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

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## ARTICLE INFO

## 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 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 inter-preted 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 among the 20 categories, whereas cars induced the weakest. It is obvious that the concepts of cars should contain higher percentages of mechanical motion properties than many other tested categories, such as faces, flowers, foods, clothes, fruits and vegetables. Thus, this finding is difficult to explain by the PLTC-motion theory and indicates that the tool-specificity in the pMTG might be driven by properties other than mechanical motion, such as knowledge of manipulation or strong mappings between the visual form and motor representations. Given that the primary goal of the current study is to test the PLTC-motion theory, we will discuss those other potential explanations in the Discussion section.

Two studies comparing PLTC activation for verbs (and nouns) with high- and low-motion properties (e.g., run vs. think) also challenged the PLTC-motion theory (Bedny et al., 2008; Grossman et al., 2002b).

In both studies, the experimental task was conceptual judgments of words. They found that the PLTC region was not activated more strongly for high-motion verbs than for low-motion verbs. Grossman et al. (2002b) even observed that one region in the PLTC showed strong activation for low-motion verbs compared with high-motion verbs. However, the PLTC-motion theory may accommodate these findings in the following ways. First, there might be functional multiplicity in the pSTS. Indeed, this region is critical to several cognitive processes, including theory of mind (Hein and Knight, 2008). The above studies used mental verbs (e.g., hope, believe) as low-motion verbs, which might activate the pSTS as a part of the "theory of mind" system, resulting in equal or stronger activation than high-motion verbs in this area. Also critically, neither study considered different types of motion properties. As previously discussed, the PLTC-motion theory assumes that the pSTS and pMTG store different types of motion knowledge (biological vs. mechanical), and each region might be sensitive to a different subset of the high-motion words used in these studies. Therefore, the motion effects in both regions may be attenuated.

In the current study, we directly tested the PLTC-motion theory by comparing activation patterns evoked by words denoting biological/articulate motion (e.g., walk) and those denoting mechanical/rigid motion (e.g., rotate). Note that both types of words are usually verbs defined by grammatical class, so we set these two conditions with verbs exclusively. A baseline condition was further included using low-motion, non-mental verbs (e.g., ferment). To ensure the conceptual processing of the words, we adapted a target-choice conceptual judgment task used in Bedny and Thompson-Schill (2006). The PLTC-motion theory predicts that verbs denoting biological motion would evoke stronger activation than the other two types of verbs in the pSTS, and those denoting mechanical motion would induce stronger activation in the pMTG. Finally, three classical noun categories with different motion types (animals, tools, and buildings) were also tested to compare with previous findings of the categorical effects in the PLTC.

## Methods

### Participants

Sixteen healthy undergraduate and graduate students (11 females) took part in the experiment. The average age of the participants was 22.6 years (SD: 2.3 years). All participants were right-handed and native speakers of Chinese. None suffered from psychiatric or neurological disorders or had ever sustained a head injury. Before the experiment, each participant read and signed the informed consent issued by the institutional review board of Beijing Normal University (BNU) Imaging Center for Brain Research.

### Design and materials

We used a conceptual association judgment task in which participants saw one target word (e.g., climb) followed by two choice words (e.g., mountain and lake) and were asked to select the choice word that was more closely related to the target by pressing a button. All target and choice words were two-character and disyllabic Chinese words (see Appendix for a complete list of materials). There were 180 target words, with 30 words for each of the six conditions: high biological-motion verbs (Bio-V, e.g., walk); high mechanical-motion verbs (Mec-V, e.g., rotate); low-motion verbs (Low-V, e.g., ferment); high biological-motion nouns (Bio-N, e.g., tiger); high mechanical-motion nouns (Mec-N, e.g., hammer); and low-motion nouns (Low-N, e.g., church). Note that we avoided mental verbs in the low-motion verb condition because, as we mentioned in the Introduction, the processing of these words might activate the pSTS via the "theory of mind" system. The target words were matched in word frequency

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); $ts$ (58)<1.50, $ps$>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 ($ts$ (58)>23.5, $ps$<.001), and for mechanical motion: Mec-V>Low-V, Mec-V>Bio-V, Mec-N>Low-N, and Mec-N>Bio-N ($ts$ (58)>12.5, $ps$<.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., 유유) 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
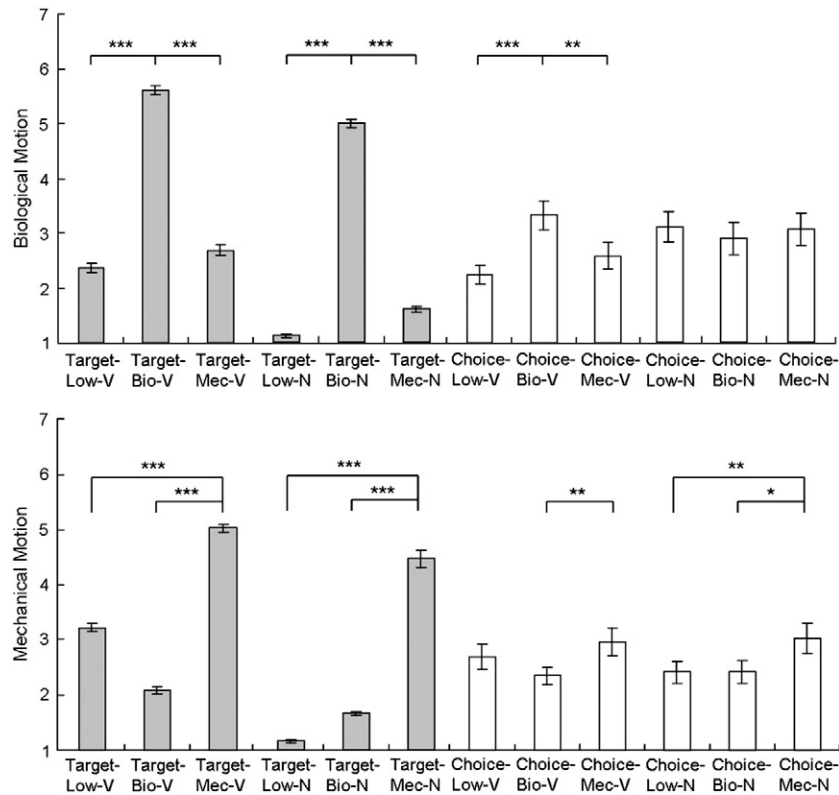


**Fig. 1.** Results of biological and mechanical motion ratings. Error bars depict the unbiased standard errors of the ratings of different types of words. The labels "Target-" and "Choice-" mean the Target- and Choice-words of a particular condition, respectively. See Table 1 for acronyms of different 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: $800 \times 600$) 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: $256 \times 256$, 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: $64 \times 64$, 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 $\alpha < 0.05$ (corrected) using the cluster-level statistical threshold estimator of Brain Voyager ($p \leq 0.01$, $k \geq 30$).

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 $\beta$-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: one for low behavioral accuracy (S1) and one for excessive head movement (S7). The mean accuracy of 16 subjects was 94.3% (SD: 2.8), and S1 was the only subject whose accuracy (88.3%) was lower than the two-SD-cutoff (88.9%). The mean translation and rotation of 16 subjects were 0.5 mm (SD: 0.4) and 0.5 degree (SD: 0.4), respectively, and S7 was the only subject whose head-movement values (2.0 mm, 1.9 degree) were larger than the two-SD-cutoffs (1.3 mm, 1.3 degree).

*Behavioral data*

The response time (RT) and accuracy data were collected when participants performed the task in the scanner. The results are shown in Fig. 2. We contrasted different types of words using a within subject paired t-test. In parallel with our whole brain analyses of fMRI data, we compared different motion conditions within nouns and verbs separately. We found that the RTs of Mec-N and Mec-V were longer than the other conditions (within nouns: $ts$ (13)>6.58, $ps<.001$; within verbs: $ts$ (13)>2.59, $ps<.05$). The accuracy for Bio-N was higher than for Low-N and Mec-N ($ts$ (13)>2.68, $ps<.05$). Other contrasts between the conditions did not reach statistical significance ($ps>.05$).

*fMRI data*

*Whole brain analyses*

The results of planned contrasts in whole brain analyses are shown in Table 1 and Fig. 3. In the Target-Choice-results, significant differences of PLTC-activation were observed in four contrasts: Bio-V>Low-V ($X = -42$,
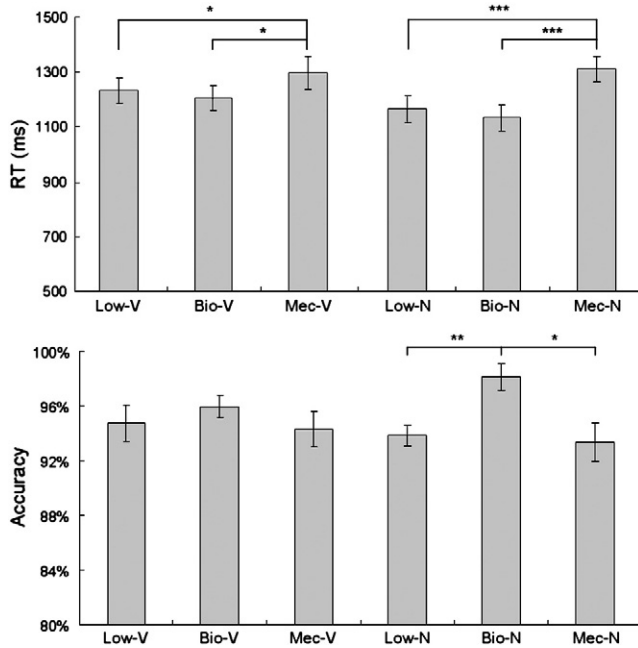
**Fig. 2.** Response time (RT) and accuracy results. Error bars depict the unbiased standard errors of RTs and accuracies of different types of words. See Table 1 for acronyms of different conditions.

$Y = -64$, $Z = 25$; $X = 51$, $Y = -64$, $Z = 19$), 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>Low-N cluster), indicating a trend of greater activation of the Mec-N than the Bio-N in the pMTG.

Compared with the Target-Choice-results, the Choice-results showed similar patterns but lower activation levels in general (see Table 1 and Fig. 3 for details). However, we did not find any significant PLTC category-specific activation in the Target-results. To explore the possible reason for the null results in the Target-results, we compared the $\beta$-values of all Target-regressors to those of Choice-regressors, and found that most brain regions showed much weaker activation for the Target-regressors than for the Choice-regressors. The relatively low activation level of the Target-regressors might lead to a low signal-to-noise ratio, making the categorical effects difficult to observe.

We scrutinized the consistency between the critical regions observed in the present study and related results in the literature. First, for the hemispheric asymmetries, the right-hemisphere dominance for Bio-N and Bio-V and the left-hemisphere dominance for Mec-N we found here were in accordance with previous findings in the published literature (for a review, see Martin, 2007). Second, we further considered the spatial localizations of our findings. To obtain a comprehensive understanding of the observed fMRI activation patterns of the two types of motion processing, we selected representative studies that investigated the following processes: 1) the visual processes of biological motion (whole body motion) and mechanical motion; and 2) the visual and conceptual processes of different categories of objects and words with a rich content of biological (animals/human) and mechanical motion (tool/artifact). For the activation pattern of each motion type, we calculated how far

the clusters we observed were from the coordinates reported in previous studies. Based on the PLTC-motion theory, the clusters specific to Bio-V should overlap with previously reported pSTS regions specific to visual processing of biological motion and conceptual processing of animals, while those specific to Mec-V should overlap with pMTG regions specific to mechanical motion and tools. Thus, the pSTS clusters were defined by Bio-V>Low-V + Mec-V. Because we did not find any Mec-V-specific cluster in the whole brain analyses, a pMTG cluster was then defined by Mec-N>Low-N to check the consistency between the tool-specific pMTG regions in our study and previous studies. These results are summarized in Table 2. The spatial localizations of critical PLTC-regions observed in the present study were largely consistent with the corresponding coordinates reported in literature.

*ROI analyses*

We carried out ROI analyses on the basis of the coordinates reported by thirteen studies shown in Table 2. These chosen coordinates were all obtained by the contrast between meaningful stimuli with biological and mechanical motions, so that the PLTC-motion theory could clearly predict which type of motion property (biological or mechanical) would be preferred. In total, 16 ROIs in bilateral pSTS for biological motion and 17 ROIs in the left pMTG for mechanical motion were included. All ROIs were defined as spheres

**Table 1**
Activations of planned whole brain contrasts in the PLTC. The false positive rate was controlled at $\alpha < 0.05$ (corrected) using the cluster-level statistical threshold estimator of Brain Voyager ($p = 0.01$, $k \geq 30$). The Talairach coordinate of peak voxel of each cluster was reported. The labels of "Low-V," "Bio-V," "Mec-V," "Low-N," "Bio-N," and "Mec-N" represent low-motion verbs, high biological-motion verbs, high mechanical-motion verbs, low-motion nouns, high biological-motion nouns, and high mechanical-motion nouns, respectively.

| Contrasts | Hemisphere | Cluster size (mm³) | Peak voxel | | | |
|---|---|---|---|---|---|---|
| | | | X | Y | Z | t-value |
| *Target-Choice results* | | | | | | |
| Within verbs | | | | | | |
| For Bio-V | | | | | | |
| Bio-V>Low-V | *Left* | 3313 | −42 | −64 | 25 | 6.97 |
| | *Right* | 7901 | 51 | −64 | 19 | 7.39 |
| Bio-V>Mec-V | *Right* | 1578 | 48 | −49 | 10 | 6.96 |
| For Mec-V | | | | | | |
| Mec-V>Low-V | *None* | – | – | – | – | – |
| Mec-V>Bio-V | *None* | – | – | – | – | – |
| Within Nouns | | | | | | |
| For Bio-N | | | | | | |
| Bio-N>Low-N | *None* | – | – | – | – | – |
| Bio-N>Mec-N | *Right* | 5551 | 45 | −55 | 19 | 7.34 |
| For Mec-N | | | | | | |
| Mec-N>Low-N | *Left* | 1738 | −45 | −52 | 4 | 6.86 |
| Mec-N>Bio-N | *None* | – | – | – | – | – |
| | | | | | | |
| *Choice-results* | | | | | | |
| Within verbs | | | | | | |
| For Bio-V | | | | | | |
| Bio-V>Low-V | *Left* | 4243 | −45 | −61 | 16 | 5.94 |
| | *Right* | 2062 | 60 | −40 | 7 | 5.44 |
| | | 983 | 57 | −55 | 28 | 5.59 |
| Bio-V>Mec-V | *Left* | 1092 | −42 | −52 | 28 | 5 |
| | *Right* | 1071 | 63 | −37 | 13 | 5.83 |
| For Mec-V | | | | | | |
| Mec-V>Low-V | *None* | – | – | – | – | – |
| Mec-V>Bio-V | *None* | – | – | – | – | – |
| Within Nouns | | | | | | |
| For Bio-N | | | | | | |
| Bio-N>Low-N | *None* | – | – | – | – | – |
| Bio-N>Mec-N | *None* | – | – | – | – | – |
| For Mec-N | | | | | | |
| Mec-N>Low-N | *Left* | 1041 | −54 | −58 | 4 | 4.53 |
| Mec-N>Bio-N | *None* | – | – | – | – | – |

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)≤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
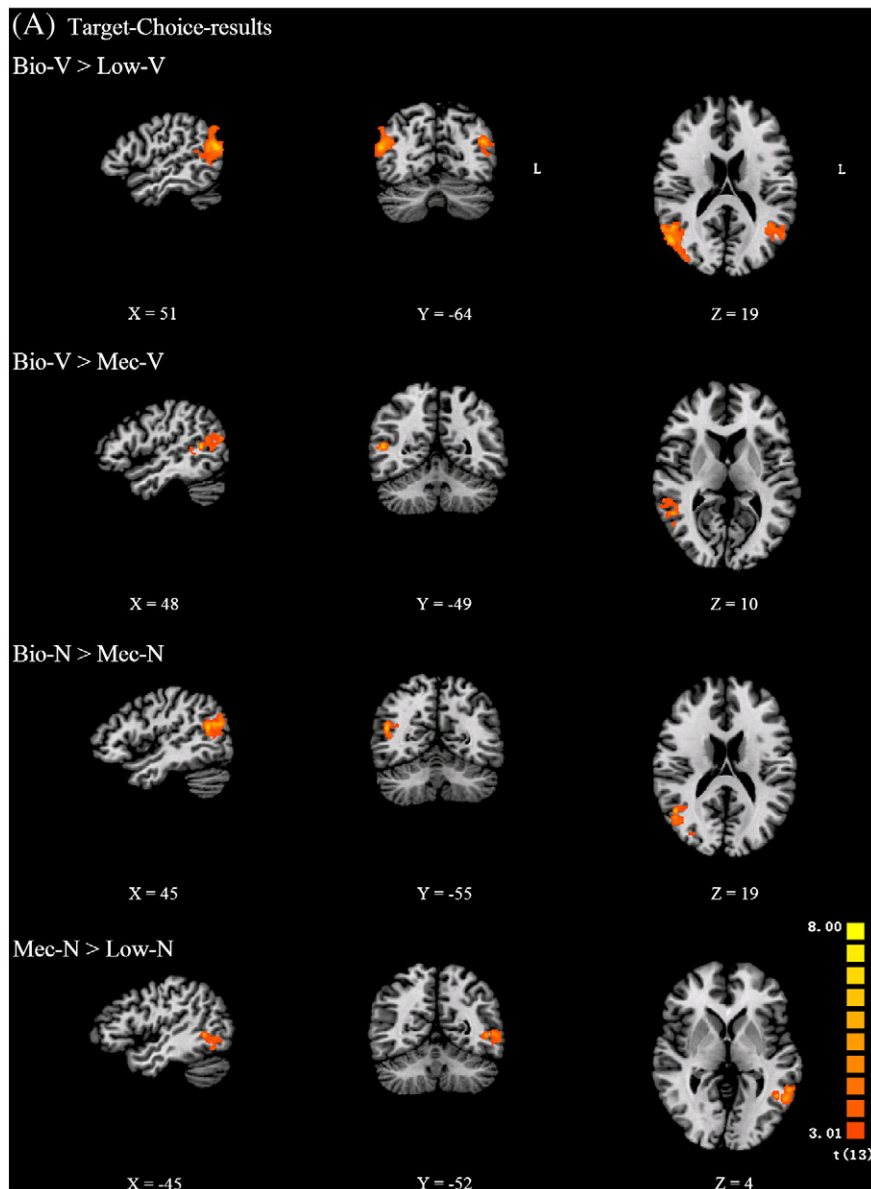


**Fig. 3.** Activations of planned whole brain contrasts in the PLTC (corrected α<0.05: $p$≤0.01, $k$≥30): (A) PLTC-activations in the Target-Choice-results; (B) PLTC-activations in the Choice-results. The presentation coordinates of results follow the coordinates of peak voxels reported in Table 1.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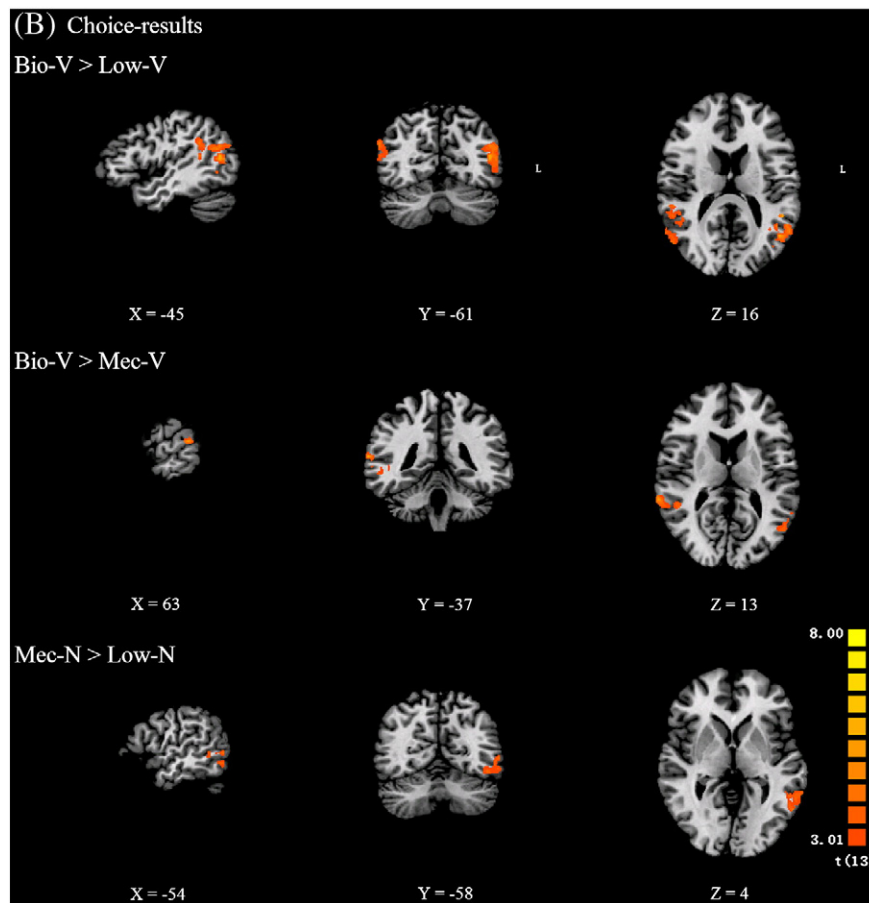
**Fig. 3** (*continued*).

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 | 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 | – |

(A)



(B)
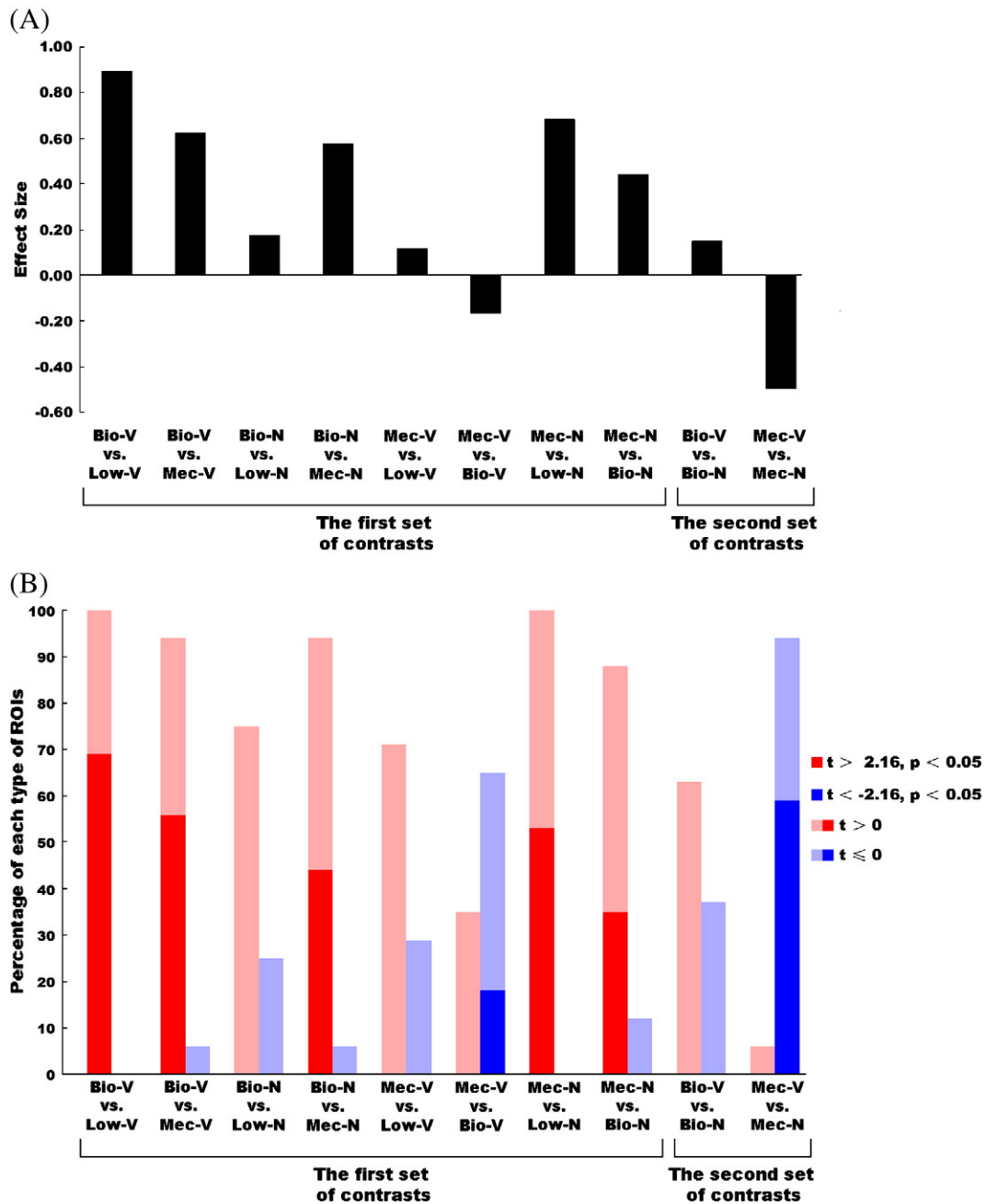


**Fig. 4.** A summary of the Target-Choice-results of the ROI analyses. The acronyms on the horizontal axis represent the contrasts conducted in the ROI analyses (see Table 1 for acronyms of different conditions). Panel (A) shows the mean effect size (the standardized mean difference d) of each contrast. 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 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.

*Categorical effects in the pMTG*

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.

## 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 (明星 Star 英雄 Hero); 溜达 Stroll (海边 Seaside 海底 Seabed); 爬行 Crawl (婴儿 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 温暖 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); 逃阳 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 (流星 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); 晃动 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 酷暑 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 白昼 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 (磨盘 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); 铁锨 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); 镰刀 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); 菜刀 Kitchen knife (案板 Chopping board 地板 Floor); 榔头 Hammer (钉子 Nail 铁丝 Iron wire); 长矛 Lance (投掷 Throw 掩埋 Bury); 勺子 Spoon (饭碗 Rice bowl 水桶 Bucket); 铅笔 Pencil (素描 Sketch 弹奏 Play); 圆规 Compass (几何 Geometry 代数 Algebra); 球杆 Choice (比赛 Game 战斗 Fighting); 汤匙 Spoon (陶瓷 Ceramics 棉毛 Interlock); 酒杯 Goblet (宴席 Banquet 会议 Meeting); 筷子 Chopsticks (饭菜 Meals 汤药 Decoction); 盾牌 Shield (弓箭 Bow and arrow 炸弹 Bomb); 扇子 Fan (夏天 Summer 冬天 Winter); 钥匙 Key (房门 Door 窗户 Window); 茶杯 Cup (干渴 Thirst 饥饿 Hunger); 鞭子 Whip (驴子 Donkey 蚊子 Mosquito); 螺丝 Screw (改锥 Screwdriver 锤子 Hammer); 钢笔 Pen (写信 Write 看书 Read); 火柴 Match (鞭炮 Firecracker 导弹 Missile); 绳子 Rope (柔软 Soft 锐利 Sharp) |
| Low-N |
| 宫殿 Palace (帝王 Emperor 老板 Boss); 花坛 Flowerbed (公园 Park 工厂 Factory); 假山 Rockery (园林 Garden 森林 Forest); 礼堂 Hall (购物 Shopping 开会 Meeting); 墙壁 Wall (挂历 Calendar 盆景 Bonsai); 城堡 Castle (贵族 Nobility 农夫 Farmer); 寺庙 Temple (和尚 Monk 政客 Politician); 堤坝 Dam (河流 River 小溪 Stream); 隧道 Tunnel (火车 Train 飞机 Aircraft); 别墅 Villa (居住 Live 办公 Work); 阳台 Balcony (晾晒 Dry 洗涤 Wash); 公墓 Cemetery (烈士 Martyr 富豪 Magnate); 天桥 Flyover (马路 Road 小巷 Alley); 花房 Greenhouse (牡丹 Peony 芦苇 Reed); 广场 Square (人群 Crowd 羊群 Sheep); 花园 Garden (散步 Take a walk 赶路 Hurry); 长城 Great Wall (山岭 Mountains 岛屿 Islands); 桥梁 Bridge (河流 River 池塘 Pond); 厂房 Factory building (设备 Equipment 档案 Archive); 教堂 Church (神父 Priest 尼姑 Nun); 地窖 Cellar (食物 Food 被褥 Bedding); 宝塔 Pagoda (寺院 Temple 庭院 Courtyard); 胡同 Alley (狭窄 Narrow 宽阔 Wide); 车站 Station (行李 Luggage 礼物 Gift); 山洞 Cave (野兽 Wild animal 美女 Beauty); 雕像 Statue (艺术 Arts 体育 Sports); 剧场 Theater (影片 Film 图片 Picture); 影院 Cinema (放映 Show (a movie); 比赛 Game); 墓地 Cemetery (葬礼 Funeral 婚礼 Wedding); 车棚 Carport (存放 Park 积攒 Accumulate) |

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