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Is the semantic category effect in the lateral temporal cortex due to motion property differences?

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abstract

Two specific areas within the posterior lateral temporal cortex (PLTC), the posterior superior temporal sulcus (pSTS) and the posterior middle temporal gyrus (pMTG), have been proposed to store different types of conceptual properties of motion: the pSTS encodes knowledge of articulated, biological motion, and the pMTG encodes knowledge about unarticulated, mechanical motion. We examined this hypothesis by comparing activation patterns evoked by verbs denoting biological motion (e.g., walk), mechanical motion (e.g., rotate), and low-motion events (e.g., ferment). Classical noun categories with different motion types (animals, tools, and buildings) were also tested and compared with previous findings of the categorical effects in PLTC. Replicating previous findings of different types of nouns, we observed stronger activation for animals than tools in the pSTS and stronger activation for tools compared to other types of nouns in the pMTG. However, such motion-type specific activation patterns only partly extended to verbs. Whereas the pSTS showed preferences for biological-motion verbs, no region within the pMTG was sensitive to verbs denoting mechanical motion. We speculate that the pMTG preference for tools is driven by properties other than mechanical motion, such as strong mappings between the visual form and motor-related representations.

Introduction

Conceptual knowledge refers to the meaning of objects, actions and words (Tulving, 1972). One of the most influential ideas about the representation of conceptual knowledge is that concepts are grounded in sensory and motor systems (for reviews, see Barsalou, 2008; Mahon and Caramazza, 2008; Martin, 2007; Thompson-Schill et al., 2006). Consistent with this notion, Beauchamp, Chao, Martin and colleagues proposed a specific hypothesis about the role of the posterior lateral temporal cortex (PLTC) in conceptual representation (Beauchamp et al., 2002, 2003; Chao et al., 1999; Martin, 2007). They suggested that two PLTC regions, the posterior superior temporal sulcus (pSTS) and the posterior middle temporal gyrus (pMTG), store different types of conceptual properties of motion. The pSTS region, which is involved in the perception of biological motion, stores knowledge of articulated, flexible motion that is usually associated with animate entities. The pMTG region that is anterior and inferior to the MT area stores knowledge about unarticulated, mechanical motion that is usually associated with artifacts. This hypothesis will be addressed as the PLTC-motion theory for simplicity.

The supporting evidence of the PLTC-motion theory comes mainly from two aspects of research. The first concerns the roles of the pSTS and pMTG in visual motion processing. The second involves studies investigating the conceptual processing of objects, actions and words. Beauchamp et al. (2002, 2003) investigated PLTC responses to video clips and point-light displays of moving humans and toolsfor humans m than in an artificial, unarticulated fashion (e.g., whole image rotating), and the pMTG showed a trend toward preferring unarticulated to articulated human motion, indicating that the effects cannot be fully attributed to the systematic differences of the specific objects being moved but rather are related to the type of motion.

These features of the PLTC in motion processing have been linked to its function in conceptual processing (Beauchamp et al., 2002; Chao

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et al., 1999). One set of evidence has shown that the PLTC encodes motion information not only in explicit visual processing but also in conceptual processing. Kourtzi and Kanwisher (2000) reported that the PLTC responded more strongly to pictures of scenes with implied motion (e.g., a picture of a cup in mid-fall) than those without, suggesting that the PLTC encodes stored information of motion (see also Senior et al., 2000). Martin and Weisberg (2003) also observed that different activation patterns in PLTC could originate from different interpretations of animations involving simple geometric shapes in motion: animations interpreted as human actions (e.g., swimming) elicited activation in bilateral pSTS, while those interpreted as artifact motions (e.g., billiards) activated the left pMTG (see also Castelli et al., 2000, 2002; Wheatley et al., 2007). Additional evidence is drawn from studies of different types of concepts. In general, the PLTC is activated when processing those concepts that contain high percentages of specific motion properties. For instance, Kemmerer et al. (2008) investigated the activation pattern of five kinds of verbs that were assumed to contain motion properties: running, speaking, hitting, cutting, and change of state. Every kind of verb, relative to the non-word baseline, activated the PLTC region more strongly. Similarly, other researchers found that the processing of actions yielded stronger activation in the PLTC than that of objects (e.g., Kable et al., 2005; Martin et al., 1995). These findings were proposed as supportive evidence for the role of PLTC in the conceptual processing of motion properties (but see Bedny et al., 2008). Within objects, tools activate the pMTG (mostly in the left hemisphere) more strongly than animals (e.g., Cappa et al., 1998; Chao et al., 1999, 2002; Devlin et al., 2002; Downing et al., 2006; Grossman et al., 2002a; Martin et al., 1996; Mummery et al., 1996, 1998; Perani et al., 1999; Phillips et al., 2002), and animals, although less frequently reported, activate the pSTS (particularly in the right hemisphere) more strongly than tools (e.g., Chao et al., 1999, 2002; Wheatley et al., 2005). These category-specific activation patterns have been reported using both picture and word stimuli across different tasks (e.g., viewing, naming, and reading), confirming the conceptual nature of the effects observed here. Indeed, ample neuropsychological literature has also documented the important role of PLTC in representing conceptual knowledge. A series of relevant studies found that patients with damage to the left PLTC typically exhibited deficits in processing action knowledge (e.g., Tranel et al., 2003) and had more difficulties in recognizing artifacts than in recognizing living things (Brambati et al., 2006; Campanella et al., 2010; Damasio et al., 2004; Gainotti, 2000). However, to our knowledge, no case presenting with category-specific deficits of animals or living things has been reported to involve a lesion in the PLTC. Therefore, the neuropsychological evidence cannot provide a clear argument for the distinct roles of pSTS and pMTG in representing concept knowledge.

The PLTC-motion theory cannot account for some findings published recently, however. For instance, Downing et al. (2006) compared pMTG activation evoked by viewing pictures of 20 different categories (e.g., tools, cars, faces, flowers, foods, clothes, fruits and vegetables). They found that tools induced the strongest activation

experimental package E-prime (Schneider et al., 2002) was used for stimulus presentation and response recording.

Magnetic resonance imaging data acquisition and analysis

In the scanner, the stimuli were back-projected via a video projector (refresh rate: 60 Hz; spatial resolution: 800 × 600) onto a translucent screen placed inside the scanner bore. Subjects viewed the stimuli through a mirror located above their eyes. Structural and functional MRI data were collected with a 3T Siemens Trio Tim scanner at the BNU MRI center. A high-resolution 3D structural data set was acquired with a 3D-MPRAGE sequence in the sagittal plane (TR: 2530 ms, TE: 3.39 ms, flip angle: 7 degree, matrix size: 256 × 256, 128 slices, voxel size: 1.33 × 1 × 1.33 mm, acquisition time: 8.12 min). BOLD signals were measured with an EPI sequence (TR: 2000 ms, TE: 30 ms, flip angle: 90, matrix size: 64 × 64, voxel size: 3.125 × 3.125 × 4 mm, inter-slice distance: 4.8 mm, number of slices: 32; slice orientation: axial).

MRI data were analyzed using BrainVoyager QX v2.0. The first six volumes of functional data in each run were discarded. The functional

Y = −64, Z = 25; X = 51, Y = −64, Z

proportion of positive results for these two contrasts was high (32/34, 94%), which indicates the consistency between the results of our study and those from the literature. In contrast, for the two contrasts related to the Mec-V condition, no ROIs showed any significantly positive effect. Three ROIs even showed a significant reversed pattern (i.e., Mec-V<Bio-V). The proportion of positive results was also at chance-level (18/34, 53%). To summarize, the general activation pattern for the pSTS ROIs is consistent with the PLTC-motion theory, while we did not observe any significant effect for the contrast of Bio-N vs. Low-N. For the ROIs in the pMTG, we failed to find any preference for verbs denoting mechanical motion from other verbs, although we replicated the previous findings of tool-specific activation.

The results of the second set of contrasts (in pSTS ROIs: Bio-V vs.

Contrasting results of previous neuroimaging studies and the current study. We calculated the distances from each coordinate derived from the published literature to every coordinate contained in the cluster we observed. The distance reported here is the minimal figure among them. The clusters in the bilateral pSTS were defined by the contrast Bio-V>Low-V + Mec-V, and the clusters in the left pMTG were defined by the contrast Mec-N>Low-N. See Table 1 for acronyms of different conditions.

Brain regions	References	Imaging methods	Stimuli	Tasks	Contrast	Talairach coordinates			Distance (mm)		No. of ROI in Supplemental Figure
						X	Y	Z	Target-Choice-results	Choice-results	
Left pSTS											
	Beauchamp et al., 2003	fMRI	video	Viewing	Human>Tool	−39	−59	15	1	4	1
	Bedny et al., 2008	fMRI	point-light	one-back task	Biological>Scrambled	−56	−53	14	0	0	-
	Chao et al., 1999	fMRI	picture	Viewing	Animal>Tool	−42	−59	19	0	2	2
			picture	Naming	Animal>Tool	−43	−63	8	8	2	3
			word	Reading	Animal>Tool	−64	−40	6	12	16	4
	Grezes et al., 2001	fMRI	point-light	direction judgment	Walker>Rotating cube	−38	−60	7	8	7	-
	Grossman and Blake, 2002	fMRI	point-light	one-back task	Biological>Scrambled	−43	−58	11	4	2	–
						−41	−53	12	3	5	–
						−47	−42	7	4	10	–
	Martin and Weisberg, 2003	fMRI	animation	viewing	Social>Mechanical	−49	−57	17	0	0	5
	Thompson et al., 2005	fMRI	mannequin	detecting gait changes	Intact>Apart	−64	−52	14	6	7	–
	Wheatley et al., 2005	fMRI	word	Reading	Living thing>Artifact	−58	−29	10	17	22	6
Right pSTS											
	Beauchamp et al.,										

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results in the pSTS and pMTG ROIs. In both regions, we observed categorical effects between word types even when they had comparable RTs, e.g., Bio-V>Low-V in the pSTS and Mec-N>Mec-V in the pMTG.

In the following section, we discuss our findings and the implications for the functional roles of the pSTS and the pMTG separately.

Categorical effects in the pSTS

The pSTS region specific to biological motion verbs observed here was overlapped with previously reported region preferring biological motion in visual perception (Beauchamp et al., 2002, 2003) as well as integration (Beauchamp et al., 2004), speech processing (Price, 2000), and face processing (Haxby et al., 2000; see a comprehensive discussion in Hein and Knight, 2008). It is possible that the function of the pSTS varies depending on task-dependent network connections (Hein and Knight, 2008). The question of how the pSTS contributes to a particular function, such as the processing of biological motion knowledge, must be further studied.

Although we replicated the previous finding of the Bio-N>Mec-N (i.e., animal>tool) effect in the pSTS (e.g., Chao et al., 1999), we did not observe a reliable preference for the Bio-N than for the Low-N (animal>building/landmark), as expected. This result is somewhat in conflict with a previous study using picture stimuli in which both buildings and tools evoked lower activation than animals in the pSTS (Chao et al., 1999). One obvious difference between these two studies is that they used pictures and we used words. It is possible that the pSTS is sensitive to explicit and implied biological motion and its response is directly tied to the nature of the visual input: pictures of animals contain implied biological motion while words do not. However, it is difficult to accommodate the whole pattern of results with this account. While the lack of pictorial visual input (e.g., no implied biological motion) in our study may explain why the difference between Bio-N words and Low-N words is smaller than when pictures were used, it does not explain why Bio-N words induced stronger activation than Mec-N words in both our study using semantic judgment and Chao et al. (1999) using word reading. We therefore speculate that the relatively high activation in the pSTS for buildings found in our study might be due to the specific characteristics of our stimuli. In Chao et al. (1999), all building stimuli were houses, and the tasks (picture viewing and matching) did not require conceptual processing explicitly. In contrast, the Low-N stimuli in our study were comprised of words denoting different types of buildings or landmarks, such as bridges, c77r

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