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Research report

Losing the sound of concepts: Damage to auditory association cortex impairs the processing of sound-related concepts

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ABSTRACT

Conceptual knowledge is classically supposed to be abstract and represented in an amodal unitary system, distinct from the sensory and motor brain systems. A more recent embodiment view of conceptual knowledge, however, proposes that concepts are grounded in distributed modality-specific brain areas which typically process sensory or actionrelated object information. Recent neuroimaging evidence suggested the significance of left auditory association cortex encompassing posterior superior and middle temporal gyrus in coding conceptual sound features of everyday objects. However, a causal role of this region in processing conceptual sound information has yet to be established. Here we had the unique chance to investigate a patient, JR, with a focal lesion in left posterior superior and middle temporal gyrus. To test the necessity of this region in conceptual and perceptual processing of sound information we administered four different experimental tasks to JR: Visual word recognition, category fluency, sound recognition and voice classification. Compared with a matched control group, patient JR was consistently impaired in conceptual processing of sound-related everyday objects (e.g., "bell"), while performance for non-sound-related everyday objects (e.g., "armchair"), animals, whether they typically produce sounds (e.g., "frog") or not (e.g., "tortoise"), and musical instruments (e.g., "guitar") was intact. An analogous deficit pattern in JR was also obtained for perceptual recognition of the corresponding sounds. Hence, damage to left auditory association cortex specifically impairs perceptual and conceptual processing of sounds from everyday objects. In support of modality-specific theories, these findings strongly evidence the necessity of auditory association cortex in coding sound-related conceptual information.

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1. Introduction

Concepts, the basic units of knowledge in human long-term memory (Barsalou et al., 2003), provide the cognitive foundation of communication, thought and action because they constitute the meaning of objects, events and abstract ideas (Humphreys et al., 1988; Levelt et al., 1999). While the significance of conceptual knowledge for higher-level cognition is generally accepted, the functional and neural representation of concepts is highly controversial. In particular, the involvement of the sensory and motor brain systems in coding conceptual knowledge is subject of a fierce debate. One class of models postulate an amodal system, where sensory or action-related inputs are transformed into common amodal representations, in which original modality-specific information is lost (Anderson, 1983; Caramazza and Mahon, 2003; McClelland and Rogers, 2003; Tyler and Moss, 2001). Amodal theories that sometimes even propose innate conceptual circuits (Mahon and Caramazza, 2009) locate storage of conceptual information in higher-level heteromodal association cortex for instance in anterior temporal areas close to the temporal pole (Rogers et al., 2004).

In contrast to this classical view of conceptual memory, more recent modality-specific models propose close links between conceptual memory on the one hand and the sensory and motor systems on the other hand (Kiefer and Barsalou, 2011). They assume that concepts are embodied mental entities (Gallese and Lakoff, 2005; Kiefer et al., 2008; Kiefer and Pulvermüller, 2011), that is they are essentially grounded in modality-specific brain areas which typically process sensory or action related information (Barsalou, 2008; James and Gauthier, 2003; Kiefer et al., 2007b; Kiefer and Spitzer, 2001; Martin, 2007; Pulvermüller and Fadiga, 2010). Activation of these modality-specific cell assemblies either bottom-up by words and objects, or top-down by thought constitutes the concept. Hence, access to concepts involves a partial reinstatement of brain activity during perception and action (Kiefer et al., 2008).

Support for modality-specific approaches comes from behavioural (Helbig et al., 2006), neuropsychological (Warrington and McCarthy, 1987), electrophysiological (Kiefer, 2005) and neuroimaging studies (Martin and Chao, 2001): They suggest that conceptual processing activates the sensory and motor brain systems. However, these findings have been questioned because they have not been consistently replicated (Gerlach, 2007). Furthermore, they could alternatively be explained by perceptual processing of the visual stimuli themselves (Gerlach et al., 1999; Kiefer, 2001), by the internal conceptual structure (Tyler and Moss, 2001) or by post-conceptual strategic processes such as visual imagery (Machery, 2007; Noppeney et al., 2006).

In an attempt to elucidate the neural basis of conceptual representations, a combined functional magnetic resonance imaging (fMRI)/event-related potential (ERP) study (Kiefer et al., 2008) has recently provided clear evidence for a link between perceptual and conceptual acoustic processing within auditory association cortex: Visual words denoting everyday objects, for which acoustic features are highly relevant (e.g., "telephone") and matched control words referring

to objects, for which sound features are less relevant (e.g., "table") were presented within a lexical decision task (word/pseudoword decision). Although orthographic and phonological processing may also contribute (Fujimaki et al., 2009), the lexical decision task induces an implicit access to conceptual word meaning (Dilkina et al., 2010; Kiefer, 2002), but does not afford explicit retrieval of specific conceptual information such as acoustic or action features (Simmons et al., 2008; Stone and Van Orden, 1993; Yap et al., 2006). It is therefore perfectly suited to study conceptual processing while minimizing strategic post-conceptual processing such as imagery.

In the Kiefer et al. (2008) study, sound-related words activated cell assemblies in left posterior superior and middle temporal gyri (pSTG/MTG) within the first 150 msec of stimulus processing, which overlapped with the activation pattern during real sound perception. Hence, sound-related concepts rapidly recruit auditory brain areas even when implicitly presented through visual words. Importantly, activity in pSTG/MTG during lexical decision increased with the ascending relevance of acoustic, but not visual or actionrelated conceptual features. This suggests that pSTG/MTG selectively codes acoustic conceptual features (Kiefer et al., 2008). In contrast to sound perception (Woolsey, 1982), conceptual acoustic information is processed in higher-level auditory cortex including pSTG/MTG (BA 21, 22), but not in lower-level auditory cortex (Heschl's gyrus). Neuroimaging studies demonstrate the involvement of pSTG/MTG in various forms of higher-level sound processing including recognition of human voices, sound recognition and music imagery (Belin et al., 2000; Kraemer et al., 2005; Lewis et al., 2004; Wheeler et al., 2000). A neuropsychological study shows that a lesion in this region impairs sound recognition (Clarke et al., 2000). The superior and middle temporal gyri receive input directly from the lower-level auditory areas and therefore form the proximal auditory association cortex (Nieuwenhuys et al., 2008). The observation that conceptual sound processing only involves auditory association cortex, but not primary auditory cortex, may reflect the absence of the vivid sound experience typically present in sound perception and sound imagery (Kiefer et al., 2008). In a continuation of this work (Hoenig et al., 2011), we showed that musical instruments activated the homologue right pSTG/MTG in musicians. This suggests that the right auditory association cortex codes acoustic conceptual features of musical instruments as a function of musical experience. The involvement of the right auditory association cortex in the representation of conceptual sound information for musical instruments is in line with findings demonstrating that this region is an essential prerequisite for music comprehension, particularly with respect to pitch perception of harmonic complex sounds such as the sounds of musical instruments - as well as for processing other aspects like contour (melody) and colour (timbre) (Halpern et al., 2004; Zatorre et al., 1992) or the semantics of music (Koelsch et al., 2004; Koelsch and Siebel, 2005). Interestingly, given that some forms of music mimic prosodic gestures, this right hemisphere region is also relevant for processing speech prosody, i.e., paralinguistic aspects of vocal processing like speaker gender, age and emotional state (Kotz et al., 2006; Schirmer and Kotz, 2006).

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