Brain & Language 122 (2012) 120–125

Contents lists available at SciVerse ScienceDirect

Brain & Language

journal homepage: www.elsevier.com/locate/b&l

Short Communication

Dissociating the representation of action- and sound-related concepts in middle temporal cortex

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ARTICLE INFO

Article history:
Accepted 24 May 2012
Available online 20 June 2012

Keywords:
Embodied cognition
Action-related concepts
Sound-related concepts
Language
Middle temporal gyrus
fMRI

ABSTRACT

Modality-specific models of conceptual memory propose close links between concepts and the sensory-motor systems. Neuroimaging studies found, in different subject groups, that action-related and sound-related concepts activated different parts of posterior middle temporal gyrus (pMTG), suggesting a modality-specific representation of conceptual features. However, as these different parts of pMTG are close to each other, it is possible that the observed anatomical difference is merely related to interindividual variability. In the present functional magnetic resonance imaging study, we now investigated within the same participant group a possible conceptual feature-specific organization in pMTG. Participants performed lexical decisions on sound-related (e.g., *telephone*) and action-related (*hammer*) words. Sound words elicited higher activity in anterior pMTG adjacent to auditory association cortex, but action-related words did so in posterior pMTG close to motion sensitive areas. These results confirm distinct conceptual representations of sound and action in pMTG, just adjacent to the respective modality-specific cortices.

1. Introduction

Conceptual representations contain categorically organized knowledge about the world, which form the central building block of human cognition and language (Humphreys, Riddoch, & Quinlan, 1988; Levelt, Roelofs, & Meyer, 1999). As concepts are essential constituents of word meaning, they provide semantic knowledge for language production and comprehension (Humphreys, Price, & Riddoch, 1999; Kiefer & Pulvermüller, 2011).

While the significance of conceptual knowledge for language and higher-level cognition is generally accepted, the functional and neural representation of concepts and word-related meanings is controversial. One class of models postulate an amodal system, where sensory or action-related inputs are transformed into a common amodal representation, in which original modality-specific information is lost (Anderson, 1983; Caramazza & Mahon, 2003; McClelland & Rogers, 2003). At a neural level, amodal theories locate storage of conceptual information in higher-level heteromodal association cortex. For instance, anterior temporal cortex (Rogers et al., 2004) as well as Wernicke's area comprised of posterior temporal and adjacent parietal cortex (de Zubicaray, Wilson, McMahon, & Muthiah, 2001; Gold et al., 2006) have been frequently considered to be the cortical seat of an amodal semantic system.

In contrast to this classical view of conceptual memory, modality-specific models propose close links between conceptual memory on the one hand and the sensory and motor systems on the other hand (Kiefer & Barsalou, 2012; Pulvermüller & Fadiga, 2010). They assume that concepts are embodied mental entities (Gallese & Lakoff, 2005; Kiefer & Pulvermüller, 2011; Pulvermüller, 2005), in the sense that they are constituted by neuronal activity in modality-specific brain areas representing sensory or action-related information (Barsalou, 2008; Kiefer, Sim, Liebich, Hauk, & Tanaka, 2007; Martin, 2007; Pulvermüller & Fadiga, 2010). Activation of these modality-specific cell assemblies forms the brain basis of concepts and word-related meanings (Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008).

The notion of a grounding of conceptual representations in modality-specific brain systems has received empirical support from an increasing number of neuropsychological and brain imaging studies (for reviews see, Kiefer & Pulvermüller, 2011; Pulvermüller & Fadiga, 2010) convincingly demonstrating that

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http://dx.doi.org/10.1016/j.bandl.2012.05.007

conceptual processing activates sensory and motor areas depending on the relevance of conceptual features (Hoenig, Sim, Bochev, Herrnberger, & Kiefer, 2008; Kiefer, 2005; Martin, Wiggs, Ungerleider, & Haxby, 1996).

One of the most consistent finding in this field of research is the involvement of a portion of posterior middle temporal gyrus (pMTG) and adjacent areas in superior temporal sulcus in the processing of manipulable objects (e.g. "hammer" or "drill") (Chao, Haxby, & Martin, 1999; Gerlach, 2007; Hoenig et al., 2008). Due to its proximity to motion-sensitive areas (Lewis, 2010), it has been suggested that this region codes action-related motion (Martin & Chao, 2001). In an anterior part of pMTG encompassing posterior superior temporal gyrus (pSTG), sound-related concepts such as "telephone" elicited higher activity compared with matched control concepts (Kiefer et al., 2008). Damage to this region selectively impaired access to sound-related concepts in a patient demonstrating the functional role of pMTG in representing conceptual sound information (Trumpp, Kliese, Hoenig, Haarmaier, & Kiefer, 2012). As pMTG is also involved in various forms of higher-level sound processing (Kraemer, Macrae, Green, & Kelley, 2005; Lewis et al., 2004), this area contributes to both perceptual and conceptual processing of sound information. In event-related potential (ERP) recordings, the processing of action-related (Pulvermüller, 2005) and sound-related concepts (Kiefer et al., 2008) compared with control concepts elicited ERP effects over fronto-central regions similar to motor and acoustically evoked potentials (Regan, 1989) within 200 ms after word onset. As these ERP effects emerged early, this activity most likely indicates rapid access to conceptual features rather than late post-conceptual imagery processes.

As MTG areas sensitive to action-related and sound-related concepts are in close neuroanatomical vicinity to each other, it could be argued that they subserve a common function in linguistic processing and do not differentially code conceptual features. In fact, activity in pMTG has been related to various aspects of semantic (Hoffmann, Pobric, Drakesmith, & Lambon Ralph, 2011), phonological (Hickok & Poeppel, 2007), and syntactic processing (Snijders et al., 2009). More specifically, pMTG has been suggested to be involved in amodal semantic processing such as activation of word meaning (Jung-Beeman, 2005), multisensory and/or amodal semantic integration (Beauchamp, Lee, Argall, & Martin, 2004; Hoffmann et al., 2011; Lewis, 2010) or semantic selection (de Zubicaray et al., 2001). According to such supramodal processing accounts of pMTG function, this area would merely serve as a modality-unspecific convergence zone (Damasio, 1989) that activates, integrates and selects distributed modality-specific features stored elsewhere in the brain into a coherent representation.

Previous work on feature-specific brain activation to action- and sound-related concepts had been performed with different subjects, thus allowing for the possibility that any difference in peak activation expressed in terms of standard neuroanatomical coordinates could certainly reflect between-subject differences or methodological differences between experimental setups. Therefore, and in spite of the fact that our previous neuroimaging study (Kiefer et al., 2008) indicated that activity in the anterior portion of pMTG selectively correlated with the relevance of sound-related (and not of action- or visual-related) conceptual features, the issue of feature-specificity of pMTG has to be further investigated.

Using functional magnetic resonance imaging (fMRI), the present study therefore assessed whether the anterior and posterior portions of pMTG, referred to as a-pMTG and p-pMTG, play a differential role in coding sound-related vs. action-related conceptual features. We investigated a possible feature-specific organization in pMTG within the same participant group, in order to rule out that interindividual anatomical differences can influence the observed activation pattern. As in our previous studies (e.g., Kiefer et al., 2008; Pulvermüller, Lutzenberger, & Preissl, 1999), we presented visual names of objects among pseudowords, on which participants performed lexical decisions. The lexical decision task induces an implicit access to conceptual-semantic word meaning (Kiefer, 2002), but does not afford explicit retrieval of specific conceptual information. Critical words named objects, for which either sound- (e.g., "telephone") or action-related conceptual features (e.g. "hammer") were of high semantic relevance (that is, they were important when defining the words' meaning; a telephone that does not ring is not a (good) telephone, and a not-graspable hammer is not a typical hammer). Control words for these critical conditions were also related to concrete well-imaginable objects but showed low semantic relevance of either acoustic ("pillow") or action features ("vase"). Word sets (high vs. low relevance of critical features) differed only with respect to the relevance of the critical conceptual features (Table 1), but were matched for confounding conceptual and linguistic variables (see Section 2). We expected that sound-related words elicit higher activity in a-pMTG compared with their control words. In contrast, action-related words should increase the MR signal in p-pMTG compared with their control words.

1.1. Results

1.1.1. Behavioral results

Separate two-tailed paired t-tests were performed on correct mean reaction time (RT) and mean error rate (ER) in the lexical decision task for action- and sound-related words (critical feature vs. corresponding control condition). This analysis yielded small, but significant differences in RT, but comparable ER (action-related vs. control words: 2.2 vs. 1.7, $t(19) = .94$, $p = .36$; sound-related vs. control words: 2.0 vs. 1.65, $t(19) = 1.0$, $p = .33$). Compared with control words, participants reacted slightly faster to action-related words (639.01 ms vs. 663.04 ms; $t(19) = -3.75$, $p < .01$). Responses to sound-related words however were slightly slower than to control words (663.79 ms vs. 653.88 ms; $t(19) = 2.77$, $p < .05$).

1.1.2. Neurophysiological results

Activity in left p-pMTG was greater for action-related words than action-control words ($t(19) = 2.18$, $p < .05$), whereas the MR signal to sound-related words did not differ from sound-control

Table 1
Conceptual and linguistic variables for the critical word sets referring to action-related and sound-related concepts as well as for the corresponding control word sets (action-control and sound-control).

	Action	Acoustic	Visual	Familiarity	Emotion	Word length	Word frequency
Action-related	4.40	1.76	4.18	4.06	2.61	7.66	29.91
Action control	1.77	1.60	4.26	3.83	2.49	7.55	33.45
p-Value	**<.001**	.31	.41	.06	.33	.79	.80
Sound-related	3.24	5.16	3.83	3.61	2.70	7.65	29.68
Sound control	3.30	1.12	3.98	3.87	2.54	7.5	28.58
p-Value	.65	**<.001**	.24	.08	.21	.74	.92