NeuroImage 55 (2011) 1853–1864

Contents lists available at ScienceDirect

NeuroImage

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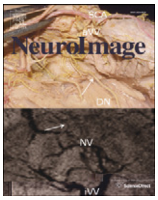

Is the semantic category effect in the lateral temporal cortex due to motion property differences?

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A R T I C L E   I N F O

Article history:
Received 17 August 2010
Revised 4 January 2011
Accepted 13 January 2011
Available online 20 January 2011

Keywords:
Semantic category
Motion knowledge
Biological motion
Mechanical motion
Posterior superior temporal sulcus (pSTS)
Posterior middle temporal gyrus (pMTG)

A B S T R A C T

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 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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doi:10.1016/j.neuroimage.2011.01.039

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 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); s (58)<1.50, 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 (s (58)>23.5, s<.001), and for mechanical motion: Mec-V>Low-V, Mec-V>Bio-V, Mec-N>Low-N, and Mec-N>Bio-N (s (58)>12.5, 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 ($\chi^2(5)=7.4$, $=0.19$). A non-word judgment condition with Korean letters (e.g., 유유) was also included but not analyzed for the present study.

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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

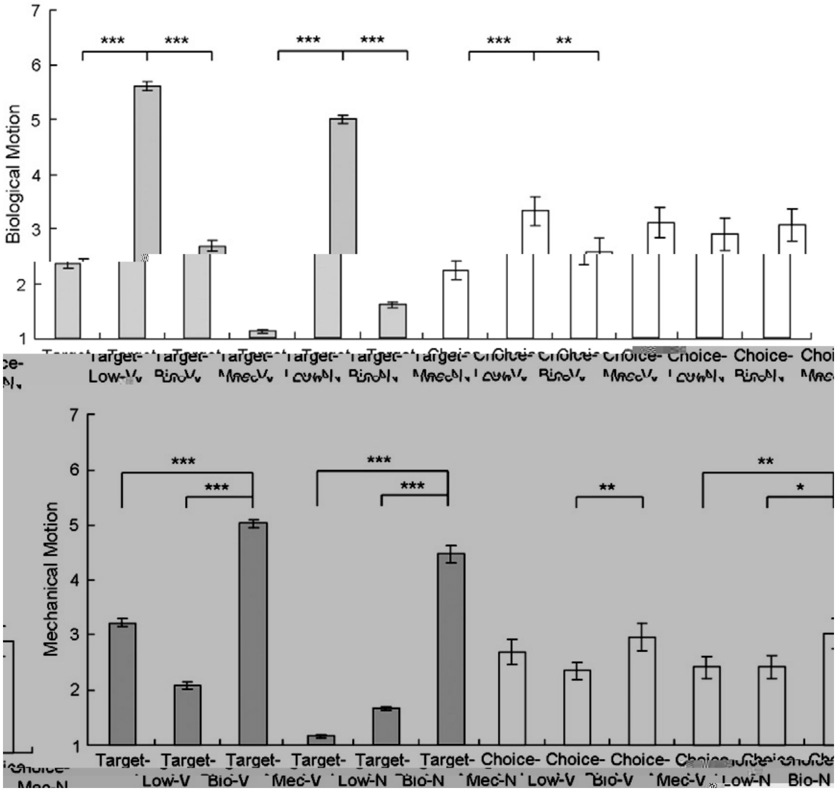

Fig. 1. Results of biological and mechanical motion ratings. Error bars depict the unbiased standard errors of the ratings of different types of words. The labels "Target-" and "Choice-" mean the Target- and Choice-words of a particular condition, respectively. See Table 1 for acronyms of different conditions.

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

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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 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 $\alpha<0.05$ (corrected) using the cluster-level statistical threshold estimator of Brain Voyager (≤ 0.01, ≥ 30).

In region-of-interest (ROI) analyses, we defined ROIs on the basis of relevant coordinates reported in the literature and then carried out analyses using mean β-values for different regressors in each ROI. Two sets of contrasts were conducted in these ROIs. The first set was similar to the one used in the whole brain analyses. For ROIs in the pSTS, the contrasts of Bio-V vs. Low-V, Bio-V vs. Mec-V, Bio-N vs. Low-N and Bio-N vs. Mec-N were conducted. And for ROIs in the pMTG, the contrasts of Mec-V vs. Low-V, Mec-V vs. Bio-V, Mec-N vs. Low-N and Mec-N vs. Bio-N were analyzed. The PLTC-motion theory predicts that the high biological- and mechanical-motion conditions would evoke stronger activation in pSTS and pMTG, respectively. The second set of contrasts included the comparisons between noun- and verb-conditions within the same motion type (i.e., Bio-V vs. Bio-N in the pSTS; Mec-V vs. Mec-N in the pMTG). If verb conditions elicited higher activation than noun conditions in the corresponding regions related to specific motion types, then the activation pattern could be attributed to either the high motion ratings of verbs relative to nouns or the grammatical effect (i.e., verb>noun) proposed by Bedny et al. (2008). However, if a reverse pattern was observed, i.e., stronger activation for nouns than for verbs, then the category-specific activation pattern observed for the Bio-N (animal) and the Mec-N (tool) in these areas could not be fully explained by the motion properties per se.

For both the whole brain and ROI analyses, we simultaneously gained two sets of results: 1) individual results of the Target-regressors and Choice-regressors, in which we investigated the effect of each of these two types of regressors independently; 2) combinational results of these two types of regressors, in which we investigated the overall effects. We assume that Target- and Choice-regressors could both capture the conceptual processing of target words in the current experimental paradigm. Specifically, the Target-regressor reflected the processing of conceptual information that was automatically activated when the target words were viewed (Meyer and Schvaneveldt, 1971), and the Choice-regressor reflected the processing of conceptual associations between target and choice words. We indeed found that combinational results showed stronger categorical-specific activation than the individual ones across our analyses (see the Results section). This result confirmed our assumption that both the Target- and Choice-regressors could reflect the conceptual processing of target-words. Even so, to have a complete picture for our result patterns, we presented these two sets of results in parallel. For the sake of simplicity, individual results of Target-regressors, those of Choice-regressors, and the combinational results are shorted in the following text as the Target-results, Choice-results, and Target-Choice-results, respectively.

Results

The data of two subjects (both females) were discarded in all subsequent analyses:a978.9(for)-203.7llo5(a920.2(bhaviortal)-210.4(c(cuacyt)-

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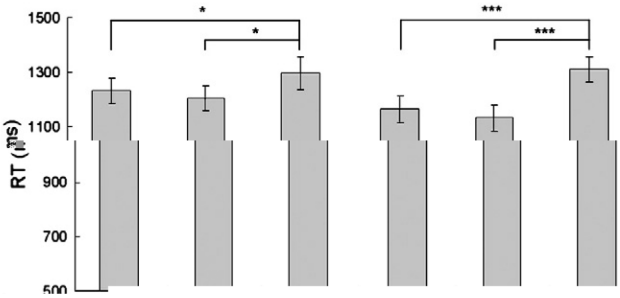

Fig. 2. Response time (RT) and accuracy 1(results.)-217.5(Error)-218.9(bars)-217.9(depict)-220.9(the)-219.2(unbiased)-228.2(standard)TJ-2.9342-1.3426TD(errors)-357.4eof RTs accuracies

=−64, =25; =51, =−64, =19), Bio-V>Mec-V (=48, = −49, =10), Bio-N>Mec-N (=45, =−55, =19), and Mec-N>Low-N (=−45, =−52, =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 et the contrasts Low-N Mec-N and Mec-N>Bio-Nt The results showed that enly the cnjunctin f Bio-V>Low-V and Bie V>Mec-V evoked significant activation (corrected ≤0.01, =20), we efur ther obse1(t)r ved

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Mec-N>Low-N and Mec-N>BiN evoked a cluster in the left pMTG (87% overlapping witt the Mec-N >Low-N activationf the Mec-N thane Bi-N einhe pMTGe.

Compared wi te similar patterns activation levels ein general (see Table 1 and Fig. 3 for details). However, we did not find any signi

possible reason for t null results in the Target-results, we compared the β-values all Target-regressors to Choice-regressors, and found that most brain regions much activation the Target-regressors than for the Choice-regressors. The relatively low activation level the Target-regressors might lead to a low8(signal-to-)TJ0-1

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We scrutinized consistency between te critical regions in the present study and related results in the literature. First, for the ehemispheric asymmetries, t eright-hemisphere dominance Bi and Bi the left-hemisphere dominance Mec-N we found here were in accordance with previous findings in

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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 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: $(13)>2.16$, <0.05; $(13)<2.16$, <0.05), and those of ROIs showing positive and negative results ($(13)>0$; $(13)\leq 0$) 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

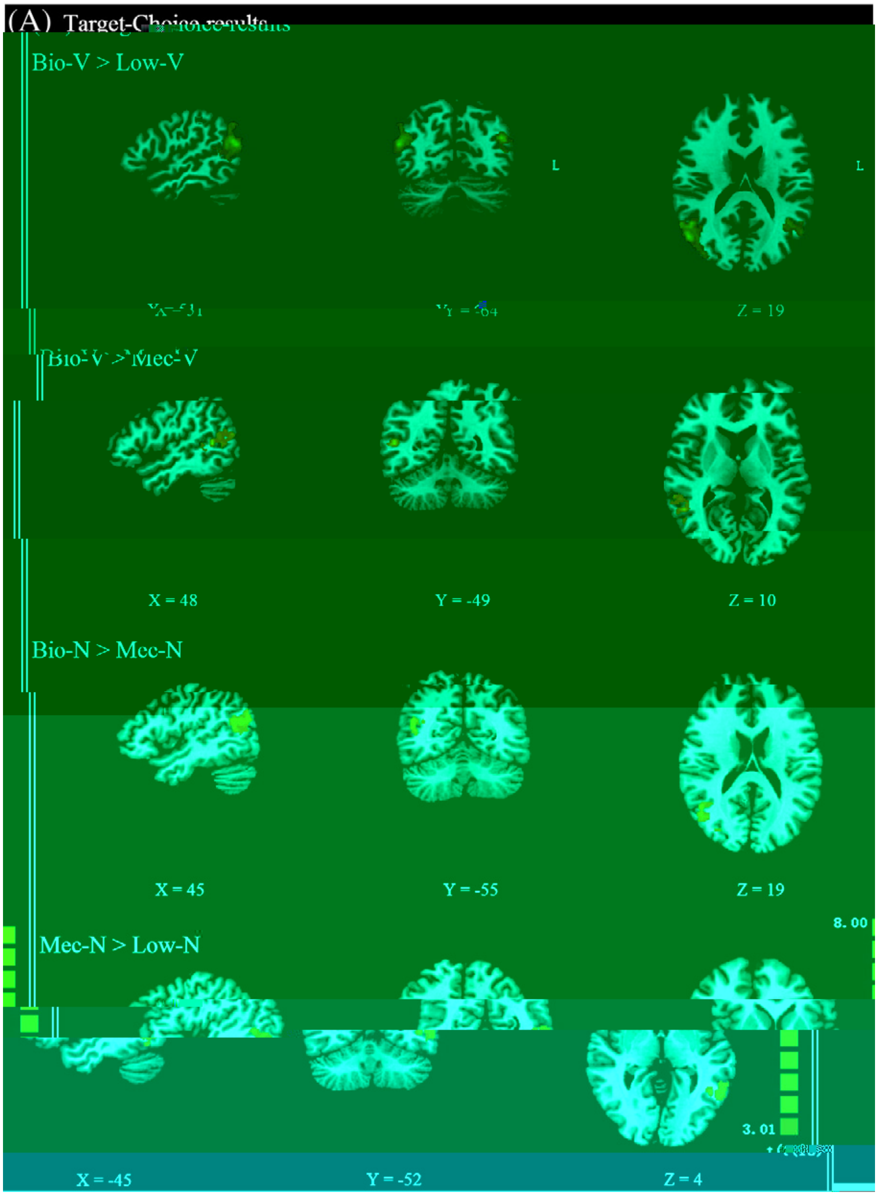

Fig. 3. Activations of planned whole brain contrasts in the PLTC (corrected $\alpha<0.05$: ≤ 0.01, ≥ 30): (A) PLTC-activations in the Target-Choice-results; (B) PLTC-activations in the Choice-results. The presentation coordinates of results follow the coordinates of peak voxels reported in Table 1. See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

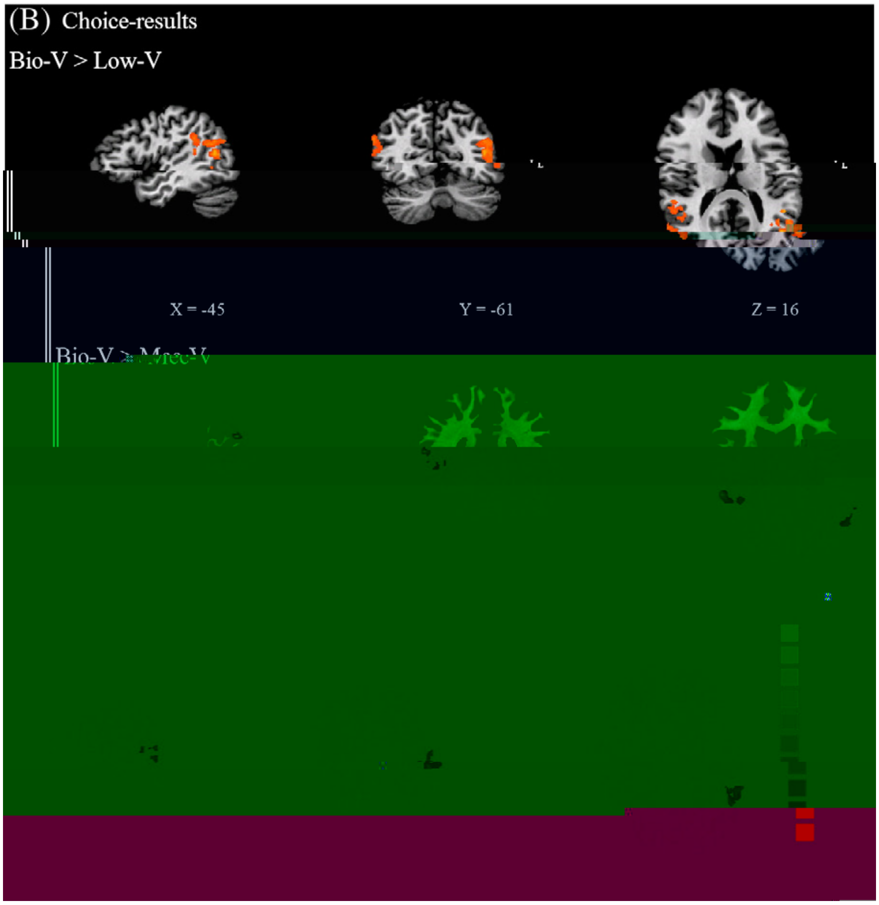

Fig. 3 (*continued*).

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
									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., 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	–

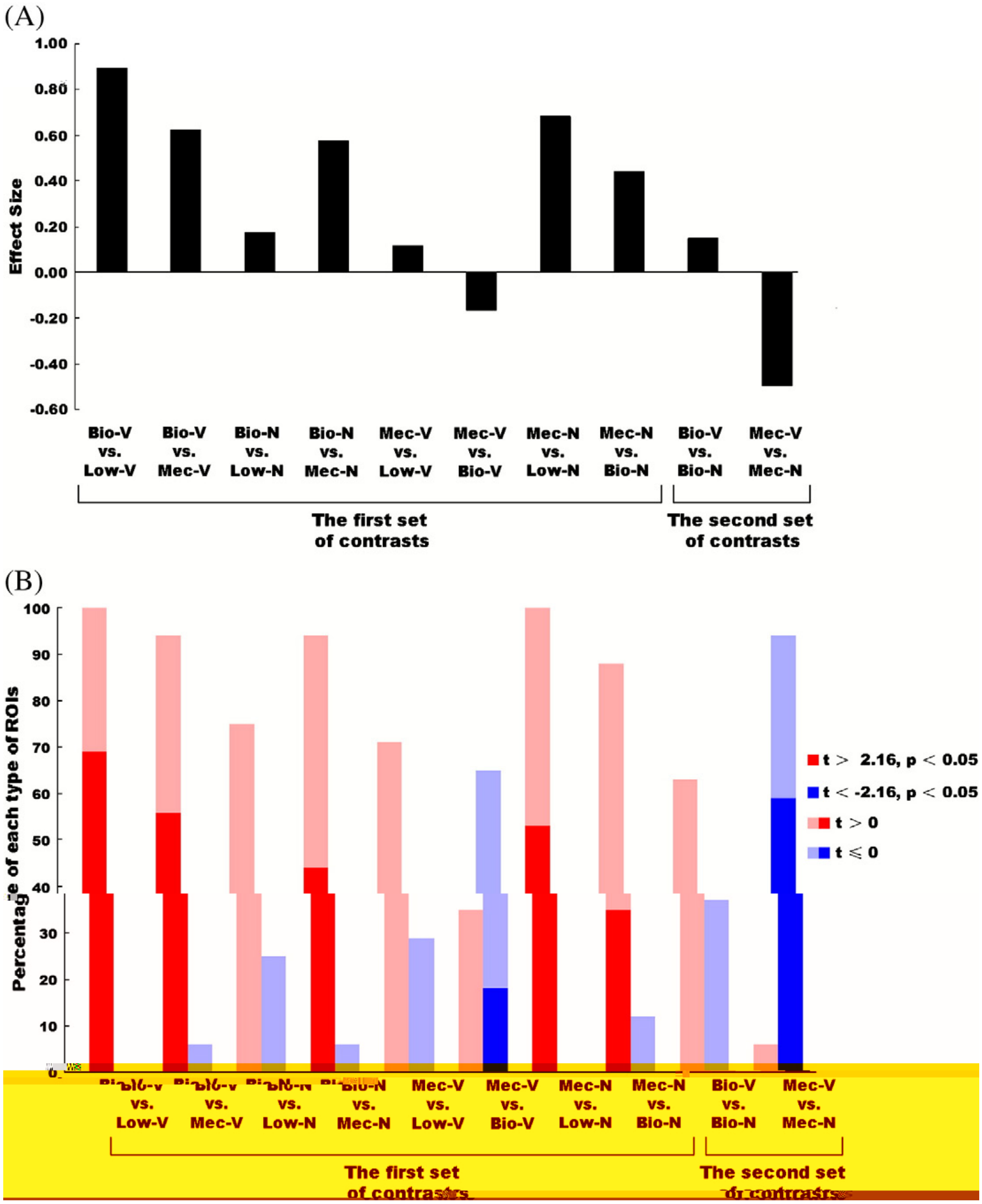

Fig. 4. A summary of the Target-Choice-results of the ROI analyses. The acronyms on the horizontal axis represent the contrasts conducted in the ROI analyses (see Table 1 for acronyms of different conditions). Panel (A) shows the mean effect size (the standardized mean difference d) of each contrast.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

e o ic e ec i e

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 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, cinemas, stations, or parks. One important component of the conceptual representation of these words is the specific human activity associated with them, which may lead to activation of systems addressing biological motion, especially in the current task that required the evaluation of the conceptual association between different concepts explicitly.

e o ic e ec i e

In contrast to the strong effect for Bio-V in the pSTS as predicted by the PLTC-motion theory, no specific effect for the Mec-V was observed in the pMTG. However, we did replicate the previous finding of the Mec-N (tool)-specific activation in the pMTG (e.g., Chao et al., 1999). To reiterate, the PLTC-motion theory explains the tool specific activation in the pMTG by assuming that the pMTG processes mechanical motion and that tools have relatively rich mechanical motion properties. It therefore directly predicts that verbs denoting such mechanical motion should induce stronger activation here than other types of verbs, but that outcome is not what we observed. This "null result" of a mechanical motion effect of verbs was not likely due to a lack of statistical power because we observed tool-specific effects here. Specifically, we examined the mechanical motion effect in verbs (Mec-V>Low-V or Mec-V>Bio-V) within 17 ROIs defined by coordinates reported in the literature and did not observe any significant effect for Mec-V. In addition, we directly compared the activation levels of Mec-N and Mec-V in those pMTG ROIs and found strong effects of higher activation for Mec-N than Mec-V, further indicating that the preference for Mec-N of the pMTG could not be fully explained by the mechanical motion effects.

If the pMTG is not sensitive to the processing of mechanical motion knowledge in general, then how can the tool-specific activation in the pMTG be explained? Previous evidence from neuroimaging as well as neuropsychological studies indicated that the tool-specificity in pMTG should be related to the manipulation of tools (Campanella et al., 2010; Kellenbach et al., 2003; Tranel et al., 2003). There are at least two other aspects of tool-manipulation that may be responsible for the pMTG activation: 1) other motion or motor properties associated with tools, such as hand movements or manipulations; or 2) the significance of visual–motor integration for tool concept processing.

For the first possibility, we may consider whether there is evidence showing that the pMTG prefers verbs denoting hand movements or manipulations. Noppeney et al. (2005) contrasted verbs denoting hand movements and those denoting whole-body movements and found that both conditions evoked similar responses in the pMTG. Saccuman et al. (2006) compared activation patterns of manipulable and non-manipulable verbs and observed that manipulable verbs showed advantages in the parietal region and the temporo-parieto-occipital junction but not the pMTG. Tyler et al. (2003) contrasted biological actions (e.g., attacking and swimming) and actions associated with tools (e.g., drilling and welding) in the ROI analyses of the pMTG and found stronger responses for biological actions. These findings suggest that the tool specific activation of the pMTG is not readily attributable to hand movements or manipulations that are associated with tools.

The second potential account for the tool-specific activation of the pMTG is that visual–motor integration is particularly important for the conceptual processing of tools and that the pMTG plays a specific role in such multi-modal integration. The pMTG region may be a suitable candidate for multi-modal integration because it is located between the primary sensory regions for hearing, motor/touch and vision (Lewis et al., 2005). Indeed, Beauchamp et al. (2004) found that pMTG regions, along with the pSTS, showed stronger activation when auditory and visual object features were presented together than when they were presented in a single modality. Interestingly, these audiovisual integrating regions were partially overlapped with regions showing categorical effects for tools in the pMTG. Another finding of potential relevance concerns the functional connectivity between the tool-specific pMTG region and other regions that are assumed to represent different types of tool properties. Mahon et al. (2007) reported that the left pMTG, left medial fusiform gyrus and left inferior parietal lobule show similar stimulus-specific repetition suppression (RS) patterns for tools and that there was strong functional connectivity among these regions, indicating that they constitute a neural circuit for tool processing. The left medial fusiform gyrus presumably processes the visual form information of tools, and the left inferior parietal lobule processes motor commands associated with tool use (Chao et al., 1999; Chao and Martin, 2000; Mahon et al., 2007). Therefore, we speculate that the pMTG plays the role of associating or mapping the visual and motor representations of concepts and that the tool-specificity of the pMTG reflects that the concepts of tools, compared with those of other objects, have stronger mappings between the visual form and motor representations (Lin et al., in press; Magnie et al., 2003).

In conclusion, we observed that the pSTS showed sensitivity for both nouns and verbs containing rich biological motion knowledge and that the pMTG showed preferences for tools but not for verbs denoting such mechanical motion properties. These results indicate that the pSTS is indeed involved in the processing of biological motion knowledge, as proposed by the PLTC-motion theory, and that the tool-specific activation in the pMTG may be explained by the properties of tools other than mechanical motion knowledge, such as strong mappings between the visual form and motor-related representations.

Supplementary materials related to this article can be found online at doi:10.1016/j.neuroimage.2011.01.039.

Acknowledgments

This study was funded by the NSFC (30770715, 30700224), BJSF (7082051) and NSSFC (07CYY009). We thank Xi Yu for helpful discussions.

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 (毛笔 Writing brush 毛刷 Brush); 冲刺 Sprint (跑步 Run 跳绳 Skip); 挣脱 Break free (牢笼 Cage 乐园 Paradise); 按摩 Massage (松弛 Relaxation 紧张 Tension); 采摘 Pick (水果 Fruit 糖果 Candy); 攀援 Climb (手臂 Arm 头颅 Head); 抄写 Copy (笔记 Notes 录像 Video); 表演 Performance (▫ ▫ Star 英雄 Hero); 溜达 Stroll (海边 Seaside 海底 Seabed); 爬行 Crawl (▫ 儿 Baby 少年 Juvenile); 踢蹬 Kick (拖鞋 Slippers 手套 Gloves); 行走 Walk (拐杖 Walking stick 熨斗 Iron); 抚摸 Caress (宠物 Pet 猛兽 Beast); 攀登 Climb (山峰 Mountain peak 湖泊 Lake); 殴打 Assault (拳头 Fist 枕头 Pillow); 搏斗 Struggle (战士 Soldier 博士 Doctor); 玩耍 Play (木马 Trojan 骡马 Mule); 追逐 Pursue (前后 Before and after 左右 Left and right); 哆嗦 Thrill (寒冷 Cold 温 ▫ Warm); 坐下 Sit down (椅子 Chair 桌子 Table); 嬉戏 Play (伙伴 Partner 老师 Teacher); 奔跑 Run (迅速 Rapid 高超 Superb); 拥抱 Hug (亲吻 Kiss 跪拜 Worship on bended knees); 搂抱 Cuddle (情侣 Couples 仇敌 Enemy); 起跑 Get off the mark (赛道 Circuit 走廊 Corridor); 搀扶 Support sb. with hand (衰老 Senescence 强壮 Strong); 躲闪 Dodge (攻击 Attack 诅咒 Curse); 逃跑 Flee (危险 Danger 骄傲 Proud); 跪下 Kneel (拜佛 To worship Buddha 乘车 Travel)
Mec-V
下降 Descend (电梯 Elevator 电话 Phone); 旋转 Rotate (电扇 Electric fan 折扇 Folding Fan); 移动 Move (运输 Transport 积压 Backlog); 流动 Flow (海水 Seawater 岩石 Rock); 反弹 Rebound (篮球 Basketball 铅球 Shot Put); 滴落 Drip (牛奶 Milk 饼干 Biscuit); 倾泻 Pour (江水 River 井水 Well water); 喷涌 Spew (石油 Petroleum 香油 Sesame oil); 倒塌 Collapse (受伤 Injure 传染 Infect); 飞溅 Splash (湖面 Lake surface 湖底 Lakebed); 飘扬 Wave (吹拂 Sway 捶打 Beat); 陨落 Fall (流 ▫ Meteor 太阳 Sun); 爆炸 Explosion (战争 War 和平 Peace); 喷射 Jet (火焰 Flame 柳絮 Catkin); 降落 Land (空军 Air force 陆军 Land force); 坠落 Fall (飞行 Flight 航海 Navigation); 滚落 Tumble (山坡 Hillside 农田 Farmland); 飘荡 Wave (旗帜 Banner 木板 Board); 倾斜 Tilt (天平 Balance 花盆 Flowerpot); 膨胀 Inflate (气球 Balloon 肥皂 Soap); 发射 Launch (军事 Military 旅游 Travel); 上升 Rise (高度 Height 长度 Length); ▫ 动 Waver (人影 Silhouette 电影 Film); 碰击 Chink (酒杯 Goblet 奖杯 Cup); 漂浮 Float (木头 Wood 石头 Stone); 平移 Translate (搬运 Transport 播撒 Sown); 流淌 Trickle (汗水 Sweat 汗衫 T-shirt); 滑落 Slide (重力 Gravity 电力 Electricity); 震颤 Tremor (大地 Earth 蓝天 Blue sky); 下沉 Sink (海洋 Ocean 陆地 Land)
Low-V
融化 Melt (雪花 Snowflake 菊花 Chrysanthemum); 轰鸣 Roar (耳朵 Ear 眼镜 Glasses); 溶解 Dissolve (白糖 Sugar 白云 Baiyun); 凝结 Condense (血液 Blood 唾液 Saliva); 笼罩 Enveloped (薄雾 Mist 微风 Breeze); 冻结 Freeze (严寒 Cold 酷 ▫ Heat); 照耀 Shine (阳光 Sunshine 月光 Moonlight); 冷却 Cool (锻造 Forge 雕刻 Engrave); 冷藏 Refrigerate (食物 Food 金钱 Money); 稀释 Dilute (药水 Liquid medicine 泉水 Fountain); 浓缩 Concentrate (溶液 Solution 粉末 Powder); 硬化 Harden (动脉 Artery 命脉 Lifeline); 腐蚀 Corrosion (损坏 Damage 修理 Repair); 浸透 Soak (衣衫 Clothes 外壳 Shell); 合成 Synthesize (化学 Chemistry 物理 Physical); 制冷 Refrigerate (冰块 Ice 火苗 Flame); 吸收 Uptake (营养 Nutrition 病毒 Virus); 辐射 Radiate (核弹 Nuclear bomb 子弹 Bullet); 浸泡 Soak (热水 Hot water 火焰 Flame); 烘干 Dry (衣服 Clothes 首饰 Jewelry); 加热 Heat (烤箱 Oven 冰箱 Refrigerator); 萎缩 Atrophy (肌肉 Muscle 肥肉 Fat); 发酵 Ferment (酸奶 Yogurt 汽水 Soda); 萌发 Bourgeon (种子 Seed 枝干 Branch); 腐烂 Rot (恶臭 Stench 清香 Fragrance); 酿造 Brew (酒窖 Wine cellar 地牢 Dungeon); 渗透 Penetrate (水滴 Bead 水花 Spray); 散热 Cool (风扇 Fan 手电 Flashlights); 熄灭 Extinguish (炉火 Fire 烟囱 Chimney); 凝固 Solidify (冷冻 Freeze 冷笑 Sneer)
Bio-N
羚羊 Antelope (草原 Grassland 冰川 Glacier); 青蛙 Frog (池塘 Pond 沙漠 Desert); 麻雀 Sparrow (飞翔 Fly 游泳 Swim); 鲸鱼 Whale (海洋 Ocean 河流 River); 蝙蝠 Bat (黑夜 Night 白 ▫ Daytime); 恐龙 Dinosaur (化石 Fossil 宝藏 Treasure); 乌龟 Tortoise (缓慢 Slow 敏捷 Agile); 山羊 Goat (犄角 Horn 爪子 Paw); 狐狸 Fox (狡猾 Cunning 笨拙 Clumsy); 兔子 Rabbit (萝卜 Radish 辣椒 Chili); 绵羊 Sheep (毛衣 Sweater 短裤 Shorts); 天鹅 Swan (美丽 Beautiful 丑陋 Ugly); 毛驴 Donkey (盘 Grindstone 水井 Well); 奶牛 Dairy cow (牧场 Ranch 鱼塘 Fish ponds); 老鼠 Mouse (奶酪 Cheese 啤酒 Beer); 螃蟹 Crab (钳子 Pliers 羽毛 Feather); 骆驼 Camel (沙漠 Desert 岛屿 Islands); 鸽子 Pigeon (书信 Letter 电报 Telegraph); 八哥 Myna (说话 Speak 弹琴 Playing); 老鹰 Eagle (天空 Sky 大地 Earth); 鲨鱼 Shark (危险 Danger 安全 Security); 孔雀 Peacock (尾巴 Tail 牙齿 Tooth); 水牛 Buffalo (小河 River 大海 Sea); 老虎 Tiger (凶猛 Fierce 温顺 Meek); 大象 Elephant (牙齿 Tooth 羽毛 Feather); 海豚 Dolphin (游泳 Swim 跑步 Run); 鸭子 Duck (鱼虾 Fish and shrimp 骡马 Mule); 熊猫 Panda (竹子 Bamboo 月季 Chinese rose); 蜜蜂 Bee (花朵 Flowers 果实 Fruit); 犀牛 Rhinoceros (冲撞 Collide 翱翔 Soar)
Mec-N
锄头 Hoe (土地 Land 沼泽 Swamp); 棒子 Stick (树枝 Branch 树叶 Leaf); 铁 Shovel (挖掘 Excavate 切割 Cut); 棍子 Stick (细长 Slender 椭圆 Oval); 尺子 Ruler (长度 Length 重量 Weight); 刀 Sickle (收割 Reap 播种 Sow); 匕首 Dagger (刺杀 Assassinate 医疗 Medical treatment); 宝剑 Sword (挥舞 Wave 瞄准 Aim); 刀子 Knife (抢劫 Robbery 诈骗 Fraud); 橡皮 Eraser (试卷 Examination paper 手绢 Handkerchief); 笤帚 Broom (簸箕 Dustpan 漏斗 Funnel);

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