NeuroImage 83 (2013) 862–869

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

A piece of the action: Modulation of sensory-motor regions by action idioms and metaphors

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ARTICLE INFO

Article history:
Accepted 13 July 2013
Available online 24 July 2013

Keywords:
Embodiment
Context sensitivity
Idiom
Metaphor
Semantics
Action
fMRI

ABSTRACT

The idea that the conceptual system draws on sensory and motor systems has received considerable experimental support in recent years. Whether the tight coupling between sensory-motor and conceptual systems is modulated by factors such as context or task demands is a matter of controversy. Here, we tested the context sensitivity of this coupling by using action verbs in three different types of sentences in an fMRI study: literal action, apt but non-idiomatic action metaphors, and action idioms. Abstract sentences served as a baseline. The result showed involvement of sensory-motor areas for literal and metaphoric action sentences, but not for idiomatic ones. A trend of increasing sensory-motor activation from abstract to idiomatic to metaphoric to literal sentences was seen. These results support a gradual abstraction process whereby the reliance on sensory-motor systems is reduced as the abstractness of meaning as well as conventionalization is increased, highlighting the context sensitive nature of semantic processing.

Introduction

The idea that the conceptual system draws on sensory and motor systems has received considerable experimental support in recent years (see Barsalou, 2008; Gallese and Lakoff, 2005; Kiefer and Pulvermüller, 2011; Pulvermüller and Fadiga, 2010). This contrasts with the traditional view that all concepts are represented in an amodal, abstract format (Anderson, 1983; Bedny and Caramazza, 2011; Fodor, 1983; Mahon and Caramazza, 2008; Pylyshyn, 1984). Current debate concerns the precise nature of the relationship between concepts and perception/action. One question is whether the involvement of sensory-motor information is obligatory (because it is an essential part of semantic representation) or context-dependent (varying with factors such as task demands or expectations due to the nature of the stimuli). Figurative action language provides an interesting vehicle for addressing this issue as it allows comparisons between concrete verbs that are used to describe physical action (e.g., *grasp a hammer*), and use of the same verbs to convey an abstract idea by analogy with an action (*grasp an idea*). Involvement of sensory-motor areas in the processing of figurative action language would lend support to embodiment theories, which hold that even abstract concepts are grounded in sensory-motor systems (Gibbs, 2006; Glenberg et al., 2008).

Neuroimaging studies of figurative action language have yielded mixed results. Activation in the premotor cortex for literal action sentences was reported by Aziz-Zadeh et al. (2006). They did not find motor activity for idiomatic/proverbial action phrases, such as 'biting off more than you can chew'. Raposo et al. (2009) also did not find motor/premotor activation for figurative action sentences, but did find it for isolated action verbs and literal sentences, and did not find somatotopy (see also Postle et al., 2008). Boulenger et al. (2009), on the other hand, found somatotopic activation for figurative and literal action sentences involving leg and arm verbs. Activation of anterior inferior parietal lobe, a higher-level motor area, for literal and metaphoric action sentences, and modulation of primary motor cortex by metaphor familiarity, was reported by Desai et al. (2011). In a MEG study, Boulenger et al. (2012) found activation of their arm ROI (and a similar trend in a leg ROI) by figurative and literal arm and leg action sentences.

Activation in or near motion processing area MT+ for literal as well as figurative or fictive motion sentences ('The man fell under her spell') compared to non-motive sentences was found in three studies (Chen et al., 2008; Saygin et al., 2010; Wallentin et al., 2005). Finally, Lacey et al. (2012) reported activation of somatosensory regions by texture metaphors ('She had a rough day.') compared to abstract sentences ('She had a bad day.').

Thus, several studies have shown activation of sensory-motor areas during processing of figurative language, while some inconsistencies also exist. An important factor that may account for some of these differing results is the extent to which the figurative stimuli are conventionalized. Idioms like "spill the beans" are an example of figurative language in which collocated (frequently co-occurring) words become "frozen" as a whole phrase that functions as a single interpretive

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1053-8119/$ – see front matter
http://dx.doi.org/10.1016/j.neuroimage.2013.07.044

unit, with the individual words only remotely related to the meaning of the expression. Phrasal verbs (e.g., *run into*, *go about*) also convey idiomatic meaning through polysemy or combinatorial structure. In contrast, the interpretation of metaphors such as "all jobs are jails" depends on the meanings of the individual words and their linkage to other types of knowledge (Glucksberg, 2003). Although the boundary between idioms and metaphors is graded rather than absolute, there are many clear examples of the difference. Imaging studies of embodiment in figurative language have not compared idioms and metaphors; some have mixed idioms and metaphors together; and in some studies 'idiom' is used to refer to familiar metaphors.

Cacciari et al. (2011) conducted a TMS study comparing literal, metaphoric, and idiomatic motion sentences. They applied a TMS pulse over the leg motor area at the end of the sentence and measured motor evoked potentials (MEPs) in leg muscles. They found increased MEPs for literal and metaphoric sentences, but not for idiomatic sentences, suggesting context sensitivity in meaning access. It is not clear, however, whether higher-level motor areas such as the anterior inferior parietal lobule, reported in several studies of action processing (Desai et al., 2009, 2011; Goldberg et al., 2006; Noppeney et al., 2005; Rueschemeyer et al., 2010; Rueschemeyer et al., 2007) for both literal and metaphoric action sentences, participates in idiomatic action sentences, as only the primary leg motor area was examined in this study.

Here, we conducted an fMRI study comparing literal, (non-idiomatic) metaphoric, and idiomatic action sentences to abstract sentences. One possibility is that to process action words, engagement of sensory-motor areas is always needed, regardless of context or task demands. An alternative is context sensitivity, where the sensory-motor roots of meaning are accessed at varying levels of depth depending on context. A further alternative, representing the traditional view, is that all concepts are represented abstractly. Once a concept is learned from sensory-motor experiences, no access to sensory-motor systems is involved, as the conceptual system functions as an independent symbolic module. Similar activation in sensory-motor areas for the literal, metaphoric, and idiomatic sentences, all of which use an action verb, would suggest that the meaning of the verb is processed by accessing its motoric basis, regardless of context. A lower level of activation for more conventionalized language such as idioms would indicate a context-sensitive abstraction process.

Methods

Participants

Participants in the fMRI experiment were 27 healthy adults (15 women; average age 24.7 years, range 18–38), with no history of neurological impairment. One additional participant was removed due to low behavioral performance in the scanner (accuracy < 75%). 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 four main conditions: literal action (Literal), non-idiomatic metaphoric action (Metaphor), idiomatic action (Idiom), and abstract sentence (Abstract). The stimuli were constructed in quadruples consisting of one sentence from each condition (examples in Table 1; complete listing provided in the Supplemental material part D).

The Literal sentence in each quadruple used a hand/arm action verb to depict a physical action. The corresponding Metaphor sentence used the same verb in a figurative but non-idiomatic manner, such that abstract meaning was conveyed. The Idiom sentence used the same action verb in an idiomatic manner. The idiomaticity of the Idiom sentences as well as the non-idiomaticity of the Metaphor sentences was verified using an online idiom dictionary compiled from the *Cambridge International Dictionary of Idioms* and the *Cambridge Dictionary of American Idioms* (http://idioms.thefreedictionary.com/). The Abstract sentence used an abstract verb (with no direct associations with physical actions). The agent in each sentence was chosen to imply either a literal or abstract/figurative interpretation of the verb. For Metaphor, Idiom, and Abstract sentences, this agent was an entity that makes literal physical actions unlikely (e.g., *the question*, *the business*). The Literal sentences, in contrast, always used a person (*the firefighter*, *the janitor*) as an agent. As in our previous study (Desai et al., 2011), this was done to facilitate nonliteral interpretation of the action verbs for Metaphor and Idiom sentences (e.g., when processing "The business is pinching pennies," a nonliteral interpretation is encouraged when *pinching* is encountered).

There are numerous constraints on the verbs and the nouns that can be used in each sentence. Most idioms only allow limited flexibility in their form in order to be interpreted naturally and idiomatically. Hence, we opted to allow some syntactic variation in the sentences belonging to the same quadruple in order to make stimuli natural to the extent possible while maintaining similar sentence length.

Forty quadruples were created, producing 40 sentences in each of the Literal, Metaphor, Idiom, and Abstract conditions. Eighty Nonsense sentences (e.g., *The speech strangled all the snow*) were created by combining action and abstract verbs with inappropriate nouns. Twenty Filler sentences (used to obscure the quadruple construction of stimuli) and 40 false font sentences were also used. The Filler sentences used variable syntax, included both action and abstract verbs, and contained both literal and figurative sentences (*Her dog is running after the rabbit*; *He finally managed to kick the habit*; *He learned a new skill to benefit the company*). The conditions of interest were matched in the number of words, syllables, phonemes, and letters (Table 2). It was not possible to match the conditions on frequency (average CELEX log per million frequency of the content words) while maintaining similar processing difficulty (see the next section). The Metaphor condition had similar frequency to the other three conditions, but the pairwise differences between the other conditions (Literal, Idiom, Abstract) were significant (all $p < 0.001$; two-tailed t-tests).

Table 1
Example stimuli.'/'separates the two parts used in presentation.

Literal	*The instructor is/grasping the steering wheel very tightly.*	*The craftsman/lifted the pebble from the ground.*
Metaphor	*The congress is/grasping the state of the affairs.*	*The discovery/lifted this nation out of poverty.*
Idiom	*The congress is/grasping at straws in the crisis.*	*The country/lifted the veil on its nuclear program.*
Abstract	*The congress is/causing a big trade deficit again.*	*The country/wanted the plan for a nuclear program.*

Table 2
The mean (s.d.) number of words, syllables, phonemes, and letters, as well as the average log per million frequency of the content words in the sentences in the conditions of interest.

Condition	#Word	#Syll	#Phon	#Lett	Freq
Literal	7.8	11.0	29.2	37.0	1.6
	(1.3)	(1.8)	(4.8)	(5.8)	(0.4)
Metaphor	7.8	11.1	29.0	36.2	2.0
	(1.2)	(2.0)	(5.0)	(6.1)	(0.3)
Idiom	7.7	10.3	27.8	34.9	1.9
	(1.3)	(2.3)	(5.5)	(6.8)	(0.3)
Abstract	7.7	11.4	29.7	35.1	2.1
	(1.3)	(2.4)	(5.5)	(6.2)	(0.3)

Stimulus norming

To assess the processing difficulty of the sentences, we tested all 260 sentence stimuli on a meaningfulness judgment task in a norming study. Participants in this study were 20 adults (10 women; average age (±s.d.) = 21.7 (±8.3) years). They were native speakers of English and did not participate in the fMRI experiment. Participants decided whether each sentence was meaningful or not with a buttonpress. Each sentence was presented visually in two parts. The first screen displayed the noun phrase (e.g., "The whole town") for 800 ms. This was replaced by the verb phrase (e.g., "tightened its belt.") on the second screen, displayed for 1500 ms. This two-part presentation was used to ensure that the first noun phrase, which suggests the literal or abstract interpretation of the verb, was read first. Mean RTs are shown in Table 3. Among the four conditions of interest, there were no significant differences between conditions in the item analysis (all $p > 0.30$ in two-tailed t-test). For the subject analysis there were no differences either, except the Metaphor condition had longer RTs than the Abstract condition ($p = 0.02$). All four conditions had overall high accuracy, but the Abstract condition had a higher accuracy than other conditions (all $p < 0.02$ in Mann–Whitney U test), and Idioms had lower accuracy (all $p < 0.04$) in both subject and item analyses. There were no accuracy differences between the Metaphor and Literal conditions ($p > 0.90$).

Action association ratings for the verbs, using a scale of 1 (not associated with action at all) to 7 (very much associated with action), were collected previously (Desai et al., 2011) and were used to ensure that abstract verbs had lower action association than action verbs. The mean (s.d.) rating for abstract and action verbs was 3.55 (0.75) and 6.02 (0.56) respectively ($p < 0.0001$).

FMRI procedure

The sentences in the imaging experiment were presented visually in two parts, as during stimulus norming. 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. To encourage attentiveness, after approximately 10% of sentences, the prompt "Makes Sense?" was presented. These probe trials were distributed equally between the four conditions of interest, and additionally also included Nonsense and Filler conditions. Subjects were instructed to press one of two buttons to indicate their response. The order of sentences was pseudo-randomized, and the interval between the sentences (including the prompt) was varied to allow optimal statistical separation of the hemodynamic response to each condition. The stimuli were presented in four runs, and 226 images were collected during each run.

Image acquisition and analysis

A 3T GE Excite scanner was used to acquire images. One volume of T2*-weighted, gradient echo, echo-planar images (acquisition time = 2.3 s, TE = 25 ms, flip angle = 77°, NEX = 1) was collected every 2.3 s. Visual sentence presentation was time-locked with the beginning of an acquisition. Volumes were composed of 35 axially-oriented 3-mm slices with a 0.5 mm interslice gap, covering the whole brain, with FOV = 192 mm and 64 × 64 matrix, resulting in 3 × 3 × 3.5 mm voxel dimensions. Anatomical images of the entire brain were obtained using a 3D spoiled gradient echo sequence (SPGR) with 0.94 × 0.94 × 1 mm voxel dimensions.

The AFNI software package (Cox, 1996) was used for image analysis. Within-subject analysis involved slice timing correction, spatial coregistration (Cox and Jesmanowicz, 1999) and registration of functional images to the anatomy (Saad et al., 2009). Voxel-wise multiple linear regression was performed with the program 3dREMLfit, using reference functions representing each condition convolved with a standard hemodynamic response function. A regressor representing the mean-centered RT for each sentence from the norming experiment was used as an additional item-wise regressor to remove variance due to time-on-task and difficulty. Reference functions representing the six motion parameters and the manual response were included as covariates of no interest. General linear tests were conducted to obtain contrasts between conditions of interest.

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 6 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 $p < 0.005$ and corrected for multiple comparisons by removing clusters with below-threshold size to achieve a mapwise corrected $p < 0.05$. Using the AlphaSim program with 5000 iterations, the cluster threshold was determined through Monte Carlo simulations that estimate the chance probability of spatially contiguous voxels exceeding the voxelwise p threshold, i.e., of false positive noise clusters. The smoothness of the data was estimated with the AFNI program 3dFWHMx using regression residuals as input. The analysis was restricted to a mask that excluded areas outside the brain, as well as deep white matter areas and the ventricles.

In addition to this whole-brain analysis, three other ROIs were defined for a more sensitive analysis. One used the area activated by a motor localizer task (physical movement of the right hand) in Desai et al. (2011). The second used primary motor and sensory cortex (M1 and S1) as defined by the HMAT atlas (Mayka et al., 2006). The third ROI was the lateral anterior temporal lobe, which is associated with semantic processing and especially idioms (Boulenger et al., 2012). Small volume correction was applied in these ROIs to achieve corrected $p < 0.05$, determined in the same manner as above (5000 Monte Carlo simulations using AlphaSim).

To examine changes in activation in accordance with hypothesized association with actions, we calculated linear trends for increasing activation from Abstract, Idiom, Metaphor, and Literal conditions, in that order, through general linear contrasts. However, a linear component can be driven by strong activation in only one condition at the end point (e.g., strong positive activation in the Literal condition and near zero activation in the other three conditions will result in a statistical linear trend). To avoid such voxels, we additionally required that the activation be strictly increasing (or decreasing) for the four conditions (Abstract < Idiom < Metaphor < Literal). The linear trend activations, masked by this required stepwise increase, were thresholded and cluster corrected in the same way as other contrasts.

Table 3
The mean (s.d.) response times and % accuracy for meaningfulness judgment in the norming experiment. n indicates the number of sentences in the condition.

Condition	n	RT	Acc
Literal	40	1628 (343)	88 (12)
Metaphor	40	1649 (358)	89 (9)
Idiom	40	1626 (353)	77 (22)
Abstract	40	1596 (356)	95 (7)
Nonsense	80	1724 (373)	88 (13)
Filler	20	1588 (366)	95 (7)

Results

In the scanner, subjects responded with a mean (s.d.) accuracy of 88% (6%). The mean (s.d.) d' was 2.35 (0.58), suggesting that they were generally attentive during the task. We now describe the fMRI results for the Literal, Metaphor, and Idiom conditions against the baseline of Abstract. 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 Tables 4 and 5.

Table 4
Activations in the main contrasts of interest. The volume of the cluster (μl), peak z-score, Talairach coordinates, and the anatomical structures that the clusters overlap are shown. L = left hemisphere, R = right hemisphere, g = gyrus, s = sulcus, ant = anterior, post = posterior, sup = superior, mid = middle, inf = inferior.

Volume	Max	x	y	z	Structure
Literal > Abstract					
13,201	5.22	−34	−8	−19	L parahippocampal g, fusiform g, inf temporal g
	5.08	−50	−48	−10	L post inf temporal g
4165	4.73	41	−66	16	R mid temporal g, angular g
	3.88	50	−44	2	R mid temporal g
3472	4.46	−45	−42	43	L supramarginal g, ant intraparietal s
3233	4.75	31	30	−6	R lat orbital g
3207	4.92	−47	26	21	L inf frontal g (pars orbitalis, triangularis)
1475	3.78	−20	7	47	L sup frontal g
990	4.37	46	6	33	R precentral g
897	4.73	29	−2	−15	R amygdala
739	3.58	−29	−56	−32	L cerebellum
360	3.90	−31	−27	54	L central s
Abstract > Literal					
5095	−5.02	−6	−44	25	L post cingulate, precuneus
	−3.12	5	−22	33	R post cingulate
2997	−4.27	−49	7	−13	L ant sup temporal g, s
Metaphor > Abstract					
2419	3.84	−42	−44	46	L supramarginal g, ant intraparietal s
	3.70	−27	−65	48	L ant intrapariatal s
1183	4.07	−17	−79	17	L sup occipital g
Abstract > Metaphor					
None					
Idiom > Abstract					
4417	5.55	−47	26	17	L inf frontal g (pars triangularis, orbitalis)
1898	4.21	55	20	8	R inf frontal g (pars triangularis)
938	3.86	−2	20	50	L sup frontal g
325	3.56	−36	−9	−24	L ant fusiform g
Abstract > Idiom					
None					

Literal–Abstract

The areas activated to a greater extent by the Literal condition relative to the Abstract condition included the left anterior inferior parietal lobule (aIPL), left parahippocampal and fusiform gyrus, bilateral posterior middle and inferior temporal gyrus, left superior and anterior inferior frontal gyri (SFG and IFG), and cerebellum, as well as the right orbital and precentral gyrus (Fig. 1). The ROI analyses revealed an additional cluster in the left central sulcus.

Abstract sentences activated the left anterior superior temporal sulcus and gyrus, as well as bilateral posterior cingulate and left precuneus.

Table 5
Areas showing a linear trend in the direction Literal > Metaphor > Idiom > Abstract, with the additional condition that the activation is strictly increasing from Abstract through Literal conditions. Negative trend indicates trend in the reverse direction.

Volume	Max	x	y	z	Structure
Positive trend					
3930	4.57	−48	−42	53	L supramarginal g, ant intraparietal s
1289	5.23	−33	−9	−18	L parahippocampal g, fusiform g
1168	4.05	−51	−53	−7	L post inf temporal g,
803	4.88	41	−65	15	R angular g
Negative trend					
1506	−4.09	−50	7	−13	L ant temporal g, s
	−3.87	−42	22	−26	L ant inf temporal g
1270	−4.33	−4	−44	26	L post cingulate g

Metaphor–Abstract

The left aIPL and the superior occipital gyrus were activated to a greater extent for the Metaphor condition, while no areas were activated more by the Abstract condition (Fig. 2).

Idiom–Abstract

The Idiom condition activated bilateral IFG, and the left medial SFG relative to Abstract sentences (Fig. 3). An additional cluster in the left anterior fusiform gyrus was identified in the ROI analyses. No areas were activated to a greater extent by the Abstract condition.

Out of the six possible pairwise contrasts, the remaining three are provided in Supplemental material (A–C). Here we note that the Literal condition, relative to the Idiom condition, activated the areas that were similar to those activated relative to the Abstract condition. These included the left aIPL, parahippocampal gyrus, and posterior middle and inferior temporal gyrus.

Linear trends

A positive linear trend, in the direction Literal > Metaphor > Idiom > Abstract was seen in aIPL, parahippocampal gyrus, posterior inferior temporal gyrus, and the right angular gyrus (Fig. 4). A negative trend (Literal < Metaphor < Idiom < Abstract) was found in the left anterior temporal lobe and posterior cingulate.

Discussion and conclusions

We examined brain activation elicited by sentences that varied in action association as well as conventionality. We can think of these sentences as establishing different levels of abstraction from action semantics. The Literal sentences described physical actions. Metaphor sentences used the same action verbs metaphorically, in a generally familiar but non-conventionalized way. The Idiom sentences used the action verbs in a highly conventionalized figurative manner. Finally, the Abstract sentences used verbs that had relatively low association with actions.

The results indicate that the involvement of sensory-motor areas in processing these sentences decreases as the level of abstraction increases. Relative to Abstract sentences, the Literal condition activated a secondary motor area in the aIPL, and also a small cluster in the primary motor cortex. Additionally, it activated regions in the posterior middle and inferior temporal gyri, close to the motion processing area MT. A large body of literature implicates the aIPL in action planning and control, complex hand–object interactions, and tool use, according to both imaging and lesion studies (see Desai et al., 2009, 2011 for further discussion). It is not organized somatotopically, but functionally (Heed et al., 2011; Jastorff et al., 2010), e.g., based on whether actions are towards or away from the body. A tool use network is formed by aIPL's structural connections to posterior middle temporal and inferior frontal regions (Ramayya et al., 2009). Rushworth et al. (2001) found activation in aIPL for planning compared to executing specific finger movements, while Johnson-Frey et al. (2005) reported aIPL activation for planning tool actions compared to preparing for random movements. Frey et al. (2005) reported aIPL activation for visually-guided grasping compared to pointing. Action judgments compared to function judgments on object pictures also activated the aIPL (Kellenbach et al., 2003). Several studies have found aIPL activation for pantomiming tool use (Johnson-Frey et al., 2005; Lewis et al., 2006; Rumiati et al., 2004). Damage to aIPL/IPL results in ideomotor apraxia (Haaland et al., 2000; Jax et al., 2006), where patients are impaired in skilled performance of motor acts, imitating gestures, performing appropriate actions in response to a visually presented object, and carrying out the action using the actual object (Buxbaum et al., 2005a, 2005b; Goldenberg and Karnath, 2006; Goldenberg and Spatt, 2009). In the model of praxis proposed by Buxbaum (2001) and

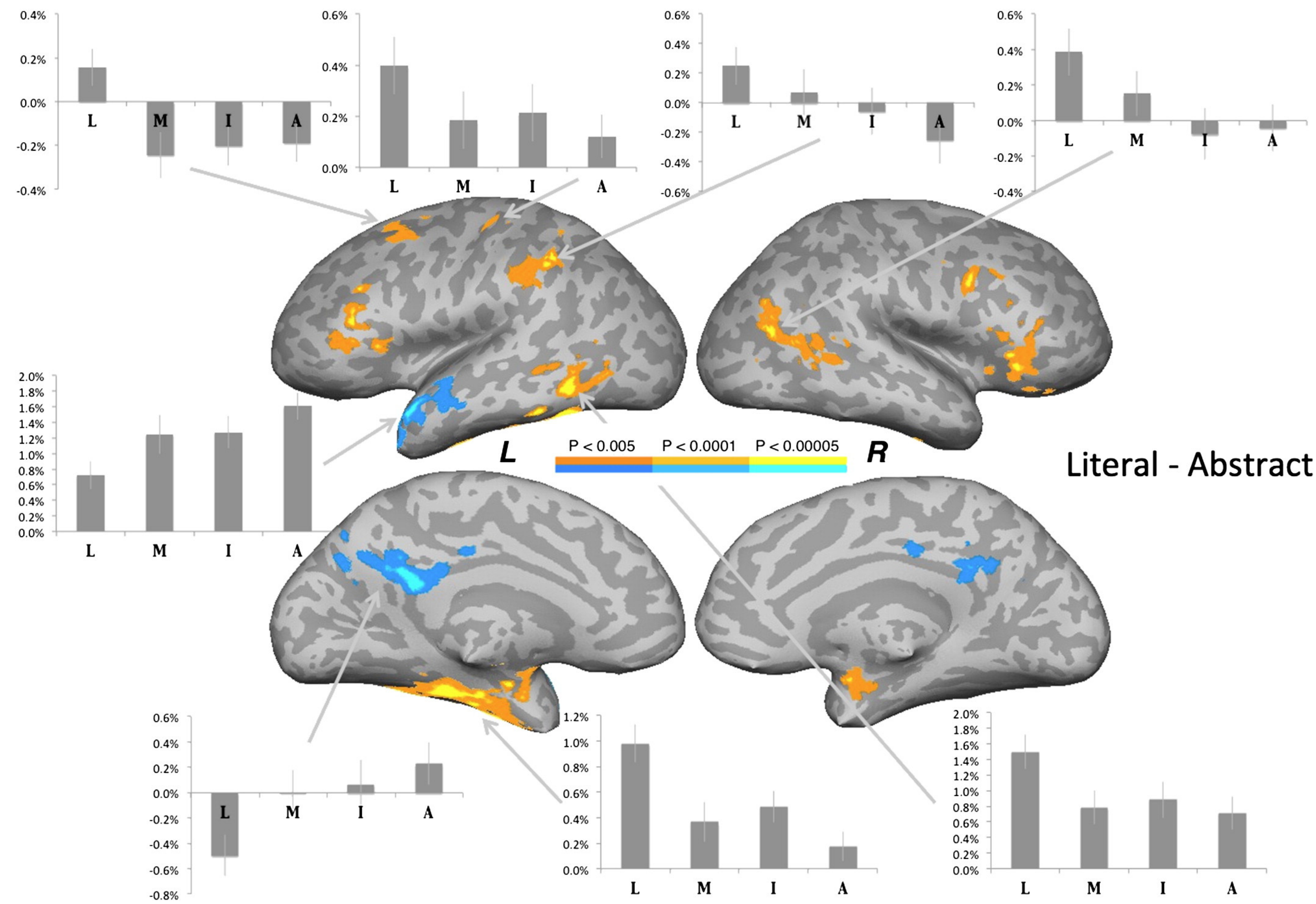

Fig. 1. Areas activated by the Literal–Abstract contrast. Yellow-orange scale shows greater activation for the first condition; blue-cyan scale shows greater activation for the second condition in the contrast. Mean percent signal change relative to rest is shown for the four main conditions for some areas, in a sphere of 5 mm radius around the peak voxel. Error bars show one standard error of the mean. (Note that differences in activation between the conditions involved in the contrast are significant by definition. The graphs are meant to show the direction of activation for these two conditions, to show the effect size, as well as illustrate the activation for the other two conditions in that region.) L = left hemisphere, R = right hemisphere. In the graphs, L = Literal, M = Metaphor, I = Idiom, A = Abstract.

Buxbaum et al. (2007), the IPL processes internal representations of movements and body part positions, and integrates object knowledge and body representations.

Thus, the activation of aIPL is consistent with the view that processing action sentences involves a form of high-level action simulation. The Metaphor sentences also activated aIPL, but not primary motor or motion-related areas. The Idiom condition, on the other hand, activated no areas commonly associated with actions. It activated the anterior IFG (pars triangularis and orbitalis; BA 45/47), which is associated with semantic retrieval and selection (as opposed to pars opercularis in the posterior IFG (BA 44/6), which is associated with tool use and is thought to be part of the mirror neuron system).

These results indicate a gradual abstraction process whereby the reliance on sensory-motor systems is reduced as the abstractness of meaning as well as conventionalization is increased. The activation of aIPL for idioms was significantly less than that for literal sentences, and numerically intermediate between metaphoric and abstract sentences, while not being significantly different from either. Our previous results

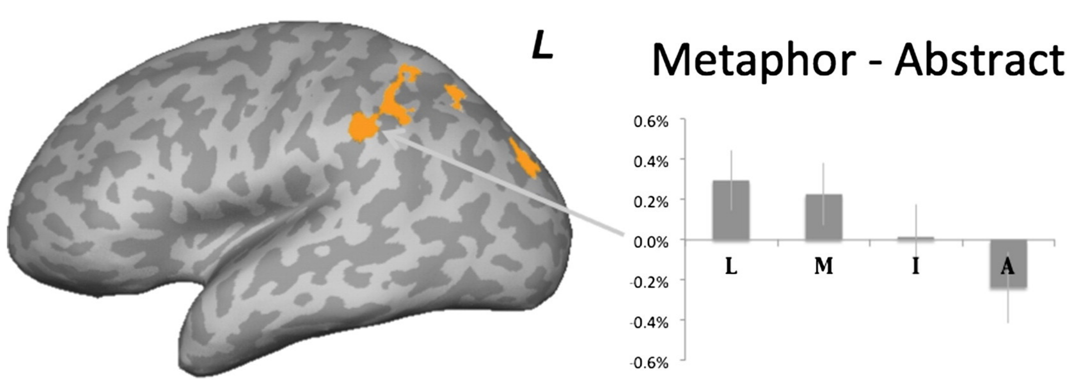

Fig. 2. Areas activated by the Metaphor–Abstract contrast. See Fig. 1 caption for other details.

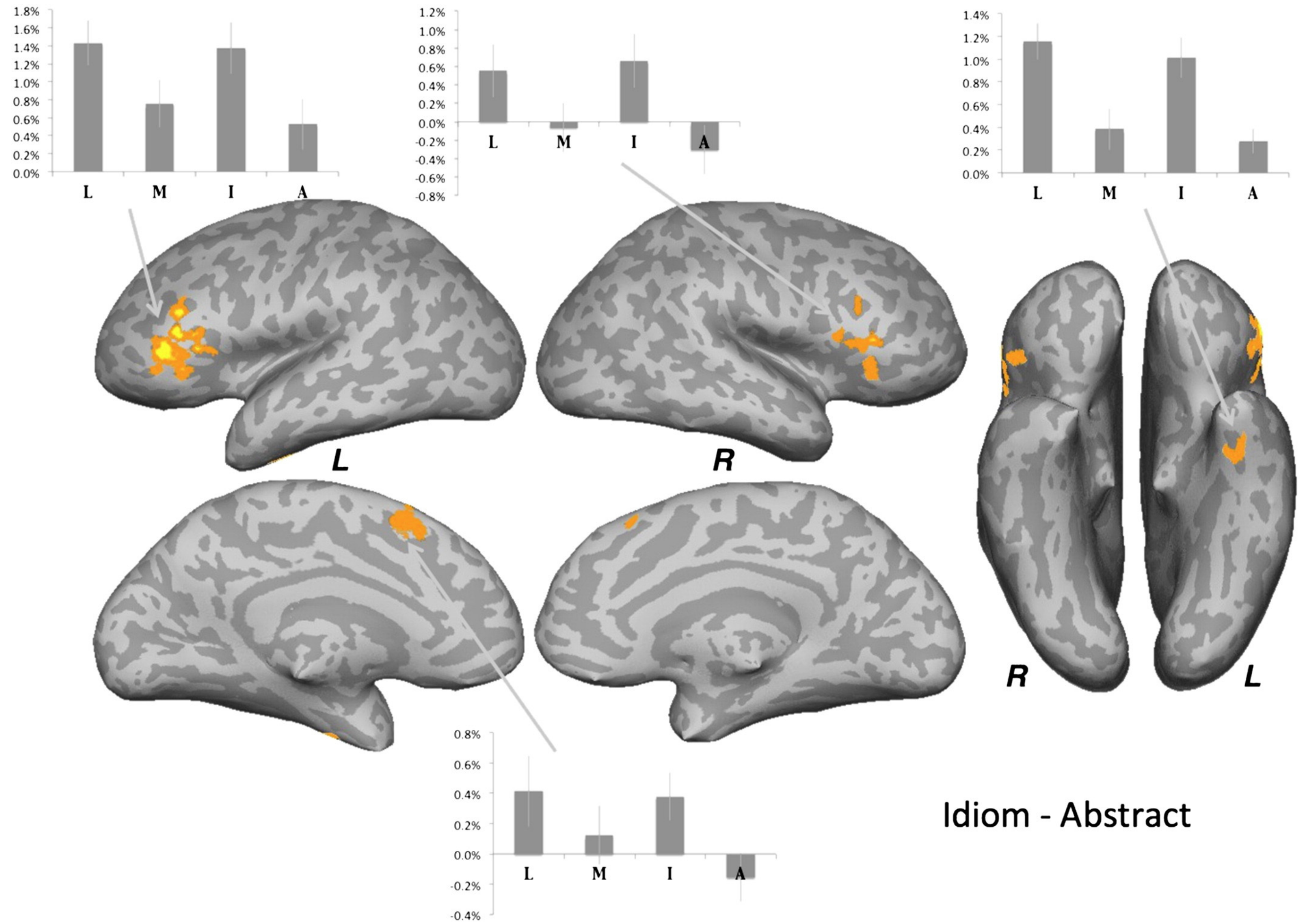

Fig. 3. Areas activated by the Idiom–Abstract contrast. See Fig. 1 caption for other details.

(Desai et al., 2011) suggested that metaphoric sentences engaged secondary sensory-motor regions, and relatively unfamiliar action metaphors even engaged primary motor regions. The present findings complement these results, in syntactically more complex sentences, by showing that when metaphors are very highly conventionalized, as is the case for idioms, engagement of sensory-motor systems is minimized

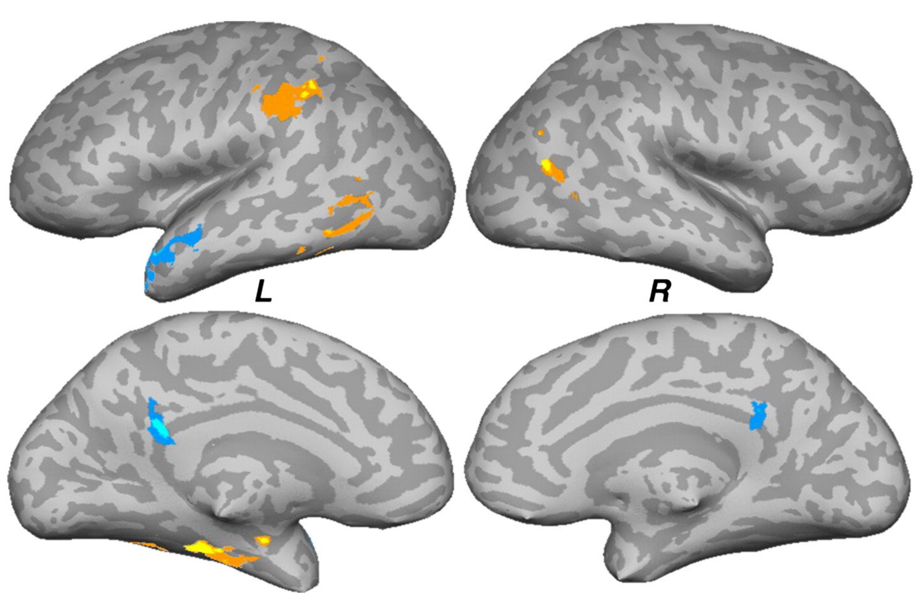

Fig. 4. Areas showing a linear trend across the four main conditions. Yellow-orange scale shows a positive trend (Literal > Metaphor > Idiom > Abstract); blue-cyan scale shows a negative trend (Literal < Metaphor < Idiom < Abstract).

or very brief. A linear trend of increasing activation from Abstract through Literal sentences was seen in the aIPL supporting a gradual abstraction, whereby the depth of simulation may vary in accordance with the degree of abstraction.

The metaphoric sentences also differ from literal sentences in noun imageability, because application of an action verb to an abstract entity is what makes the use metaphoric. However, activation in aIPL is unlikely to reflect noun imageability, given that it is present in the Metaphor > Abstract comparison, and also in a Motor > Visual comparison in a previous study (Desai et al., 2009) where both conditions contained identical concrete nouns. On the other hand, greater activation in the parahippocampal and fusiform gyri for literal sentences, and greater activation in posterior cingulate and the anterior temporal lobe for metaphoric sentences, could be partly due to noun imageability differences, as these regions are commonly implicated in concreteness effects (Wang et al., 2010). The region close to area MT, activated for Literal sentences, was also not activated for metaphoric sentences. This suggests that the inferior temporal activations are related to applications of action on concrete objects. 'Idea' in 'grasp an idea' is not seen as a physical object with the same level of visual detail as, say, a hammer, while the act of grasping retains some of its relationship with the motor and visuomotor integration system, making metaphors more strongly grounded in the motor and the dorsal visual stream than in the ventral visual "what" stream. However, both the posterior inferior temporal and the parahippocampal regions showed Abstract through Literal linear trends, suggesting that visual grounding is not completely eliminated for metaphors, and these activations are not just reflections of noun imageability, but are related to visual details in sentence comprehension that are reduced as the abstractness of meaning increases.

These results are consistent with other studies showing effects of context on sensory-motor activations. For example, van Dam et al. (2012) showed modulation of sensory-motor regions, including aIPL, based on whether motoric or visual features of the same items were emphasized by the task. In another study, morphologically simple motor verbs activated motor areas to a greater extent than abstract verbs, but this difference was absent for morphologically complex verbs based on motor stems (e.g., *begreifen*, to understand, based on *greifen*, to grasp) compared to complex abstract verbs (Rueschemeyer et al., 2007). In a behavioral study by Sato et al. (2008), a semantic task caused interference with button presses for hand action verbs relative to foot action verbs, but this was not the case for a lexical decision task.

Note that verbs in the Abstract condition were not completely "abstract" in the sense of having no association with actions, as they received a mean action rating of 3.55 on a scale of 1 to 7. There is evidence that abstract verbs denoting some type of transfer (e.g., *delegate*) involve motor systems (Glenberg et al., 2008). Nonetheless, abstract verbs used here clearly had a lower action association than action verbs, and Idiom sentences were processed much like Abstract sentences in terms of access to sensory-motor regions.

Idiom sentences differed from Abstract in their activation of the anterior IFG, medial SFG, and ventral anterior temporal lobe. These regions are possibly involved in the retrieval or selection of a second level of meaning that is available only after processing the group of words forming the idiom. However, the fact that Literal sentences activated these regions to the same extent does not support the view that they are specialized for idiomatic meaning storage or retrieval. One likely possibility is that the Literal and Idiom sentences both made greater demands on selection compared to the other conditions. Like literal sentences, idioms generally feature phrases with concrete objects (e.g., "plug" in "pull the plug"), allowing the possibility of a literal interpretation. This may require re-interpretation of the verb in light of the phrase-level context and retrieval of idiomatic meaning, requiring more cognitive control, although this process must happen efficiently such that response times are not affected and results in rapid and automatic comprehension of idioms and metaphors (Glucksberg, 2003). By design, lower frequency words were used in Literal sentences (in order to match them to other conditions in overall difficulty), and this lower lexical frequency may have resulted in IFG activation. In contrast, metaphors typically have a more abstract object (e.g., "support" in "pull the support"), which makes interpretation less ambiguous. The activation of the left anterior fusiform gyrus for Idiom and Literal (but not Abstract and Metaphoric) sentences may also be related to their higher noun imageability.

The dorsal/middle portion of the anterior temporal lobe was activated by Idiom > Literal sentences (Supplementary material, Fig. A). The same region was also activated by Metaphor > Literal (Supplementary material, Fig. B), and by the Abstract > Literal contrasts, and showed a linear trend of decreasing activation from Abstract through Literal sentences. This suggests a role of this region in abstract semantic processing, rather than a specialization for idiomatic processing. The posterior cingulate/precuneus region showed a similar activation profile: greater activation for Abstract, Metaphor, and Idiom relative to the Literal condition, and a negative linear trend. This region figures prominently in semantic processing (Binder et al., 2009) and has been identified as a connectivity hub (Buckner et al., 2009; Sporns et al., 2007). Disproportionally numerous connections in hubs make them suitable for integrating information from diverse sources. Lacking a direct connection to perceptual input, figurative and abstract language may rely more on integration of associated and contextual cues for their comprehension.

The results also speak to the issue of how the activation of sensory-motor areas for processing action metaphors should be interpreted. According to one view, metaphoric sentences activate motor regions not because the metaphoric meaning is grounded in motor systems, but because an alternative homonymous action meaning is activated simply due to the presence of the action verb in the sentence (Marslen-Wilson and Tyler, 1980; Swinney, 1979; Traugott and Dasher, 2002). The lack of motor activation for Idiom sentences, containing the same action verbs, demonstrates that the mere presence of an action verb is not sufficient for activating sensory-motor regions, at least as measured by fMRI. This highlights the important role context plays in semantic processing. In literal context and apt (but not completely conventionalized) metaphoric context, secondary sensory-motor systems are accessed and provide a basis for understanding even the figurative meaning. In a conventionalized, idiomatic context, this access is minimal in terms of magnitude or timing, as the abstract meaning conveyed by the idiom is more firmly established.

Various conditions had similar but not identical syntactic structure, and this can potentially contribute to some of the differences between the conditions (e.g., Keller et al., 2001). This is necessitated by the desire to keep the sentences readily interpretable, given that idioms and metaphors severely limit the syntactic and lexical choices. The modulation of regions such as aIPL, parahippocampal gyrus, and ITG is, however, consistent with our previous studies (Desai et al., 2009, 2011) that did use syntactically matched sentences.

Another limitation of the study stems from the temporal resolution of fMRI. The activations observed here represent responses temporally integrated over the entire event of sentence processing, and responses to individual words cannot be easily separated. Hence the possibility of brief access to motor systems for action verbs even in the idiomatic context cannot be ruled out. Indeed, Fernandino et al. (2013) found small but significant impairment for action idioms in Parkinson's patients relative to abstract sentences. Nonetheless, by showing clear modulation of activation for different types of sentences involving the same action verbs, the results demonstrate the flexible and context-sensitive nature of the semantic system. The findings argue for a graded view of conceptual embodiment (Binder and Desai, 2011), whereby the depth of reference to the source domain is modulated by factors such as familiarity, context, and task demands.

Acknowledgments

We thank William Graves for the script for ratings collection, and Edward Possing for his help with fMRI scanning. Supported by grants R03 DC008416 (RHD), R01 DC010783 (RHD), and R01 NS033576 (JRB) from the NIH.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.07.044.

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