

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.

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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 tools and reported two critical findings about the roles of the PLTC in visual motion processing. First, both the pSTS and pMTG responded more strongly to moving humans and tools than to static ones and moving radial gratings. They also showed significant activation for point-light displays, which did not contain any color or form information. These results indicate that both the pSTS and pMTG regions contribute to the processing of high-level visual motion. Second, the pSTS was more strongly activated by video clips and point-light displays of human motion compared to those of tool motion, and the pMTG showed the reverse pattern. Critically, the pSTS demonstrated stronger activation for humans moving in a natural, articulated fashion (e.g., jumping) 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

within each grammatical class (Mean frequency count (SD): Bio-V 10.03 (13.29), Mec-V 17.23 (28.25), Low-V 8.83(12.38), Bio-N 11.93 (20.48), Mec-N 8.27 (13.12), and Low-N 11.53 (13.35); $t_s(58) < 1.50$, $p_s > 0.14$; Sun et al., 1997).

To confirm the motion property variations of our stimuli, we asked sixteen students to rate the motion contents of our stimuli. To illustrate the characteristics of different motion types, subjects were shown several cartoon examples of biological movements (e.g., a dog running or a man dancing), mechanical movements (e.g., scissors cutting), and still images with no movements (e.g., a standing guard or a house). Subjects were then asked to rate the extent to which the meaning of the target word brought to mind biological or mechanical motion on a 7-point scale (“1”: very low; “7”: very strong). Each subject saw each word twice in two separate blocks, one block to rate the biological motion and the other block to rate the mechanical motion, and the presentation orders of the two blocks were counterbalanced between subjects. The rating results were consistent with our intended manipulation for biological motion: Bio-V>Low-V, Bio-V>Mec-V, Bio-N>Low-N, and Bio-N>Mec-N ($t_s(58) > 23.5$, $p_s < .001$), and for mechanical motion: Mec-V>Low-V, Mec-V>Bio-V, Mec-N>Low-N, and Mec-N>Bio-N ($t_s(58) > 12.5$, $p_s < .001$) (see Fig. 1).

Whereas the target words were clearly manipulated into the six conditions varying by motion content and grammatical class, the corresponding choice words were not manipulated in the same way. Rather, the choice words were constructed so that they did not differ systematically across different conditions or, in the few cases where they did, the pattern paralleled that of the target words. In other words, they did not jeopardize the target manipulations. All conditions had choice words with low ratings for both biological and mechanical motions (ratings collected in the same way as the target words with 16 new subjects were between 2.24 and 3.33 for all

conditions, see Fig. 1). Although choice words were mostly nouns, words belonging to other grammatical classes were also included to prevent the participants from guessing the choice words before their presentation. Considering that the noun/verb differences were potential variables affecting the activation of some PLTC regions (e.g., Bedny et al., 2008), we examined the percentage of choice words that were more frequently used as verbs than nouns across the six experimental conditions and found that the distributions did not differ significantly ($\chi^2(5) = 7.4$, $p = 0.19$). A non-word judgment condition with Korean letters (e.g., 유포유포) was also included but not analyzed for the present study.

Procedure

The experiment consisted of 6 runs of 35 trials (30 word trials) presented in a pseudorandom order such that no more than three consecutive trials belonged to the same condition. In each trial, participants saw a target word followed by a pair of choice words. The target word appeared for 2, 4 or 6 s (randomized, mean = 4 s) after which it was replaced by a pair of choice words that appeared for 2 s. The word pairs were presented in a left–right fashion. Participants were instructed to choose which word was more closely related to the preceding target by pressing a button with either the right index or middle finger. A jittered trial interval of 2, 4 or 6 s (randomized, mean = 4 s) followed before the next trial started. The background was always black with a red dot fixation point presented at the center of the screen, and all words were white. Each participant first completed a practice run outside of the scanner, for which the procedure was identical to the trial runs in the formal experiment, but with different stimuli. Then they received a structural scan followed by the functional scan runs (i.e., the task). There were no trials during the first 12 s and the last 10 s of each run. Each run lasted 6.2 min. The

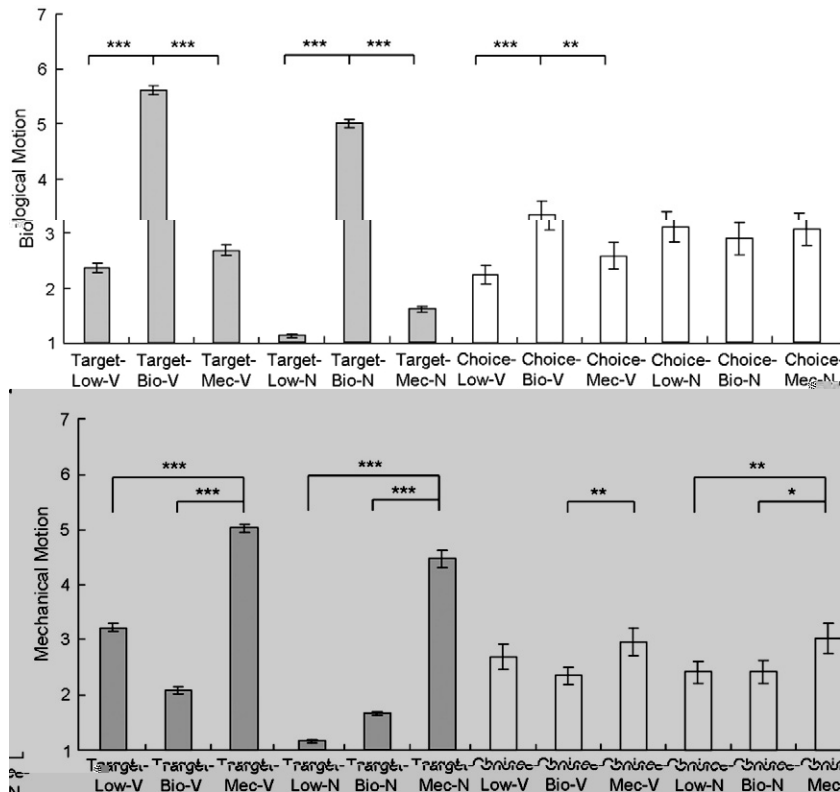


Fig. 1. Results of biological and mechanical motion ratings. Error bars depict the unbiased standard errors of the ratings of different types of words. The labels “Target-” and “Choice-” mean the Target- and Choice-words of a particular condition, respectively. See Table 1 for acronyms of different conditions.

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: $1.33 \times 1 \times 1.33$ 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: $3.125 \times 3.125 \times 4$ 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 data underwent preliminary processing that included slice scan time correction (temporal interpolation by cubic spline function), 3D motion correction (co-registration of each volume of the time series to the first remaining volume of the first run by three-plane mechanical body transformations and trilinear spatial interpolation), spatial smoothing (Gaussian filter, 6-mm Full Width Half Maximum), and temporal filtering (high-pass (GLM-Fourier): 2 sines/cosines). For each participant, functional data were then registered to her/his anatomical data. Finally, functional and anatomical volumes were transformed into a standardized space (Talairach and Tournoux, 1988).

All functional data were then analyzed using the general linear model (GLM). We included a total of 15 regressors, 6 corresponding to the onsets of the target words in each of the six conditions (called "Target-regressors" in the following text), 6 corresponding to the onsets of the choice words in each of the six conditions (called "Choice-regressors"), 2 corresponding to the target non-words and choice non-words, and 1 to model the amount of time that each target word was presented. A random effect GLM analysis was conducted to analyze the group data. Because previous literature has shown that grammatical class may be a variable affecting activation patterns of the PLTC (e.g., Bedny et al., 2008), and our primary interest lies in the differences among motion-type knowledge processing in whole brain analyses, we contrasted the motion type conditions within each grammatical class separately. Specifically, we planned the following contrasts comparing each motion type against the other two within nouns and verbs independently: Bio-V>Low-V, Bio-V>Mec-V, Mec-V>Low-V and Mec-V>Bio-V; and Bio-N>Low-N, Bio-N>Mec-N, Mec-N>Low-N and Mec-N>Bio-N. To further elucidate the regions showing specific preferences for certain motion conditions, we also conducted conjunction analyses on several contrasts involving the same condition (e.g., Bio-V>Low-V and Bio-V>Mec-V) with the "random effects of conjunction" analysis method in BrainVoyager. The false positive rate in whole brain analyses was controlled at

$Y = -64, Z = 25; X = 51, Y = -64, Z = 19$), Bio-V>Mec-V ($X = 48, Y = -49, Z = 10$), Bio-N>Mec-N ($X = 45, Y = -55, Z = 19$), and Mec-N>Low-N ($X = -45, Y = -52, Z = 4$). We further conducted a random effect analysis of the conjunction of different contrasts for each high-motion condition. For example, for the Mec-N, we analyzed the conjunction of the contrasts Mec-N>Low-N and Mec-N>Bio-N. The results showed that only the conjunction of Bio-V>Low-V and Bio-V>Mec-V evoked significant activation (corrected $\alpha < 0.05$: $p \leq 0.01, k \geq 30$) in the PLTC ($k = 127$, in right pSTS). Using a more lenient cluster threshold ($p \leq 0.01, k = 20$), we further observed that the conjunction of Mec-N>Low-N and Mec-N>Bio-N evoked a cluster in the left pMTG (87% overlapping with the Mec-N>

with a 6-mm diameter centered in the established coordinates (see Table 2 for the coordinates).

Again, the Target-Choice-results generally showed stronger effects than the Target- and Choice-results. The patterns of the Choice-results were similar to those of the Target-Choice-results, and the Target-results showed weak or no effects (see Supplemental material). In the following text, we will focus on and discuss the pattern of the Target-Choice-results.

The outcomes of the first set of contrasts (in pSTS ROIs: Bio-V vs. Low-V, Bio-V vs. Mec-V, Bio-N vs. Low-N and Bio-N vs. Mec-N; in pMTG ROIs: Mec-V vs. Low-V, Mec-V vs. Bio-V, Mec-N vs. Low-N and Mec-N vs. Bio-N) are summarized in Fig. 4 (see Supplemental material for detailed results of each contrast in each ROI). Two complementary statistical approaches were used to compile the results of ROI analyses. The first calculated the mean effect size of each contrast across different ROIs. We used standardized mean difference d as a measure of effect size (Rosenthal, 1991, p. 15 Table 2.2 Equation 2.13). As shown in Fig. 4(A), five of eight contrasts (Bio-V vs. Low-V, Bio-V vs. Mec-V, Bio-N vs. Mec-N, Mec-N vs. Low-N and Mec-N vs. Bio-N) identified large or medium positive effect sizes, while the other three

(Bio-N vs. Low-N, Mec-V vs. Low-V and Mec-V vs. Bio-V) showed very small effect sizes. While the effect size provided a quantitative measure of the overall activation difference across ROIs, the result might be driven by effect in one or two specific ROIs. We therefore further presented the percentages of ROIs showing significant positive and negative results (threshold: $t(13) > 2.16$, $p < 0.05$; $t(13) < 2.16$, $p < 0.05$), and those of ROIs showing positive and negative results ($t(13) > 0$; $t(13) \leq 0$) in Fig. 4(B). For ROIs in the pSTS, significant results for advantage of biological motion were observed in three of the four contrasts: Bio-V vs. Low-V (significant in 11 ROIs), Bio-V vs. Mec-V (significant in 9 ROIs), and Bio-N vs. Mec-N (significant in 7 ROIs). We further calculated the proportion of positive results. Among the 64 results (4 contrasts multiplied by 16 ROIs), 58 were positive (i.e., Bio-V > Low-V, Bio-V > Mec-V, Bio-N > Low-N, and Bio-N > Mec-N). This high proportion (91%) of positive results indicates that the overall activation pattern of pSTS ROIs is consistent with the expectation of the PLTC-motion theory. For ROIs in the pMTG, significant results for advantage of mechanical motion were only found in the two contrasts related to the Mec-N condition: Mec-N vs. Low-N (significant in 9 ROIs) and Mec-N vs. Bio-N (significant in 6 ROIs). In addition, the



Fig. 3. Activations of planned whole brain contrasts in the PLTC (corrected $\alpha < 0.05$; $p \leq 0.01$, $k \geq 30$): (A) PLTC-activations in the Target-Choice-results; (B) PLTC-activations in the Choice-results. The presentation coordinates of results follow the coordinates of peak voxels reported in Table 1. See Table 1 for acronyms of different conditions.

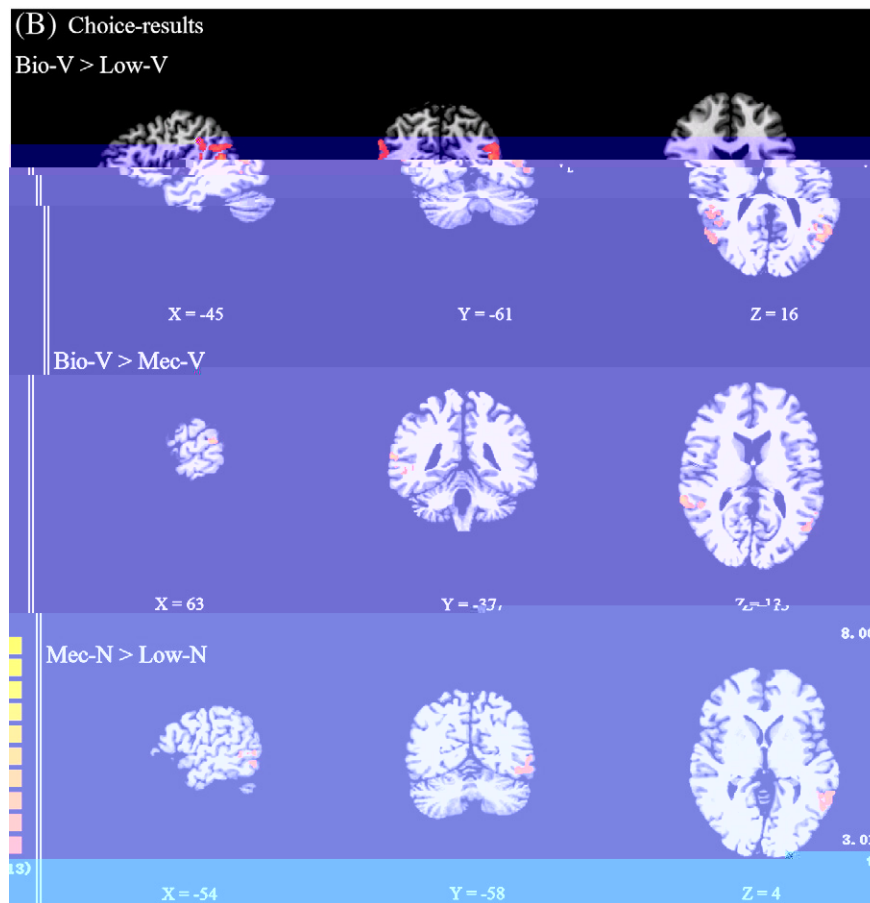


Fig. 3 (continued).

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. Bio-N; in pMTG ROIs: Mec-V vs. Mec-N) are shown in Fig. 4 (see Supplemental material for detailed results of each contrast in each ROI). As shown in Fig. 4(A), the effect size of the contrast between the Bio-V and Bio-N conditions was small, while a medium negative effect size was obtained when contrasting the Mec-V and Mec-N conditions. The percentage summarization of ROI results showed a similar pattern (Fig. 4(B)). Of the sixteen ROIs in the pSTS, one showed a marginally significant effect of BV > BN ($t(13) = 2.11$, $p = 0.05$), and none showed an effect of BV < BN. These indicate that the activation pattern of the pSTS was consistent with the biological motion account. Of the seventeen ROIs in the pMTG, we observed ten significant and one marginally significant ($t(13) = 2.10$, $p = 0.06$) effects of Mec-V < Mec-N, and we did not find any significant effect of Mec-V > Mec-N. In addition, the positive result

(i.e., Mec-V > Mec-N) was only observed in one ROI ($t(13) = 1.39$, $p = 0.19$). These indicate that the specificity for the Mec-N (tool) in the pMTG could not be fully explained by mechanical motion effects per se.

Discussion

In this fMRI study, we examined the PLTC-motion theory (Beauchamp et al., 2002, 2003; Chao et al., 1999; Martin, 2007), which hypothesizes that two regions (the pSTS and pMTG) in the PLTC process two different types of motion knowledge (biological vs. mechanical motion), using verbs denoting these different types of motion. We found that verbs denoting biological motion evoked higher activation than verbs denoting mechanical motion and low-motion events in bilateral pSTS, which is consistent with the predictions of the PLTC-motion theory. However, we did not observe any differences between verbs denoting mechanical motion and other types of verbs in the PLTC, even from analyses of 17 different ROIs defined by tool-specific, established coordinates in the pMTG. The manipulation of word categories also replicated some classical effects, such as the tool-selective activation in the left pMTG and the animal-selective activation in the right pSTS (e.g., Beauchamp et al., 2002, 2003; Chao et al., 1999), indicating the effectiveness of our design.

We further inspected whether the observed category-specific activation in the PLTC could be explained as an artifact of item difficulty reflected by the response times (RT). Indeed, the Mec-V induced a longer RT than Bio-V and Low-V, and Mec-N than Bio-N and Low-N. However, the RT differences cannot readily explain our categorical

Table 2
 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 picture	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., 2002	fMRI	video	same/different judgment	Human>Tool	47	-64	10	1	1	7
			video	human/tool judgment	Human>Tool	51	-69	10	4	0	8
	Beauchamp et al., 2003	fMRI	video	Viewing	Human>Tool	47	-56	15	0	3	9
	Bedny et al., 2008	fMRI	point-light	one-back task	Biological>Scrambled	57	-47	14	2	1	-
	Bonda et al., 1996	PET	point-light	Viewing	Biological>Random	56	-54	8	1	3	-
	Chao et al., 1999	fMRI	picture	Viewing	Animal>Tool	53	-54	16	0	1	10
			picture	Naming	Animal>Tool	52	-59	15	0	1	11
			picture	Matching	Animal>Tool	43	-61	12	2	5	12
	Chao et al., 2002	fMRI	picture	Naming	Animal>Tool	43	-40	19	8	3	13
	Grezes et al., 2001	fMRI	point-light	direction judgment	Walker>Rotating cube	51	-58	8	0	4	-
	Grossman and Blake, 2002	fMRI	point-light	one-back task	Biological>Scrambled	46	-48	12	0	2	-
						49	-53	11	1	2	-
						50	-33	4	6	3	-
	Martin and Weisberg, 2003	fMRI	animation	viewing	Social>Mechanical	56	-58	19	0	2	14
	Santi et al., 2003	fMRI	point-light	Viewing	Biological>Scrambled	63	-44	2	3	2	-
	Thompson et al., 2005	fMRI	mannequin	detecting gait changes	Intact>Apart	44	-40	16	5	1	-
	Vaina et al., 2001	fMRI	point-light	direction judgment	Walker>Letter	42	-56	14	2	4	-
	Wheatley et al., 2005	fMRI	word	Reading	Living thing>Artifact	47	-55	18	0	1	15
						60	-37	7	0	0	16
Left pMTG											
	Beauchamp et al., 2002	fMRI	video	human/tool judgment	Tool>Human	-46	-70	-4	3	6	1
			video	same/different judgment	Tool>Human	-38	-63	-6	6	6	2
	Beauchamp et al., 2003	fMRI	video	Viewing	Tool>Human	-50	-62	-6	2	1	3
	Cappa et al., 1998	PET	word	visual/functional knowledge judgment	Tool>Animal	-48	-64	-8	4	3	4
	Chao et al., 1999	fMRI	picture	Viewing	Tool>Animal	-46	-55	3	0	4	5
			picture	Matching	Tool>Animal	-47	-54	6	1	4	6
			word	Reading	Tool>Animal	-49	-52	-3	2	1	7
			picture	Naming	Tool>Animal	-45	-57	7	3	6	8
	Chao et al., 2002	fMRI	picture	Naming	Tool>Animal	-44	-55	2	0	4	9
	Downing et al., 2006	fMRI	picture	Viewing	Artifact>Animal	-49	-60	4	2	2	10
	Grossman et al., 2002a	fMRI	word	pleasantness decision	Tool>Animal	-60	-52	12	5	7	11
	Mahon et al., 2007	fMRI	picture	Naming	Tool RS	-49	-61	-7	3	1	-
	Martin and Weisberg, 2003	fMRI	animation	Viewing	Mechanical>Social	-49	-56	-9	3	1	12
						-34	-58	-7	10	7	13
	Martin et al., 1996	PET	picture	Naming	Tool>Animal	-36	-50	4	5	10	14
	Mummery et al., 1996	PET	word	category fluency	Artifact>Living thing	-42	-62	0	2	6	15
	Mummery et al., 1998	PET	word	attribute similarity judgment	Artifact>Living thing	-54	-54	0	0	3	16
	Perani et al., 1999	PET	word	matching	Tool>Animal	-44	-56	0	0	4	17
	Phillips et al., 2002	PET	picture and word	action/size knowledge judgment	Tool>Fruit	-55	-66	7	7	8	-

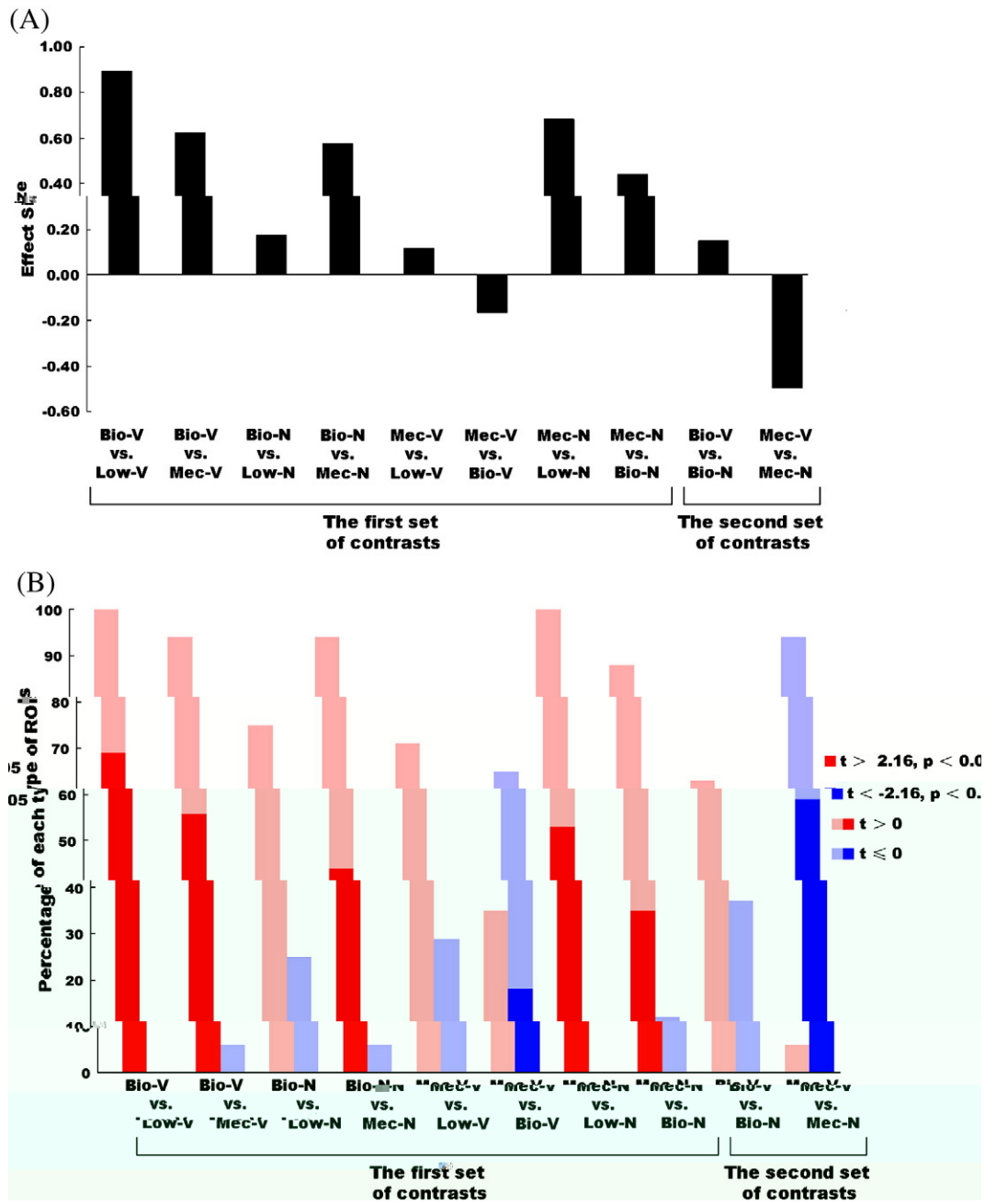


Fig. 4. A summary of the Target-Choice results of the ROI analyses. The acronyms on the horizontal axis represent the contrasts conducted in the ROI analyses (see Table 1 for acronyms of different conditions). Panel (A) shows the mean effect size (the standardized mean difference *d*) of each contrast. Panel (B) shows the percentages of ROIs showing 1) significant positive results ($t > 2.16, p < 0.05$; the red bar), 2) significant negative results ($t < -2.16, p < 0.05$; the dark blue bar), 3) positive results ($t > 0$; the combination of the red and pink bars) and 4) negative results ($t \leq 0$; the combination of the dark and light blue bars). See Supplemental Figure for the detailed results of each contrast in each ROI.

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 that preferring objects or words of animals (Chao et al., 1999) (see Table 2 and the section ROIs analysis). It has been commonly assumed that the latter effect can be explained by the former effect, i.e., the conceptual processing of animal items more strongly involves attributes of biological motion encoding/processing. Our current methods using verbs denoting such motion attributes provide direct evidence to support this hypothesis and consolidate the role of the pSTS in the conceptual processing of biological motion knowledge. The pSTS is also known to be involved in many other aspects of cognitive processing, such as theory of mind (Saxe, 2006), audiovisual

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 specifi

Appendix A. Materials used in the experiment

Target words (Choice words)

Bio-V

跌倒 Fall (路面 Pavement 湖心 Mid-lake); 临摹 Copy (毛 Writing brush 毛刷 Brush); 冲刺 Sprint (跑步 Run 跳绳 Skip); 脱 Break free (牢 Cage 乐园 Paradise); 摩 Massage (松弛 Relaxation 紧张 Tension); 采摘 Pick (水果 Fruit 糖果 Candy); 攀 Climb (手臂 Arm 头颅 Head); 抄写 Copy (记 Notes 录像 Video); 表演 Performance (明星 Star 英雄 Hero); 溜达 Stroll (海边 Seaside 海底 Seabed); 爬行 Crawl (婴儿 Baby 少年 Juvenile); Kick (拖鞋 Slippers 手套 Gloves); 行走 Walk (拐杖 Walking stick 熨斗 Iron); 抚摸 Caress (宠物 跌脱StrollJuvenile0TD)nt2537,

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