perisylvian region, who generally show greater processing deficits for abstract words (Goodglass et al., 1969; Katz and Goodglass, 1990; Franklin et al., 1995).

Correlations with Familiarity

Activation in a number of sensory-motor regions, overlapping with the localizer activation, were 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 superior temporal sulcus was also correlated with both Lit and Met familiarity, and is implicated in biological motion (Grossman and Blake, 2002; Saygin, 2007). 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 the 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 lab 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 et al., in press).

While 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 and Gennari, 2010) and force (Frak et al., 2010) required for an action, and semantic context (van Dam et al., in press) 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.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

References

Andrews M, Vigliocco G, Vinson D. Integrating experiential and distributional data to learn semantic representations. Psychol Rev. 2009; 116:463–498. [PubMed: 19618982]

Aziz-Zadeh L, Damasio A. Embodied semantics for actions: Findings from functional brain imaging. Journal of Physiology-Paris. 2008; 102:35–39.

Aziz-Zadeh L, Wilson SM, Rizzolatti G, Iacoboni M. Congruent embodied representations for visually presented actions and linguistic phrases describing actions. Curr Biol. 2006; 16:1818–1823. [PubMed: 16979559]

Barsalou LW. Grounded cognition. Annu Rev Psychol. 2008; 59:617–645. [PubMed: 17705682]

Beeman M, Friedman R, Grafman J, Perez E, Diamond S, Lindsay M. Summation priming and coarse semantic coding in the right hemisphere. Journal of Cognitive Neuroscience. 1994; 6:26–45.

Bergen, BK. Mental simulation in literal and figurative language understanding. In: Coulson, S.; Lewandowska-Tomaszczyk, B., editors. The Literal/Non-Literal Distinction. Berlin: Peter Lang; 2007.

Binder, JR. Effects of word imageability on semantic access: Neuroimaging studies. In: Hart, J.; Kraut, MA., editors. Neural basis of semantic memory. Cambridge, UK: Cambridge University Press; 2007. p. 149-181.

Binder JR, Desai RH, Graves WW, Conant LL. Where Is the Semantic System? A Critical Review and Meta-Analysis of 120 Functional Neuroimaging Studies. Cereb Cortex. 2009

Boulenger V, Hauk O, Pulvermuller F. Grasping Ideas with the Motor System: Semantic Somatotopy in Idiom Comprehension. Cereb Cortex. 2009; 19:1905–1914. [PubMed: 19068489]

Bowdle B, Gentner D. The career of metaphor. Psychological Review. 2005; 112:193–216. [PubMed: 15631593]

Buckner RL, Sepulcre J, Talukdar T, Krienen FM, Liu H, Hedden T, Andrews-Hanna JR, Sperling RA, Johnson KA. Cortical hubs revealed by intrinsic functional connectivity: mapping, assessment of stability, and relation to Alzheimer's disease. J Neurosci. 2009; 29:1860–1873. [PubMed: 19211893]

Buxbaum LJ, Kyle KM, Menon R. On beyond mirror neurons: internal representations subserving imitation and recognition of skilled object-related actions in humans. Brain Res Cogn Brain Res. 2005; 25:226–239. [PubMed: 15996857]

Calhoun VD, Stevens MC, Pearlson GD, Kiehl KA. fMRI analysis with the general linear model: removal of latency-induced amplitude bias by incorporation of hemodynamic derivative terms. Neuroimage. 2004; 22:252–257. [PubMed: 15110015]

Chen E, Widick P, Chatterjee A. Functional-anatomical organization of predicate metaphor processing. Brain Lang. 2008; 107:194–202. [PubMed: 18692890]

Cox RW. AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. Computers and Biomedical Research. 1996; 29:162–173. [PubMed: 8812068]

Cox RW, Jesmanowicz A. Real-time 3D image registration of functional MRI. Magnetic Resonance in Medicine. 1999; 42:1014–1018. [PubMed: 10571921]

Cross ES, Hamilton AF, Grafton ST. Building a motor simulation de novo: observation of dance by dancers. Neuroimage. 2006; 31:1257–1267. [PubMed: 16530429]

Decety J, Grezes J, Costes N, Perani D, Jeannerod M, Procyk E, Grassi F, Fazio F. Brain activity during observation of actions: Influences of action content and subject's strategy. Brain. 1997; 120:1763–1777. [PubMed: 9365369]

Desai RH, Binder JR, Conant LL, Seidenberg MS. Activation of Sensory-Motor Areas in Sentence Comprehension. Cerebral Cortex. 2009

Fischer MH, Zwaan RA. Embodied language: A review of the role of the motor system in language comprehension. The Quarterly Journal of Experimental Psychology. 2008; 61:825–850. [PubMed: 18470815]

Frak V, Nazir T, Goyette M, Cohen H, Jeannerod M. Grip force is part of the semantic representation of manual action verbs. PLoS ONE. 2010; 5:e9728. [PubMed: 20300535]

Franklin S, Howard D, Patterson K. Abstract word anomia. Cognitive Neuropsychology. 1995; 12:549–566.

Gibbs R. Metaphor Interpretation as Embodied Simulation. Mind & Language. 2006; 21:434–458.

Glover S. Separate visual representations in the planning and control of action. Behav Brain Sci. 2004; 27:3–24. discussion 24–78. [PubMed: 15481943]

Glucksberg, S. Understanding Figurative Language. New York: Oxford University Press; 2001.

Goodglass H, Hyde MR, Blumstein S. Frequency, picturability and availability of nouns in aphasia. Cortex. 1969; 5:104–119. [PubMed: 5824429]

Graves WW, Binder JR, Desai RH, Conant LL, Seidenberg MS. Neural correlates of implicit and explicit conceptual combination. Neuroimage. in press.

Grossman ED, Blake R. Brain Areas Active during Visual Perception of Biological Motion. Neuron. 2002; 35:1167–1175. [PubMed: 12354405]

Haaland KY, Harrington DL, Knight RT. Neural representations of skilled movement. Brain. 2000; 123 (Pt 11):2306–2313. [PubMed: 11050030]

Kable JW, Kan IP, Wilson A, Thompson-Schill SL, Chatterjee A. Conceptual representations of action in the lateral temporal cortex. Journal of Cognitive Neuroscience. 2005; 17:1855–1870. [PubMed: 16356324]

Katz RB, Goodglass H. Deep dysphasia: Analysis of a rare form of repetition disorder. Brain and Language. 1990; 39:153–185. [PubMed: 2207619]

Kemmerer D. The spatial and temporal meanings of English prepositions can be independently impaired. Neuropsychologia. 2005; 43:797–806. [PubMed: 15721192]

Kemmerer, D. Visual and motor features of the meanings of action verbs: A cognitive neuroscience perspective. In: de Almeida, RG.; Manouilidou, C., editors. Verb concepts: Cognitive science perspectives on verb representation and processing. Oxford, UK: Oxford University Press; in press

Lakoff, G.; Johnson, M. Metaphors We Live By. Chicago: University of Chicago Press; 1980.

Lakoff, G.; Johnson, M. Philosophy in the Flesh: The Embodied Mind and its Challenge to Western Thought. New York: Basic Books; 1999.

Landauer TK, Dumais ST. A solution to Plato's problem: The Latent Semantic Analysis theory of the acquisition, induction, and representation of knowledge. Psychological Review. 1997; 104:211–240.

Lyons IM, Mattarella-Micke A, Cieslak M, Nusbaum HC, Small SL, Beilock SL. The role of personal experience in the neural processing of action-related language. Brain and language. 2010; 112:214–222. [PubMed: 19628276]

Mahon BZ, Caramazza A. A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. Journal of Physiology-Paris. 2008; 102:59–70.

Martin A. The representation of object concepts in the brain. Annu Rev Psychol. 2007; 58:25–45. [PubMed: 16968210]

Mayka MA, Corcos DM, Leurgans SE, Vaillancourt DE. Three-dimensional locations and boundaries of motor and premotor cortices as defined by functional brain imaging: a meta-analysis. Neuroimage. 2006; 31:1453–1474. [PubMed: 16571375]

Moody CL, Gennari SP. Effects of implied physical effort in sensory-motor and pre-frontal cortex during language comprehension. Neuroimage. 2010; 49:782–793. [PubMed: 19660559]

Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia. 1971; 9:97–113. [PubMed: 5146491]

Onifer W, Swinney D. Accessing lexical ambiguity during sentence comprehension: Effects of frequency of meaning and contextual bias. Memory and Cognition. 1981; 9:225–236.

Paivio, A. Mental representations: A dual-coding approach. New York: Oxford University Press; 1986.

Peeters R, Simone L, Nelissen K, Fabbri-Destro M, Vanduffel W, Rizzolatti G, Orban GA. The representation of tool use in humans and monkeys: common and uniquely human features. J Neurosci. 2009; 29:11523–11539. [PubMed: 19759300]

Pulvermuller F. Brain mechanisms linking language and action. Nat Rev Neurosci. 2005; 6:576–582. [PubMed: 15959465]

Pynte J, Besson M, Robichon F-H, Poli J. The time-course of metaphor comprehension: An event-related potential study. Brain and Language. 1996; 55:293–316. [PubMed: 8954602]

Ramayya, AG.; Glasser, MF.; Rilling, JK. Cerebral cortex. New York, NY: 2009. A DTI Investigation of Neural Substrates Supporting Tool Use; p. 507-516.1991

Raposo A, Moss HE, Stamatakis EA, Tyler LK. Modulation of motor and premotor cortices by actions, action words and action sentences. Neuropsychologia. 2009; 47:388–396. [PubMed: 18930749]

Rastle K, Harrington J, Coltheart M. 358,534 nonwords: The ARC Nonword Database. Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology. 2002; 55:1339–1362.

Saad ZS, Glen DR, Chen G, Beauchamp MS, Desai R, Cox RW. A new method for improving functional-to-structural MRI alignment using local Pearson correlation. Neuroimage. 2009; 44:839–848. [PubMed: 18976717]

Saygin AP. Superior temporal and premotor brain areas necessary for biological motion perception. Brain. 2007; 130:2452–2461. [PubMed: 17660183]

Saygin AP, McCullough S, Alac M, Emmorey K. Modulation of BOLD Response in Motion-sensitive Lateral Temporal Cortex by Real and Fictive Motion Sentences. Journal of cognitive neuroscience. 2010; 22:2480–2490. [PubMed: 19925197]

Schmidt GL, Seger CA. Neural correlates of metaphor processing: the roles of figurativeness, familiarity and difficulty. Brain Cogn. 2009; 71:375–386. [PubMed: 19586700]

Seidenberg M, Tanenhaus MK, Leiman JL, Bienkowski M. Automatic access of the meanings of ambiguous words in context: Some limiations of knowledge-based processing. Cognitive Psychology. 1982; 14:470–519.

Sporns O, Honey CJ, Kotter R. Identification and classification of hubs in brain networks. PLoS ONE. 2007; 2:e1049. [PubMed: 17940613]

Squire LR, Stark CE, Clark RE. The medial temporal lobe. Annu Rev Neurosci. 2004; 27:279–306. [PubMed: 15217334]

Talairach, J.; Tournoux, P. Co-planar Stereotaxic Atlas of the Human Brain. New York: Thieme Medical; 1988.

Tranel D, Kemmerer D, Adolphs R, Damasio H, Damasio A. Neural correlates of conceptual knowledge for actions. Cognitive Neuropsychology. 2003; 20:409–432. [PubMed: 20957578]

Tranel D, Martin C, Damasio H, Grabowski TJ, Hichwa R. Effects of noun-verb homonymy on the neural correlates of naming concrete entities and actions. Brain Lang. 2005; 92:288–299. [PubMed: 15721961]

van Dam WO, Rueschemeyer SA, Lindermann O, Bekkering H. Context effects in embodied lexical-semantic processing. Front Cognition. in press.

Van Essen DC, Drury HA, Dickson J, Harwell J, Hanlon D, Anderson CH. An integrated software suite for surface-based analyses of cerebral cortex. Journal of American Medical Informatics Association. 2001; 8:443–459.

Wallentin M, Lund TE, Ostergaard S, Ostergaard L, Roepstorff A. Motion verb sentences activate left posterior middle temporal cortex despite static context. Neuroreport. 2005; 16:649–652. [PubMed: 15812326]

Yang FG, Edens J, Simpson C, Krawczyk DC. Differences in task demands influence the hemispheric lateralization and neural correlates of metaphor. Brain Lang. 2009; 111:114–124. [PubMed: 19781756]

Zhang Y, Brady M, Smith S. Segmentation of brain MR images through a hidden Markov random field model and the expectation-maximization algorithm. IEEE Trans Med Imaging. 2001; 20:45–57. [PubMed: 11293691]
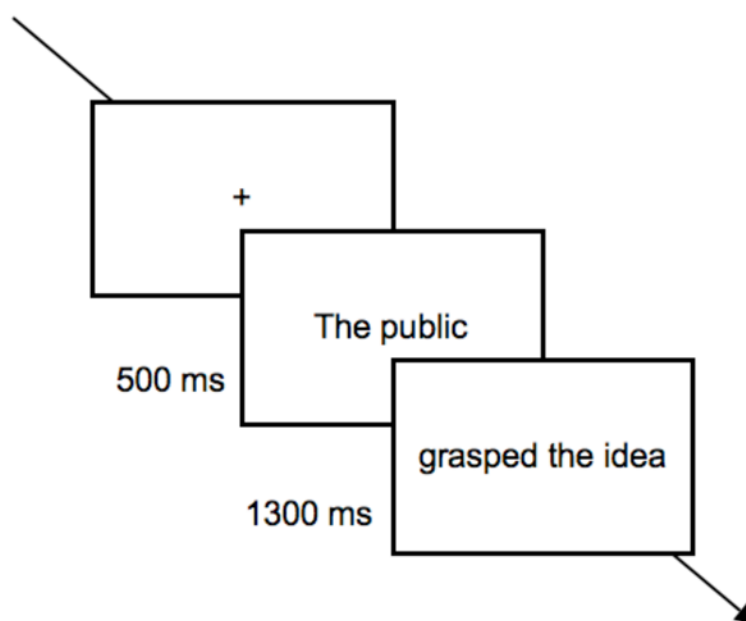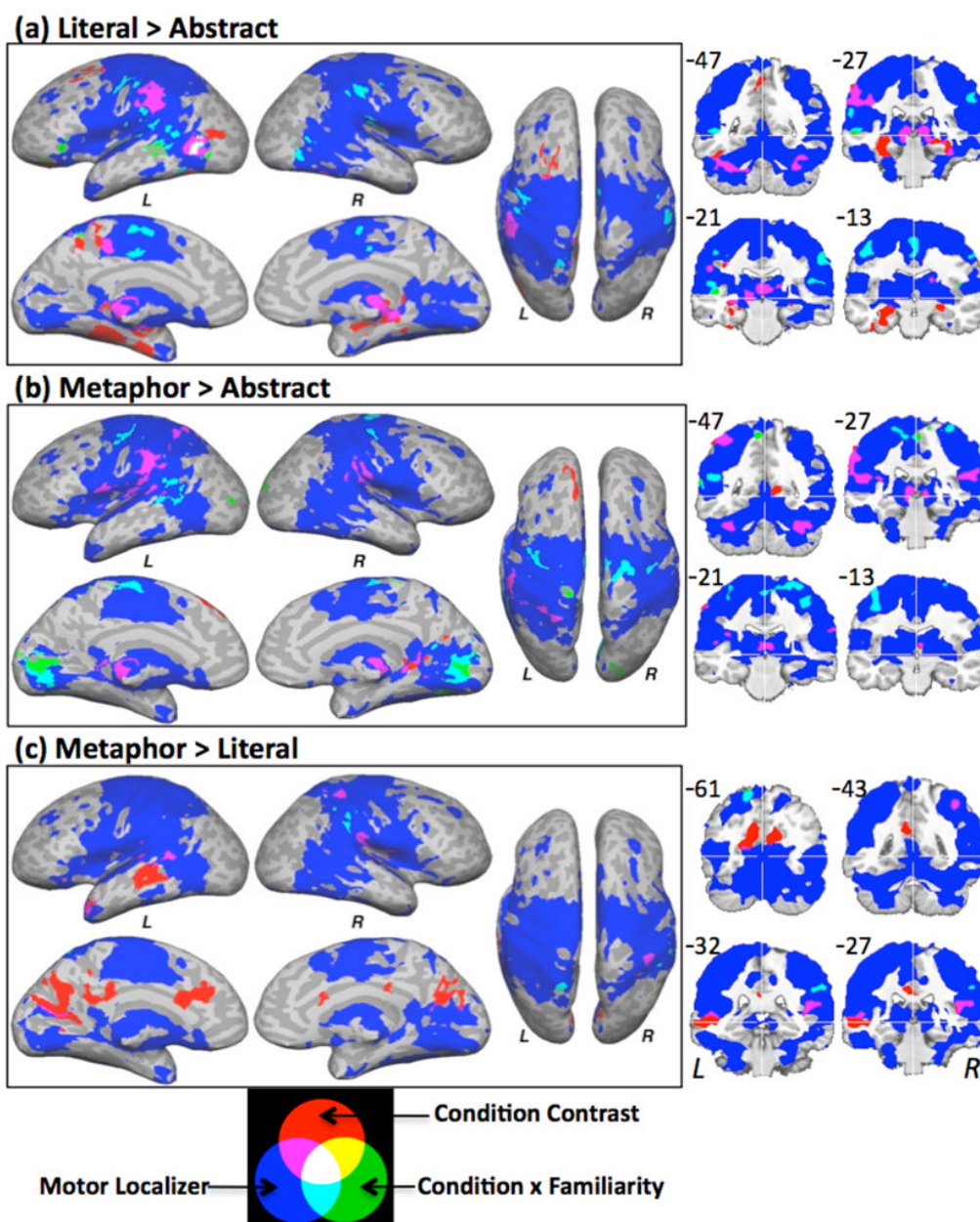
Figure 1.
The presentation of the stimuli. The first noun phrase of the sentence was displayed for 500 ms, followed by the remaining sentence for 1300 ms. The sentences were separated by variable intervals.
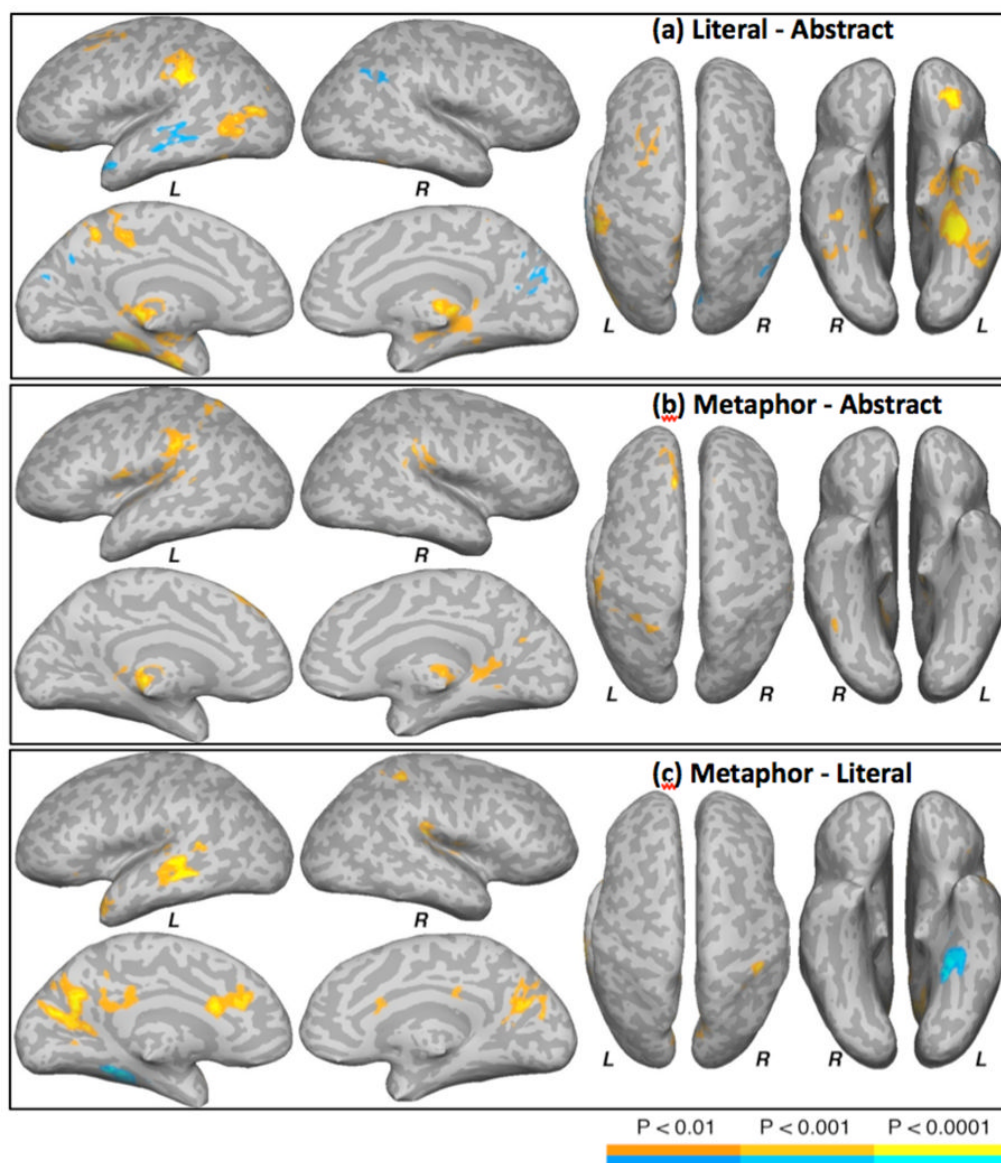
Figure 2.
Areas activated by condition contrasts. Yellow-orange scale shows greater activation for the first condition; blue-cyan scale shows greater activation for the second condition in the contrast. L = left hemisphere, R = right hemisphere.

Figure 3.
The overlap of condition contrasts, condition x familiarity interactions, and the motor localizer. Interactions in (a) and (b) show greater negative correlation to familiarity for Lit and Met conditions respectively. Talairach *y* coordinates are indicated in the upper left corner of each slice. Stereotaxic *x* and *z* axis are shown in white.

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*

Table 2

The mean (s.d.) RTs in the Meaningfulness Judgement 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)	-

Table 3

A summary of the main results. '×' indicates regions that are activated or correlated with familiarity, or overlap with the localizer activation.

Area	Contrast				
	Lit > Abs	Met > Abs	Lit-Abs × Fam	Met-Abs × Fam	Loc. Overlap
L dorsomedial prefrontal	×				
L parahippocampal/fusiform g	×				
L aIPL	×	×			×
Bilateral thalamus	×	×			×
Bilateral cerebellum	×	×			×
L p mid temporal g	×		×		×
Bilateral parietal operc.		×	×		×
R aIPL		×	×		×
L sup parietal lobule		×	×		×
R p mid temporal g			×		×
L central s			×	×	×
L p sup temporal s			×	×	×
Bilateral SMA			×	×	×
R central s				×	×
Bilateral Lingual g				×	×