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Engagement of the left extrastriate body area during body-part metaphor comprehension



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ABSTRACT

Grounded cognition explanations of metaphor comprehension predict activation of sensorimotor cortices relevant to the metaphor's source domain. We tested this prediction for body-part metaphors using functional magnetic resonance imaging while participants heard sentences containing metaphorical or literal references to body parts, and comparable control sentences. Localizer scans identified body-part-specific motor, somatosensory and visual cortical regions. Both subject- and item-wise analyses showed that, relative to control sentences, metaphorical but not literal sentences evoked limb metaphor-specific activity in the left extrastriate body area (EBA), paralleling the EBA's known visual limb-selectivity. The EBA focus exhibited resting-state functional connectivity with ipsilateral semantic processing regions. In some of these regions, the strength of resting-state connectivity correlated with individual preference for verbal processing. Effective connectivity analyses showed that, during metaphor comprehension, activity in some semantic regions drove that in the EBA. These results provide converging evidence for grounding of metaphor processing in domain-specific sensorimotor cortical activity.

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1. Introduction

The idea that knowledge is represented in abstract codes, distinct from the sensory modalities through which it was acquired (Fodor, 1975), is challenged by theories of grounded cognition. Such theories suggest that knowledge is anchored in modalityspecific codes derived from sensorimotor experience and that cognitive processes involve perceptual simulations (Barsalou, 2008). One approach to grounded cognition, conceptual metaphor theory (Lakoff & Johnson, 1980), argues that knowledge is structured into concepts by metaphorical mappings from sensorimotor experience. For example, when we speak of falling 'behind' schedule or looking 'forward' to an event, we are using our experience of the

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concrete domain of space to organize and understand the abstract domain of time (Boroditsky, 2000; Casasanto & Boroditsky, 2008).

These opposing views make very different predictions about the neural basis of metaphor processing. If mapping to sensorimotor experience is involved, then metaphor comprehension should activate brain regions involved in processing the sensorimotor domain from which the metaphor is derived. Consistent with this, textureselective somatosensory cortex was indeed activated during comprehension of metaphors related to texture (Lacey, Stilla, & Sathian, 2012). By contrast, if sensorimotor mappings are not involved, metaphor processing should involve only classical language regions. Studies reporting such a distribution of activity (e.g., Eviatar & Just, 2006; Lee & Dapretto, 2006; Rapp, Leube, Erb, Grodd, & Kircher, 2004) employed metaphors drawn from a variety of source domains and thus could not properly test the idea of domain-specific sensorimotor cortical recruitment.

A modified version of grounded cognition is suggested by the finding that, as the sense of a word becomes more abstract, neural processing is shifted to the anterior part of the region processing the relevant sensorimotor domain (Chatterjee, 2010; Chen, Widick, & Chatterjee, 2008). For example, motion-related metaphors activated the anterior portion of the middle temporal gyrus, a region known to be visually motion-sensitive (Chen et al., 2008). The finding that activation magnitude in motor-related brain regions decreases as the familiarity of metaphorical and literal sentences using action verbs increases (Desai, Binder, Conant, Mano, & Seidenberg, 2011) fits with the notion that the perceptual simulations underpinning grounded cognition are weaker or less detailed for more familiar metaphors, reflecting their conventionalization (Bowdle & Gentner, 2005).

The philosopher-rhetorician Giambattista Vico argued in 1744 that the "greater part of the expressions relating to inanimate things are formed by metaphor from the human body and its parts and from the human senses and passions" (Donoghue, 2014, p. 89). Body-related metaphors would thus seem ideal to test the different theories of the neural basis of metaphor. Previous imaging studies have concentrated on metaphorical or idiomatic uses of bodyrelated action verbs rather than explicitly named body parts. Action-related metaphors recruit cerebellar and left inferior parietal regions known to be active during movement (Desai, Conant, Binder, Park, & Seidenberg, 2013; Desai et al., 2011), and left premotor cortex shows body-part congruent activations for action metaphors (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006). But while action metaphors elicited somatotopic activation in motor cortex in one study (Boulenger, Hauk, & Pulvermüller, 2009), other studies failed to find activation in motor areas by action metaphors (Raposo, Moss, Stamatakis, & Tyler, 2009) or motion-related idioms, which instead activated a cortical region near visual motion-responsive areas (Chen et al., 2008). However, these studies are limited by the absence of functional localizers (Chen et al., 2008; Desai et al., 2013) or of control sentences matched for meaning (Aziz-Zadeh et al., 2006; Boulenger et al., 2009; Chen et al., 2008; Desai et al., 2011, 2013; Raposo et al., 2009).

Here, we used functional magnetic resonance imaging (fMRI) while participants listened to sentences containing body metaphors referring to faces, arms, or legs. A priori, grounded cognition accounts predict activity at or near several cortical loci during processing of body metaphors, not only in somatosensory and motor cortex, but also in visual cortex, particularly, the face-selective fusiform face area (FFA) (Kanwisher, McDermott, & Chun, 1997) and the extrastriate body area (EBA). The EBA responds selectively to images of whole bodies and body parts and is located in lateral occipitotemporal cortex (Downing, Jiang, Shuman, & Kanwisher, 2001), in the inferior temporal sulcus/middle temporal gyrus (ITS/MTG: Myers & Sowden, 2008; Taylor, Wiggett, & Downing, 2007; Weiner & Grill-Spector, 2011). Participants heard sentences using body-part words used in either metaphorical or literal contexts, with control sentences matched for meaning and also matched on lexical, semantic, and acoustic variables. In separate sessions, they underwent motor, somatosensory, and visual functional localizer scans. This design aimed to isolate the brain regions underlying both metaphorical and literal use of body-part words, and to determine whether they were in or near the visual, somatosensory or motor regions identified by the localizers. Thus, we could test the grounded cognition hypothesis that comprehension of body-part metaphors should engage sensorimotor cortices involved in processing body parts. Even though this hypothesis makes no specific prediction as to whether body-part metaphor comprehension is grounded in visual, somatosensory, or motor experience, our design covered all the possibilities. In addition, we collected resting-state fMRI data to examine whether body-selective areas active during metaphor processing exhibit functional connectivity with language-related areas and how this relates to individual preferences for visual imagery and verbal processing. Finally, we also carried out effective connectivity analysis of task-state fMRI data, in order to gain converging evidence with respect to the neural basis of metaphor processing.

2. Methods

2.1. Participants

Twelve people (six male, six female; mean age 23 years 6 months) took part in the main imaging experiment of this study. All were right-handed based on the validated subset of the Edinburgh handedness inventory (Raczkowski, Kalat, & Nebes, 1974) and none had taken part in the metaphor selection process described below. We excluded volunteers for whom American English was a second or non-native language in order to avoid potential confounds due to variable language ability. All participants gave informed consent and all procedures were approved by the Emory University Institutional Review Board.

2.2. Metaphor selection

We compiled a list of sentences containing body-part metaphors via deliberation, internet searches, and creating novel metaphors. We also compiled control sentences that matched the metaphorical ones for meaning. Wherever possible we minimized syntactic differences between metaphorical and control sentences (see below). A schematic of the stimulus generation and preparation process is provided in Fig. 1a.

The metaphors were restricted to those related to arms, legs and faces (or sub-parts thereof) because these body parts have readily identifiable cortical associations in motor, somatosensory, and visual cortex. The list was further constrained by the need for all of the sentences to be relatively short and, ideally, for each control sentence to be formed by substitution of a single word e.g., by changing 'she shouldered responsibility' to 'she took responsibility' - in order to minimize syntactic differences, which was possible in approximately 75% of the initial list. In the remainder, the metaphor consisted of a phrase and the control sentence contained a substituted, non-metaphorical phrase - e.g., 'she turned a blind eye' vs. 'she took no notice'. This exercise resulted in 69 metaphor-control pairs. We analyzed the numbers of words and syllables in each sentence, and the frequency and imageability of the operative word in each sentence (e.g., 'he had to foot the bill' vs. 'he had to pay the bill'), using the MRC Psycholinguistic Database 2.0 (Coltheart, 1981; Wilson, 1988) and cross-checking with published ratings (Gilhooly & Logie, 1980; Kucera & Francis, 1967; Toglia & Battig, 1978). We assumed a frequency of 1 for any word without a published frequency and conducted our own imageability ratings for words without a published rating, using instructions adapted from Toglia and Battig (1978). After making adjustments to reduce differences between metaphorical and control sentences for these linguistic variables, we tested the interpretability of the 69 metaphorical sentences, as outlined below, before selecting the final list.

Ten participants read each metaphorical sentence and provided their own interpretation of its meaning. Three independent judges read each participant's interpretations of each metaphorical sentence and rated them as plausible or not (regardless of the intended control sentence). We then calculated an interpretability score for each metaphorical sentence as the number of judges who rated an interpretation as plausible for each participant; thus the maximum score for each metaphorical sentence was 30 (10 participants \times 3 judges). A cut-off score of 21 (70%) gave 60 metaphorical sentences that were deemed easily interpretable. Of these, 23 related to the arm, 20 to the head, and 17 to the leg. (In order to

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