Brain & Language 119 (2011) 167–174

Contents lists available at ScienceDirect

Brain & Language

journal homepage: www.elsevier.com/locate/b&l

Dissociation and association of the embodied representation of tool-use verbs and hand verbs: An fMRI study

Jie Yang [a,*], Hua Shu [a], Yanchao Bi [a], Youyi Liu [a], Xiaoyi Wang [b]

[a] State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing 100875, China
[b] Department of Radiology, Xuanwu Hospital, Capital Medical University, Beijing 100053, China

ARTICLE INFO

Article history:
Accepted 5 June 2011
Available online 7 July 2011

Keywords:
Embodied theory
Chinese tool-use action verbs
Chinese hand action verbs
Semantic knowledge

ABSTRACT

Embodied semantic theories suppose that representation of word meaning and actual sensory-motor processing are implemented in overlapping systems. According to this view, association and dissociation of different word meaning should correspond to dissociation and association of the described sensory-motor processing. Previous studies demonstrate that although tool-use actions and hand actions have overlapping neural substrates, tool-use actions show greater activations in frontal–parietal–temporal regions that are responsible for motor control and tool knowledge processing. In the present study, we examined the association and the dissociation of the semantic representation of tool-use verbs and hand action verbs. Chinese verbs describing tool-use or hand actions without tools were included, and a passive reading task was employed. All verb conditions showed common activations in areas of left middle frontal gyrus, left inferior frontal gyrus (BA 44/45) and left inferior parietal lobule relative to rest, and all conditions showed significant effects in premotor areas within the mask of hand motion effects. Contrasts between tool-use verbs and hand verbs demonstrated that tool verbs elicited stronger activity in left superior parietal lobule, left middle frontal gyrus and left posterior middle temporal gyrus. Additionally, psychophysiological interaction analyses demonstrated that tool verbs indicated greater connectivity among these regions. These results suggest that the brain regions involved in tool-use action processing also play more important roles in tool-use verb processing and that similar systems may be responsible for word meaning representation and actual sensory-motor processing.

1. Introduction

The brain mechanism of word meaning is an important topic that has attracted increasing attentions. Embodied semantic theories claim that word meaning is grounded in sensory-motor systems (Barsalou, 1999; Glenberg, 1997; Pulvermüller, 2005). This opinion is supported by neuroimaging studies, which reveal that reading or listening to words can activate sensory-motor regions that enact the word meaning. For instance, color knowledge processing induced by color words can elicit activations in color perceiving areas in fusiform gyrus (FG) (Pulvermüller & Hauk, 2006; Simmons et al., 2007). Moreover, numerous studies indicate that viewing verbs that describe actions of different body parts (such as *pick*, *lick* and *kick*) can elicit effects in motor and premotor areas in a somatotopic way (Hauk, Johnsrude, & Pulvermüller, 2004; Pulvermüller, Härle, & Hummel, 2001; Raposo, Moss, Stamatakis, & Tyler, 2009). These results support the view that neurons responsible for sensory-motor information and word forms strongly link to each other (Pulvermüller, 2001) or the view that language comprehension is mediated by implicit sensory-motor simulation (Barsalou, 1999; Glenberg & Kaschak, 2002). The findings of motor and premotor activation are extended from the processing of single verbs to the processing of phrases, sentences and even figurative language that contain body-schema verbs (Aziz-Zadeh, Wilson, Rizzolatti, & Iacobonni, 2006; Boulenger, Hauk, & Puvermüller, 2009; Tettamanti et al., 2005; but see Raposo et al., 2009). However, for verbs that depict complex actions, such as tool-use action verbs (tool verbs for short), whether their meaning is ground in sensory-motor systems, and what difference between their meaning and the meaning of hand verbs are still unclear (Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008; Tyler et al., 2003).

As a defining characteristic of humans, tool-use introduces challenges on motor skill and tool knowledge compared with hand actions without tools. This is because the goal of tool-use is not enhancing movements of the upper limbs, but implementing qualitatively different mechanical actions (Frey, 2007). Such extra requirements are demonstrated by recent neuroimaging studies, which find that tool-use processing elicits stronger effects than hand action processing in both dorsal (frontal–parietal) stream

* Corresponding author. Address: Sackler Institute, Department of Psychiatry, Weill Cornell Medical College, 525 East 68th Street, New York, NY 10065, United States.
E-mail address: yangjiepsy@gmail.com (J. Yang).

0093-934X/$ - see front matter © 2011 Elsevier Inc. All rights reserved.
doi:10.1016/j.bandl.2011.06.001

and ventral (posterior temporal) stream (Frey, 2008). The dorsal stream is mainly responsible for motor skill processing in tool-use. Left superior parietal lobule and inferior parietal lobule (SPL and IPL) are responsible for tool-use motor skill planning (Chaminade, Meltzoff, & Decety, 2005; Choi et al., 2001; Fridman et al., 2006; Goldenberg & Hagmann 1998; Johnson-Frey, Newman-Norlund, & Grafton, 2005). Left middle frontal gyrus (MFG) and inferior frontal gyrus (IFG, BA 44/45) are responsible for integrating the actor's prospective goals (Buccino et al., 2004; Duncan & Owen, 2000; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000). The ventral stream is responsible for tool information processing. The medial FG is responsible for tool shape processing (Beauchamp, Lee, Haxby, & Martin, 2002; Mahon et al., 2007), and the left posterior middle temporal gyrus (MTG) is responsible for tool knowledge processing (Damasio et al., 2001; Mahon et al., 2007; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Martin, Wiggs, Ungerleider, & Haxby, 1996). In a word, these studies indicate that although tool-use actions and hand actions have overlapping neural substrates, tool-use shows greater activations in frontal, parietal and posterior temporal regions that are responsible for action goal integration, motor-skill planning and tool knowledge processing.

According to the embodied semantic view, the representation of word meaning and actual sensory-motor processing are implemented in overlapping systems. If this is true, the association and the dissociation of different word meaning should correspond to the association and the dissociation of the described sensory-motor processing. Thus, we hypothesize that (1) reading tool verbs and hand verbs should elicit common activity in hand motion areas and (2) tool verbs and hand verbs should elicit different effects in tool-use related regions, such as IFG (BA 44/45), MFG, SPL/IPL, medial FG and left posterior MTG. However, previous studies about tool verbs have not indicated clear findings about the two above hypotheses. For example, Tyler et al. (2003) used a semantic categorization task and found that tool verbs (such as *drilling*) and biological verbs (such as *swimming*) showed similar frontal–temporal activities and no difference was found. With a semantic similarity judgment task, Kemmerer et al. (2008) found that biological verbs (such as *running*) and tool verbs (such as *cutting*) elicited similar effects in frontal–temporal areas, in addition the tool verbs elicited activation in left angular gyrus (AG). However, the study did not directly compare the tool verbs with the biological verbs. Thus, it is still unclear whether the regions responsible for tool-use functions are more involved in tool verb processing, i.e. whether tool verbs elicit stronger effects than hand verbs in areas of left SPL/IPL, left MFG/IFG (BA 44/45) and left posterior MTG.

One possible reason for the difficulty of seeing the involvement of tool-use network in reading tool verbs may be that the tool-use network contains much more information compared with biological motions, and that tool-use occurs much later than biological actions in the history of human evolution and ontogenetic development. Thus, the combination between the word form and the tool-use network might be relatively vulnerable and easily disturbed. To investigate whether the tool-use network engages in the semantic representation of tool verbs, both the elaborate semantics specifying the manners of how hand interacts with tools and the strong association between word form and word meaning may be necessary. In the current study, we used single-character Chinese action verbs, which emphasize on very specific manual action manner and refer to a limited range of actions. As a typical ideographic writing system, Chinese written word forms have strong connections with word meaning. For instance, many single-character words have semantic radicals in their word forms to indicate meaning (Zhang & Chen, 2008). Most of single-character hand verbs contain a hand-related semantic radical, such as *nie* (*pinch*) (Fig. 1A). Single-character tool verbs can be divided into two types based on their semantic radicals (Zhang & Chen, 2008). In one type, each tool verb contains a hand-related semantic radical, such as *wa* (dig) (Fig. 1B). In the other type, each tool verb contains a tool-related semantic radical, such as *bang* (bind, here stresses the rope) (Fig. 1C). To examine the semantic representation differences between tool verbs and hand verbs thoroughly, both types of tool verbs were compared with hand verbs in the present study. A passive reading task was used to avoid confounding from motor response and to investigate the automatic access from word form to word meaning (Aziz-Zadeh et al., 2006; Hauk et al., 2004). A hand motion task was conducted after the passive reading task to localize hand motor areas and to examine whether hand verbs and tool verbs elicit effects in hand motor areas (Aziz-Zadeh et al., 2006; Hauk et al., 2004; Raposo et al., 2009). To eximageability for each verb using Likert 7-point scales (1 = very low, 7 = very high). They additionally rated (1) whether the action was a hand action and (2) whether the action required tool-use on two dichotomous scales (1 = yes, 0 = no). If a verb described a hand action, these Chinese speakers then rated (3) to what extent the verb reminded them to think of hand on a Likert 7-point scale (1 = very low, 7 = very high). If the action required tool-use, they then rated (4) to what extent the action relied on tools on a Likert 7-point scale (1 = very low, 7 = very high). Word frequency information was obtained from Language Corpus System of Modern Chinese Studies (LCSMCS, Sun, Huang, Sun, Li, & Xing, 1997).

Forty-eight verbs were selected as the experimental materials. They included (1) 16 hand verbs that described hand actions without tool-use, such as *nie (pinch), reng (throw), fu (touch)*; (2) 16 tool verbs, and their semantic radicals indicated hand involvement [tool verbs (hand part) for short], such as *sao (sweep), wa (dig), dao (smash)* and (3) 16 tool verbs, and their semantic radicals indicated the tools or materials [tool verbs (tool part) for short], such as *bang (bind), ke (carve), ge (cut)* (Table 1). Rating scores for three conditions were submitted to one-way analysis of variance (ANOVA) with verb condition as a between-subject factor. Significant effects were followed up with the planned comparisons. Results showed that three types of verbs had no differences in word frequency, familiarity, stroke, concreteness and imageability (all $Fs < 1$). The hand verbs had higher hand action ratio than the two types of tool verbs (both $ps < 0.001$), but no difference of hand action ratio was found between the two types of tool verbs ($p > 0.1$). What is more, the hand verbs had higher hand-reminding degree than the two types of tool verbs (both $ps < 0.001$), and the tool verbs (hand part) had higher hand-reminding degree than the tool verbs (tool part) ($p < 0.01$). As for tool-use ratio and tool-use degree, the tool verbs (tool part) had higher scores than the tool verbs (hand part) and the hand verbs (both $ps < 0.001$), and the tool verbs (hand part) had higher scores than the hand verbs ($p < 0.001$).

2.3. Design and task

We employed a block design for the passive reading task and the hand motion task because such design is found to indicate superior statistical power (Friston, Zarahn, Josephs, Henson, & Dale, 1999). In addition, block designs may be more appropriate because our goal is to detect subtle differences across different experimental conditions (Chee, Venkatraman, Westphal, & Siong, 2003). The passive reading phase began with an 8 s rest followed by six experimental blocks. Each block lasted 20 s, and was followed by 16 s rest. Each block consisted of eight words from one condition (thus the 16 words were divided into two blocks), and each word was displayed for 2 s, followed by 0.5 s blank. The order of the blocks was randomized. Participants were instructed to view each word carefully without making any response. After the fMRI experiment, each participant read a word list and was asked to select the words they had read during the experiment. The aim of this posttest was to examine whether participants read each word carefully during the experiment.

To test whether passively viewing tool verbs and hand verbs would elicit activations in hand motor areas, we instructed all participants to perform a hand-motion localizer task after the passive reading session. In each of the six hand motion blocks, participants were asked to pantomime grasping action ten times according to the frequency of a signal consisted of three asterisks (***) with their left or right hand. At the beginning of each block, an instruction appeared on the computer screen to tell participants which hand they should use. The order of hand motion was randomized.

2.4. Image acquisition

Imaging acquisition was performed on a 3.0-T Scanner (Siemens, Trio Tim) in the Imaging Center for Brain Research of Beijing Normal University. A gradient echo planar imaging (EPI) sequence was used to acquire the functional images (32 axial slices), with the following parameters: TR = 2000 ms, TE = 30 ms, FA = 90°, FOV = 200×200 mm^2, matrix = 64×64, thickness = 4 mm, inter-slice gap = 0.8 mm, voxel size = $3.125 \times 3.125 \times 4.8$ mm^3. A MPRAGE sequence was used to acquire high-resolution anatomical images of the entire brain with the following parameters: TR = 2530 ms, TE = 3.39 ms, FA = 7°; 128 sagittal slices; $1.33 \times 1.33 \times 1.33$ mm^3 resolution.

2.5. Data analysis

AFNI software package was used to preprocess and analyze the imaging data (Cox, 1996). After slice timing, a six-parameter rigid-body transformation was employed to correct head motion of the EPI images (Cox & Jesmanowicz, 1999). The anatomical image of each participant was registered to a standard Talaiarach template (TT_N27_atlas) (Talairach & Tournoux, 1988), and then the EPI images were aligned with the anatomical image. A 6-mm FWHM Gaussian kernel was used to spatially smooth the EPI data. Finally, all functional images were resampled to $2 \times 2 \times 2$ mm^3 voxel size.

Individual GLM-based analysis was used to estimate beta coefficient and statistical *t*-map for each experimental condition (three conditions for the passive reading task, and two conditions for the hand motion task) in each participant. Voxel-wise scaled coefficients were calculated with standard hemodynamic response function model (single gamma function) and then were submitted into a two-way, mixed-factor ANOVA with condition as a fixed factor and participant as a random factor.

The group statistical map of each condition was generated by contrasting individual *t*-maps against a constant value of 0. The

the reported peak coordinates for contrast of each condition relative to rest were reported.

To examine whether all verbs show effects in hand motor areas, we first performed a single contrast of left and right hand motion relative to rest, and then the contrast of each verb condition relative to rest was inclusively masked by left and right hand motion effects. To show common areas of activations in three verb conditions within the hand motion mask, we performed a single contrast of all three conditions relative to rest within hand motion mask, and the contrast result was inclusively masked by the effect of each condition related to rest within the hand motion mask. We reported *Z*-score and effect size at each reported peak coordinate for contrast of each condition relative to rest.

Results of simple contrasts between each tool verb condition and the hand verb condition was inclusively masked by the effect of each condition relative to rest to assure that the areas identified were activated by the condition of interest relative to rest and were not the results of de-activation. The resulting maps for the simple contrasts were thresholded at a voxel-wise, uncorrected, two-tailed probability of $t = 3.860$ ($p < 0.001$). We also reported *Z*-scores at the reported peak coordinates. Effect size for each condition in each identified region reported.

Two PPI analyses (Friston et al., 1997) were performed to find brain regions showing enhanced connectivity with the regions for the tool verbs conditions as compared with the hand verb condition. Two clusters were selected as seed regions for their significant presence in the initial contrast analysis and for their proposed theoretical importance in tool-use processing (Frey, 2007; Lewis, 2006). One was in left MFG (−45, 19, 40), which showed stronger effect in the tool verbs (hand part) than the hand verbs, and the other was in left posterior ITG/MTG (−49, −47, −10), which indicated stronger activation in the tool verbs (tool part) than the hand verbs. In two separated PPI analyses, the physiological variable was defined as the time course of the voxel whose *t*-value peaked within each cluster. The psychological variable was a vector coding for contrast effect [contrast between the tool verbs (hand part) and the hand verbs or contrast between the tool verbs (tool part) and the hand verbs] convolved with the hemodynamic response function (single gamma function). The psychophysiological interaction was calculated as the product of the deconvolved seed time-series (Gitelman, Penny, Ashburner, & Friston, 2003) and the vector of the psychological variable. Each PPI analysis was based on a general linear model with separate regressors for the psychological, physiological, and psychophysiological interaction variable. We then assessed the interaction effect in a random effects analysis using one-sample *t*-test. Results were reported on a height threshold of $p < 0.001$ (uncorrected) with 10 voxels minimum extend.

3. Results

3.1. Behavioral results

The aim of the behavioral test after the FMRI experiment was to see whether participants read every presented word carefully. Accuracy of word recognition was expressed as *d*-prime scores. Scores of each participant in each condition were submitted to repeated-ANOVA with verb condition as a within-subject factor. The overall average *d*-prime was 2.57 (SD = 1.46). The *d*-prime of hand verbs recognition was 2.51 (SD = 1.36); for tool verbs (hand part) the *d*-prime was 2.71 (SD = 1.52), and for tool verbs (tool part) the *d*-prime was 2.48 (SD = 1.41). ANOVA showed that there was no significant condition effect ($F < 1$).

3.2. Brain activation results

3.2.1. Common activation of three verb conditions versus rest

Fig. 2 presents the common activities for three verb conditions relative to rest. All conditions revealed effects in areas of bilateral FG/IOG (BA 19), precentral gyrus (BA 6), left MFG (BA 9), left IFG (p. opercularis)/IFG (p. triangularis) (BA 44/45), supplementary motor areas (SMA, BA 6) and cerebellum. In addition, all verb conditions elicited effects in an area of left IPL/SPL (BA 40/7). *Z*-scores at the reported peak coordinates for the contrast of each condition relative to rest were also reported (Table 2).

Left hand movement elicited activations in right motor areas, including right precentral gyrus (BA 4/6), postcentral gyrus (BA 3), supplementary motor areas (SMA, BA 32/24) and cerebellum. Brain areas in bilateral temporal lobe and right occipital lobe also showed effects. Right hand movement elicited effects in left SMA (BA 32/24), left precentral gyrus (BA 6/4), left postcentral gyrus (BA 3) and cerebellum. Brain areas in right temporal lobe and left occipital lobe also showed strong effects.

Within the hand-motion effect mask, all three types of verbs showed common activations in bilateral precentral gyrus (BA 4), MFG (BA 6), lingual gyrus (BA 18/19), SMA (BA 6) and cerebellum. *Z*-score and effect size at the each reported peak coordinate for contrast of each condition relative to rest were also reported (Table 3).

3.2.2. Contrast analyses

3.2.2.1. Tool verbs (hand part) vs. hand verbs. The contrast analysis between the tool verbs (hand part) and the hand verbs demonstrated that the tool verbs (hand part) had stronger effects in areas of left MFG (BA 8/9), left SPL/IPL (BA 19/7) and left caudate nucleus (BA 32/24). Additionally, the hand verbs elicited stronger activation in left postcentral gyrus/precentral gyrus (BA 3/2) and right postcentral gyrus (BA 3/2) (Table 4). The effect size for each condition in each region was plotted in Fig. 3.

3.2.2.2. Tool verbs (tool part) vs. hand verbs. The comparison between the tool verbs (tool part) and the hand verbs revealed that the tool verbs (tool part) had stronger effects in areas of left posterior ITG/MTG (BA 37), left SPL (BA 7) and right ITG/FG (BA 20). No stronger effect was revealed in the hand verb condition (Table 4). The effect size for each condition in each region was plotted in Fig. 4.

3.2.3. Results of PPI analyses

The area in left MFG (−45, 19, 40) showed stronger effect in the tool verbs (hand part) and was taken as a seed region in PPI

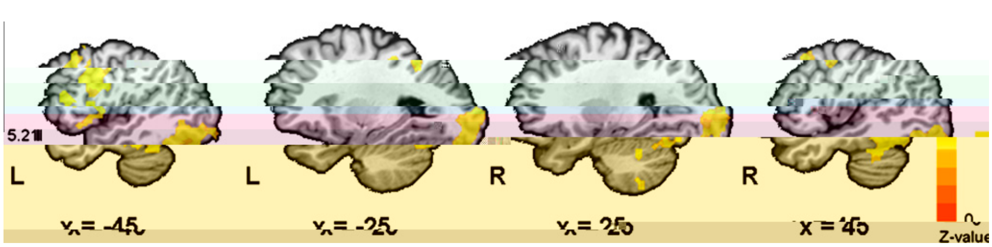

Fig. 2. Common significant activities for three verb conditions versus rest (FDR corrected to $p < 0.01$). L = left, R = right.

Table 2
Talaiarach coordinates (*x*, *y*, *z*) of common significant clusters (FDR corrected to $p < 0.01$) for three verb conditions versus rest. *Z*-scores at each reported peak coordinate for contrast of each condition relative to rest were also reported.

Voxel	Brain region	BA	*Z*-value	*Z*-HV	*Z*-TVH	*Z*-TVT	*x*	*y*	*z*
2425	L FG/IOG	19	5.22	4.37	4.43	4.33	−27	−81	−16
1387	L Prec G/MFG/IFG(ope)/IFG(tri)	6/9/44	5.22	3.98	4.43	4.16	−45	3	36
116	L IFG(tri)	46/10	4.60	2.71	3.32	2.8	−47	35	14
84	L IPL/SPL	40/7	4.34	2.75	2.68	3.42	−27	−57	42
136	R Prec G	6	4.48	3.54	2.74	3.43	49	3	44
2498	R FG/LOG	19	5.21	4.17	3.77	4.08	43	−69	−14
479	R SMA	6	5.06	3.22	2.69	3.67	1	5	58
166	Cerebellum		4.70	3.19	3.49	3.56	27	−53	−46

L = left; R = right; FG = fusiform gyrus; IFG(ope) = inferior frontal gyrus (p. opercularis), IFG(tri) = inferior frontal gyrus (p. triangularis), IOG = inferior occipital gyrus, IPL = inferior parietal lobule; MFG = middle frontal gyrus, Prec G = precentral gyrus; SMA = supplementary motor areas; SPL = superior parietal lobule. HV = hand verbs, TVH = tool verbs (hand part), TVT = tool verbs (tool part).

Table 3
Talaiarach coordinates (*x*, *y*, *z*) of common significant clusters (FDR corrected to $p < 0.01$) of three verb conditions versus rest in hand motion task. *Z*-score and effect size at each reported peak coordinate for contrast of each condition relative to rest were also reported.

Voxel	Brain region	BA	*Z*-value	*Z*-HV	*Z*-TVH	*Z*-TVT	EF-HV	EF-TVH	EF-TVT	*x*	*y*	*z*
331	L Prec G/MFG	6	4.78	3.66	3.8	3.87	1.57	1.81	1.66	−37	−3	34
220	L SMA	6	4.87	3.75	3.56	4.29	1.66	1.60	2.02	−1	3	52
91	L LG	18/19	5.29	4.54	4.73	4.49	2.47	2.91	2.46	−27	−83	−16
77	R Prec G/MFG	6/4	4.21	4.32	3.85	4.49	2.21	1.86	2.39	45	−1	44
50	R LG	18/19	4.98	3.45	2.95	3.47	1.39	1.14	1.26	19	−85	−10
177	Cerebellum		4.78	4.32	3.72	4.34	2.20	1.73	2.09	33	−57	−24

L = left; R = right; MFG = middle frontal gyrus; LG = lingual gyrus; Prec G = precentral gyrus; SMA = supplementary motor areas. HV = hand verbs, TVH = tool verbs (hand part), TVT = tool verbs (tool part), EF, effect size.

Table 4
Talaiarach coordinates (*x*, *y*, *z*) of significant clusters ($p < 0.001$ uncorrected) in contrast analyses.

Voxel	Brain region	BA	*Z*-value	*x*	*y*	*z*
Tool verb (hand part) > hand verb						
31	L SPL	19/7	4.37	−27	−79	44
21	L MFG	8/9	4.16	−45	19	40
Hand verb > tool verb (hand part)						
51	L Postc G/Prec G	3/2	−4.27	−49	−9	22
21	R Post G	3/2	−4.40	61	−9	20
Tool verb (tool part) > hand verb						
27	L SPL	7	3.94	−15	−47	64
22	L posterior ITG/MTG	37	3.66	−49	−47	−10
26	R ITG/FG	20/21	4.24	39	−7	−20
Hand verb > tool verb (tool part)						
–						

L = left, R = right, FG = fusiform gyrus; ITG = inferior temporal gyrus, MFG = middle frontal gyrus, MTG = middle temporal gyrus, Postc G = postcentral gyrus, Prec G = precentral gyrus, SPL = superior parietal lobule.

analysis. The results indicated that areas in left MFG (BA 9), left IPL (BA 40) and right AG (BA 39) showed stronger coupling with left MFG when the tool verbs (hand part) compared with the hand verbs (Table 5).

The area in left posterior ITG/MTG (−49, −47, −10) showed stronger effect in tool verbs (tool part) and was used as a seed region. The results of PPI analysis demonstrated that areas in left IFG (p. opercularis) (BA 44/45), left MOG (BA 19) and right MFG (BA 46/10) showed stronger coupling with left posterior ITG/MTG when the tool verbs (tool part) compared with the hand verbs. At a lower threshold of $p < 0.005$ uncorrected, area in left IPL (BA 40/7) also indicated enhanced connectivity (Table 6).

4. Discussion

The current study aimed to explore the dissociation and the association of the semantic representation of tool verbs and hand verbs. To achieve this goal, we employed two types of Chinese tool verbs, a group of hand verbs and a passive reading task. We predicted that the tool verbs and the hand verbs would elicit significant differences in tool-use related areas, but they would also elicit common effects in hand motion areas.

The results of the present study confirmed the prediction. The comparison between the tool verbs (hand part) and the hand verbs indicated that areas in left SPL and left MFG showed greater effects in the tool verb condition. The SPL plays an important role in planning and executing tool-use movements (Choi et al., 2001; Johnson-Frey et al., 2005) or preparing motor actions in tool-use (Chaminade et al., 2005; Goldenberg & Hagmann, 1998). Previous studies demonstrate that left MFG, as well as IFG (BA 44/45), is responsible for the integration of actor's prospective goals (Buccino et al., 2004; Duncan & Owen, 2000; Rowe et al., 2000) or the visuomotor transformations of grasping and manipulating objects (Binkofski et al., 2000). Additionally, the PPI analysis indicated that left IPL and right AG showed enhanced connectivity with left MFG. This result is consistent with previous studies, which indicate that left dorsal stream (frontal–parietal) plays a key role in tool-use planning (Johnson-Frey et al., 2005), pantomime (Choi et al., 2001; Moll et al., 2000), imagination (Johnson-Frey et al., 2005), viewing (Manthey, Shubotz, & von Cramon, 2003) and sound listening (Lewis, Brefczynski, Phinney, Janik, & DeYoe, 2005). Together, these results suggest that the meaning of tool verbs (hand part) might emphasize more on the action planning and action goal integration and require more involvement of the dorsal stream that is important during tool-use executing (Frey, 2007).

The contrast between the tool verbs (tool part) and the hand verbs demonstrated that the tool verbs (tool part) showed stronger activations in left posterior ITG/MTG, a brain area that is involved in tool naming (Mahon et al., 2007; Martin et al., 1996), tool action words generation (Martin et al., 1995) and tool questions answering (Chao, Haxby, & Martin, 1999). This region is supposed to represent the conceptual knowledge of tools. The result is consistent with the semantic radical information that indicates the tools or

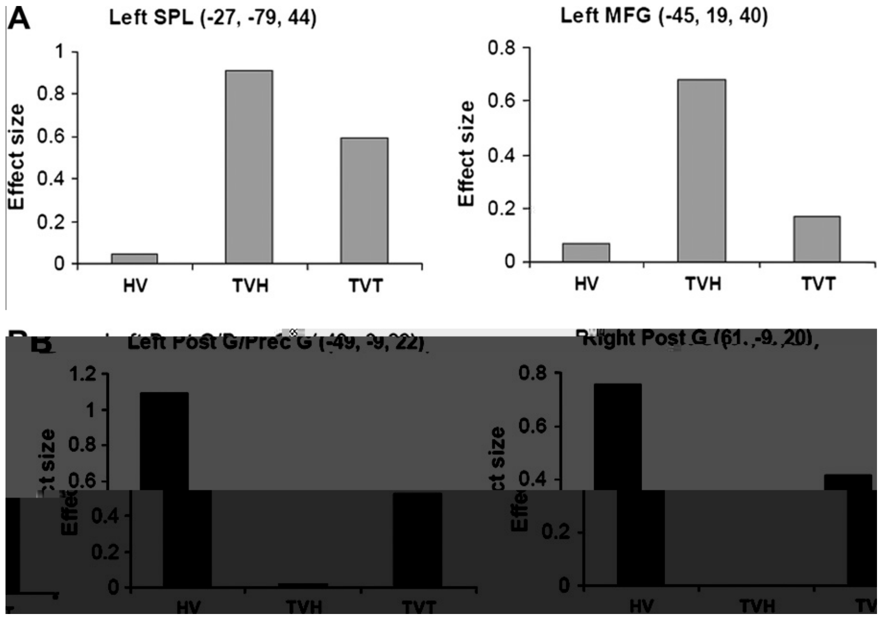

Fig. 3. Effect sizes for all conditions in each region that identified by the contrast between the tool verbs (hand part) and the hand verbs. (A) Effect sizes in brain regions in which the tool verbs (hand part) showed stronger effect than the hand verbs. (B) Effect sizes in brain regions in which the hand verbs showed stronger effect than the tool verbs (hand part).

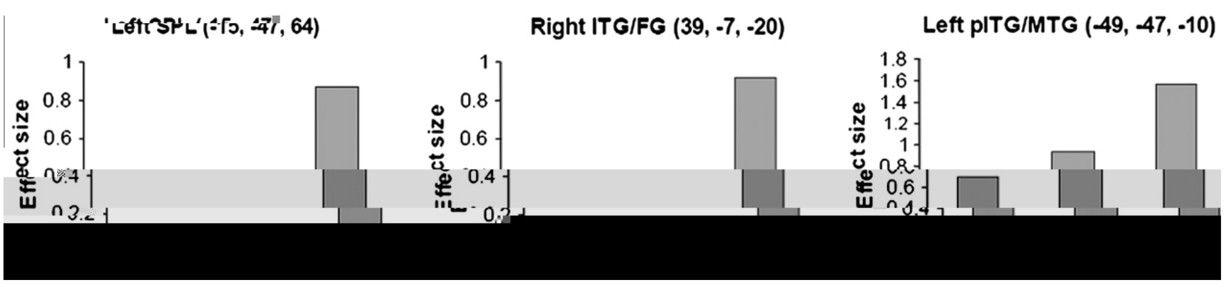

Fig. 4. Effect sizes for all conditions in each region that identified by the contrast between the tool verbs (tool part) and the hand verbs.

Table 5
Results of PPI analysis: Talaiarach coordinates (x, y, z) for regions showing significantly greater coupling with left MFG in the contrast results of tool verbs (hand part) > hand verbs. The threshold is $p < 0.001$ uncorrected with 10 voxels minimum extend.

Voxel	Brain region	BA	Z-value	x	y	z
113	L MFG	9	4.09	−21	39	30
60	L IPL	40	3.4	−45	−47	38
105	R AG	39	4.09	43	−61	40
43	R AG	40/39	3.73	47	−67	26

L = left; R = right; AG = angular gyrus; IPL = inferior parietal lobule; MFG = middle frontal gyrus.

Table 6
Results of PPI analysis: Talaiarach coordinates (x, y, z) for regions showing significantly greater coupling with left posterior ITG/MTG in the contrast results of tool verbs (tool part) > hand verbs. The threshold is $p < 0.001$ uncorrected with 10 voxels minimum extend.

Voxel	Brain region	BA	Z-value	x	y	z
11	L IFG(ope)	44/45	3.53	−47	11	20
52	L IPL*	40/7	3.23	−41	−55	44
13	L MOG	19	3.76	−39	−81	−2
49	R MFG	46/10	3.7	41	37	18

L = left; R = right; IFG (ope) = inferior frontal gyrus (p. opercularis), IPL = inferior parietal lobule; MFG = middle frontal gyrus.
* $p < 0.005$.

materials. The result is also consistent with the rating results, which showed highest scores in tool involvement in this type of tool verbs. In addition, the tool verbs (tool part) also have stronger effect in left SPL, and this result suggests that there is a connection between left posterior MTG and the dorsal areas. Direct evidence of this connection comes from the PPI analysis, which showed that left IFG (p. opercularis) and left IPL had greater coupling with left posterior ITG/MTG. This result suggests that areas in dorsal stream (frontal-parietal cortex) and ventral stream (posterior temporal cortex) play important roles in representing the meaning of tool verbs (tool part).

Together, the contrasts between tool verbs and hand verbs and the functional connectivity results suggest that the meaning of tool verbs is represented in a more complex tool-use network, and the brain regions that play important roles in tool-use are more involved in the meaning of tool verbs.

Despite these differences, the tool verbs and the hand verbs also indicated common neural substrates. The contrast analysis of each verb condition relative to rest indicated activities in left MFG, IFG, bilateral precentral gyrus, FG/IOG, and left SPL/IPL. Additionally, all verb conditions elicited activities in premotor areas within the mask of hand motion effects. This result is consistent with previous studies about manual action language (Aziz-Zadeh et al., 2006; Hauk et al., 2004; Raposo et al., 2009; Tettamanti et al., 2005) and confirms that hand motor areas engage in the representation of manual action verbs.

The dissociation and the association of the embodied representation of tool verbs and hand verbs relate to the classic debate of how different semantic knowledge is distributed over the neocortex. One point of view supposes that different semantic knowledge is represented in distinct systems. For example, Allport (1985) sup-

Lewis, J. W. (2006). Cortical networks related to human use of tools. *The Neuroscientist, 12*, 211–231.

Lewis, J. W., Brefczynski, J. A., Phinney, R. E., Janik, J. J., & DeYoe, E. A. (2005). Distinct cortical pathways for processing tool versus animal sounds. *Journal of Neuroscience, 25*, 5148–5158.

Mahon, B. Z., Milleville, S. C., Negri, G. A. L., Rumiati, R. I., Caramazza, A., & Martin, A. (2007). Action-related properties of objects shape object representations in the ventral stream. *Neuron, 55*, 507–520.

Manthey, S., Shubotz, R. I., & von Cramon, D. Y. (2003). Premotor cortex in observing erroneous action: an fMRI study. *Cognitive Brain Research, 15*, 296–307.

Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science, 270*, 102–105.

Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature, 379*, 649–652.