Premotor Cortex Activation Elicited during Word Comprehension Relies on Access of Specific Action Concepts

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Abstract

■ The relationship between the lexical-semantic and sensory-motor systems is an important topic in cognitive neuroscience. An important finding indicating that these two systems interact is that reading action verbs activates the motor system of the human brain. Two constraints have been proposed to modulate this activation: the effector information associated with the action concepts and statistical regularities between sublexical features and grammatical classes. Using fMRI, we examined whether these two types of information can activate the motor system in the absence of specific motor-semantic content by manipulating the existence of a sublexical cue, called the hand radical, which strongly indicates the semantic feature "hand-related" and grammatical class "verb." Although hand radical characters referring to specific manual actions evoked stronger activation in the premotor cortex than the control characters, hand radical pseudocharacters did not evoke specific activation within the motor system. These results indicated that activation of the premotor cortex during word reading relies on the access of specific action concepts. ■

INTRODUCTION

The relationship between lexical-semantic and sensory-motor processing is an important topic in cognitive neuroscience. One influential idea, called the embodied cognition hypothesis, suggests that semantic knowledge is, at least partially, grounded in the sensory-motor system (Kemmerer & Gonzalez-Castillo, 2010; Pulvermüller et al., 2010; Barsalou, 2008; Martin, 2007; Pulvermüller, 2005). In contrast, the disembodied cognition hypothesis suggests that semantics is amodal and symbolic and is processed outside the sensory-motor system (Mahon, 2015; Caramazza, Anzellotti, Strnad, & Lingnau, 2014).

To examine the embodied cognition hypothesis, many studies investigated the activation of the motor system during comprehension of verbs, phrases, or sentences that denoted actions (e.g., Desai, Conant, Binder, Park, & Seidenberg, 2013; Desai, Binder, Conant, & Seidenberg, 2010; Kemmerer, Gonzalez-Castillo, Talavage, Patterson, & Wiley, 2008; Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Hauk, Johnsrude, & Pulvermüller, 2004). Numerous studies have observed activation within the motor system, and this observation is often presented in support of the embodied cognition hypothesis, that is, action verb comprehension necessarily and automatically involves the motor system because action semantic knowledge is grounded in it (Kemmerer & Gonzalez-Castillo, 2010; Barsalou, 2008; Pulvermüller, 2005). By contrast, researchers holding the disembodied view have proposed alternative explanations. One disembodied explanation, hereinafter referred to as Disembodied Explanation I, suggests that semantic knowledge is represented in amodal brain regions, and its activation can spread to the motor system (Mahon, 2015). Despite the important difference between the embodied cognition hypothesis and Disembodied Explanation I, discriminating between them based on fMRI data is difficult (Hauk & Tschentscher, 2013). In this study, we focused on their difference with another disembodied explanation, hereinafter referred to as Disembodied Explanation II, which suggests that the activation reflects the processing of statistical regularities between ortho-phonological features and grammatical classes, but not action semantic processing or its spreading activation (de Zubicaray, Arciuli, & McMahon, 2013).

The core evidence in support of the view that motor system activation during action verb processing is, directly or indirectly, evoked by action semantic processing is the somatotopic organization of the activation. Hauk et al. (2004) found that passive reading of hand, foot, and mouth action words (e.g., pick, kick, and lick) activates the motor system in a somatotopic manner. This somatotopic activation pattern was then reported by several follow-up studies (Wu, Mai, et al., 2013; Pulvermüller, Cook, & Hauk, 2012; Aziz-Zadeh et al., 2006; Tettamanti et al., 2005), thereby indicating that the body-specific semantic features associated with action verbs can modulate motor system activation during verb processing.

Meanwhile, de Zubicaray et al. (2013) argued that the peaks of the so-called somatotopically organized action verb activations reported by previous studies are inconsistent

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and overlap with those reported for nonword processing. More importantly, they found that the motor system activates not only during processing of verbs, but also during processing of verb-like nonwords. In their study, participants were instructed to judge the grammatical class ("noun" or "verb") of 40 verbs that denoted manual actions, 40 nouns that denoted nonmanipulable entities, and 80 nonwords. Half of the nonwords had endings probabilistically associated with verb status (e.g., "-eve") and the other half of them had endings probabilistically associated with noun status (e.g., "-age"). It was found that the brain regions in the left precentral gyrus that exhibited stronger activation to verbs than to nouns also exhibited stronger activation to verb-like nonwords than to noun-like nonwords. Because nonwords do not have any semantic content, the authors proposed that motor system activation that occurs during verb processing reflects implicit processing of ortho-phonological statistical regularities which help to distinguish the grammatical class of a word.

The paradigm used by de Zubicaray et al. (2013) is elegant and provides a new way to examine brain activation during word processing. A sublexical cue shared by a group of different words has stronger probabilistic associations to the shared features of these words than to the unshared ones. Therefore, by manipulating sublexical cues embedded in nonwords, one can dissociate some shared features of words from their unshared semantic content. However, grammatical class is not the only type of information that has probabilistic associations with sublexical cues. For example, for most words there is a natural association between their grammatical category (noun/verb) and their semantic category (entity/event or object/action). If probabilistic learning links grammatical classes to sublexical cues, it should also link semantic features to sublexical cues. Therefore, it is possible that some semantic information associated with the sublexical cues evoked the activation of the motor system that de Zubicaray et al. (2013) observed.

In this study, we examined the sublexical modulation effect on the motor system activation using Chinese, a language in which the mapping between sublexical cues and semantic features is typically highly selective. About 81% of the 7000 frequently used Chinese characters are semantic-phonetic compounds (Li & Kang, 1993). These compounds have a distinct composition in which a semantic radical indicates the meaning of the character and a phonetic radical indicates the pronunciation of the character. Semantic radicals typically indicate specific semantic features, and importantly, some semantic radicals are "embodied," meaning that they refer to effectors, such as hand, foot, or mouth. These embodied semantic radicals are frequently used to constitute action verbs. The semantic radical "扌" (hereinafter referred to as "hand radical") indicates the semantic feature "hand-related." Most characters containing the hand radical refer to manual actions, such as hit ("打"), grasp ("握"), or dig ("挖"). Therefore, the hand radical has strong probabilistic associations with the semantic feature "hand-related" and the grammatical class "verb" (see Table 1 for the distribution of hand radical characters in different grammatical classes). However, there are also radicals that refer to objective features of objects and actions. For example, the ancient Chinese believed that five elements (mental, wood, water, fire, and earth) constitute the world, and in Chinese there are five radicals that refer to each of these elements. The semantic radical "氵" (hereinafter referred to as "water radical") indicates the semantic feature "water-related." Characters containing the water radical can refer to water-related entities, such as river ("河"), sea ("海"), or soup ("汤"), or they can refer to water-related events, such as swim ("游"), wash ("洗"), or flow ("流"). Behavioral studies of Chinese reading have demonstrated that the semantics of radicals can be automatically processed during character reading (Luo, Proctor, & Weng, 2015; Zhou, Peng, Zheng, Su, & Wang, 2013; Feldman & Siok, 1999; Zhou & Marslen-Wilson, 1999). The clear and specific mapping between semantic radicals and semantic features make Chinese an ideal language in which to investigate whether the effector and grammatical class information indicated by sublexical cues can activate the motor system.

Although previous studies have investigated activation of the motor system during processing of single-character Chinese verbs (Wu, Chan, et al., 2013; Wu, Mai, et al., 2013; Yang, Shu, Bi, Liu, & Wang, 2011), these studies may not accurately reflect activation evoked by sublexical cues, because the effects of sublexical cues may be attenuated by activation related to whole character meanings (Zhou et al., 2013). Therefore, similar to the study by de

Table 1. Total Numbers and Frequencies of Single Character Words Containing the Hand Radical and Water Radical for Each Grammatical Class

	Hand Radical ("扌")			*Water Radical ("氵")*		
	Verb	*Noun*	*Other*	*Verb*	*Noun*	*Other*
Total type frequency	197	23	40	83	78	56
Total token frequency (per million)	8833	442	3836	2164	1518	1990
Total log-changed token frequency	229	10	26	68	60	37

These data were obtained from the Language Corpus System of Modern Chinese Studies (Sun et al., 1997).

Zubicaray et al. (2013), this study included pseudocharacters in addition to normal characters as stimuli. We focused on the hand radical, a sublexical cue that strongly indicates the semantic feature "hand-related" and the grammatical class "verb." If the specific motor system activation for action verbs, as suggested by Disembodied Explanation II, can be reduced to processing of the sublexical cues indicating grammatical class information, then we can observe an equal level of activation differences between hand radical and control characters and between hand radical and control pseudocharacters. On the contrary, if we observe significant activation difference between hand radical and control characters but no activation difference between hand radical and control pseudocharacters, then the motor system activation during action verb processing relies on the access of specific motor semantic content rather than on the effector or grammatical class information that can be indicated by sublexical cues.

METHODS

This study contains an fMRI experiment (the main experiment) and a supplemental behavioral experiment to provide additional RT data.

The fMRI Experiment

Participants

Twenty healthy undergraduate and graduate students (13 women) participated in the experiment. The average age of the participants was 22.5 years ($SD = 2.0$ years). All participants were right-handed and were native Chinese speakers. No participant suffered from psychiatric or neurological disorders or had ever sustained a head injury. Before the experiment, each participant read and signed an informed consent form issued by the institutional review board of the Beijing Normal University Imaging Center for Brain Research.

Design and Materials

We used the hand radical as the sublexical cue of interest, and the water radical served as its control. The water radical was chosen to be our control semantic radical for two reasons. First, unlike the hand radical, the water radical does not indicate effector or grammatical class information. Second, using the water radical can help in examining whether the sublexical effects observed by de Zubicaray et al. (2013) have a grammatical ambiguity explanation.

In the study by de Zubicaray et al. (2013), the grammatical ambiguity of sublexical cues was highly unbalanced between conditions. As shown by their behavioral data, the cueing effect of verb-like endings is much weaker than that of noun-like endings (correctly classified verb-like nonword: 57%; correctly classified noun-like nonword: 79%). Therefore, even if grammatical class information in sublexical cues does mediate the activation of the left precentral gyrus, there are still two possible explanations for why this occurs. One is that the brain regions that exhibit stronger activation to verbs and verb-like nonwords specifically represent statistical regularities between sublexical cues and the grammatical class "verb." The other is that the activation of these brain regions reflects grammatical ambiguity of the sublexical cues: The sublexical cues with high grammatical ambiguity evoke stronger activation in the left precentral gyrus than those with low grammatical ambiguity.

We dissociated the potential grammatical ambiguity explanation for the sublexical effects observed by de Zubicaray et al. (2013) from the alternative explanations investigated here by reversing the relative grammatical ambiguity across sublexical cue categories. As shown in Table 1, statistical regularities between the hand radical and grammatical classes are relatively unambiguous: The majority of hand radical characters are verbs [verb/noun/other (%): type frequency: 76/9/15; token frequency: 67/3/29; log-changed token frequency: 86/4/10]. In contrast, the statistical regularities between the water radical and grammatical classes are ambiguous: Characters with the water radical include roughly equal numbers of nouns and verbs [verb/noun/other (%): type frequency: 38/36/26; token frequency: 38/27/35; log-changed token frequency: 41/36/22]. Therefore, if the semantic feature "hand-related" or grammatical class "verb" can modulate the activation of the motor system, then hand radical characters and pseudocharacters should evoke stronger activation of the motor system than water radical ones; in contrast, if the activation observed by de Zubicaray et al. (2013) reflects grammatical ambiguity of sublexical cues, then water radical characters and pseudocharacters should evoke stronger activation of the motor system than hand radical ones.

Four conditions were used in this experiment: the hand radical character condition, the water radical character condition, the hand radical pseudocharacter condition, and the water radical pseudocharacter condition. Each condition included 42 items, with 14 items not repeated (14 items total) and 14 items repeated once (28 items total) to ensure sufficient signal detection (Thompson et al., 2007). All characters and pseudocharacters were left–right structured semantic-phonetic compounds, with the hand radical "扌" or water radical "氵" as the semantic radical on the left side (see Figure 1 for examples of our stimuli). The stroke number was matched between all conditions [mean stroke number (SD): hand radical characters, 9.5 (3.0); water radical characters, 9.5 (2.7); hand radical pseudocharacters, 9.5 (3.0); water radical pseudocharacters, 9.5 (2.7); $ts(82) < 1$]. For the two character conditions, all characters used were single-character words. Word frequency was obtained from the Language Corpus System of Modern Chinese Studies (Sun, Huang, Sun, Li, & Xing, 1997) and was matched between the two conditions [mean frequency

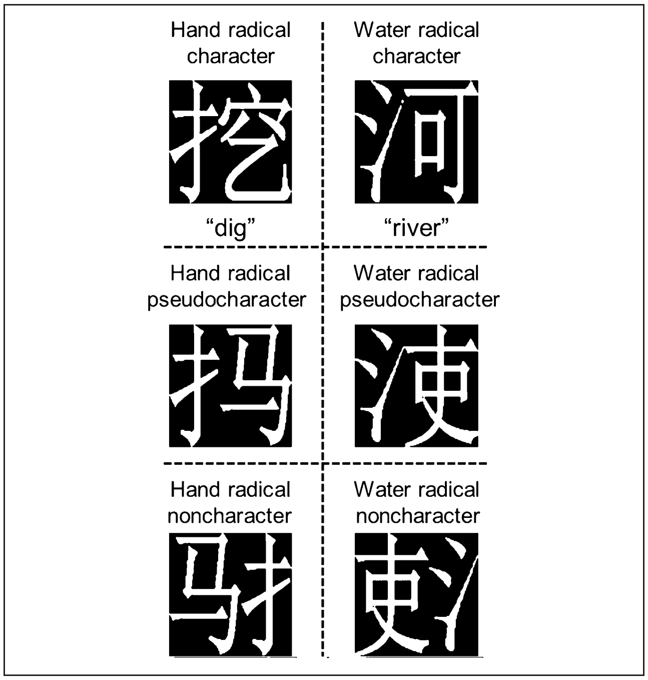

Figure 1. Examples of the experimental stimuli.

count per million (*SD*): hand radical characters, 35.0 (28.5); water radical characters, 33.7 (38.6); $t(82) < 1$]. In general, hand radical characters were verbs and water radical characters were nouns; noun/verb homographs were avoided, but when used the selected hand radical characters were used as a noun in less than 20% of their total frequency and the selected water radical characters were used as a verb in less than 20% of their total frequency. The imageability of each character was rated using a 7-point scale (1 = *very low*, 7 = *very high*) by a group of 16 participants [12 women; age = 22.5 years (*SD* = 1.0)] who did not take part in the fMRI experiment. The imageability was matched between the two conditions [mean rating (*SD*): hand radical characters, 4.6 (0.6); water radical characters, 4.5 (1.0); $t(82) < 1$]. The pseudocharacters were produced by combining the hand or water radical with real phonetic radicals. In a pseudocharacter, the radicals were always positioned legally, that is, positioned where they may appear in real characters. For about three quarters of the pseudocharacters, we simply adopted their phonetic radicals from the character items and exchanged the semantic radicals.

Task

We used the lexical decision task, but not the grammatical judgment task, that was used by de Zubicaray et al. (2013). The reason we did not use the grammatical judgment task is that the cognitive processes underlying grammatical judgment of nonwords are unclear, because nonwords do not belong to any grammatical class. As assumed by de Zubicaray et al. (2013), participants can judge the grammatical classes of nonwords on the basis of implicit statistical regularities between sublexical cues and grammatical classes. However, the behavioral data showed that the participants failed to "correctly" classify a considerable proportion of the nonwords (21% noun-like nonwords and 43% verb-like nonwords), indicating that the statistical regularities between sublexical cues and grammatical classes might not be strong enough to allow the participants to make accurate decisions. Therefore, it is possible that participants use some strategies to make their judgments, such as associating a target nonword to its orthographically neighboring words. If so, the brain activation evoked by nonwords may partially reflect processing of words.

We believe that the lexical decision task largely discourages participants from associating a target nonword with its orthographically neighboring words. Participants cannot benefit from associating a target nonword to a word when making their responses; rather that strategy will only disrupt their performance when deciding a pseudocharacter to be pseudo. Therefore, if we observe similar sublexical effects across characters and pseudocharacters in the lexical decision task, we will be able to exclude a confounding strategy effect.

Procedure

We used an event-related design with three runs lasting 6 min 52 sec each. Each run included 56 trials, 14 for each of the four conditions. In each trial, the target character/pseudocharacter appeared for 1 sec, followed by a 1-sec blank. Participants were instructed to perform a lexical decision task and to withhold their response until the response options appeared. Next the response options "real" and "pseudo" were presented on either side of the center of the screen for 2 sec. The left/right positions of the labels and the correct responses were randomized and counterbalanced across trials to prevent consistent response mapping (de Zubicaray et al., 2013). Each trial was followed by a jitter interval of at least 2 sec. No trial was conducted during the first and last 10 sec of each run. The order of test trials and the length of jitter intervals were optimized using optseq software (surfer.nmr.mgh.harvard.edu/optseq/) and were counterbalanced across participants.

In the scanner, the stimuli were back-projected via a video projector (refresh rate = 60 Hz; spatial resolution = 800 × 600) onto a translucent screen placed inside the scanner bore. Participants viewed the stimuli through a mirror located above their eyes. The background was black and all stimuli were white. Participants were instructed to make their choices by pressing a button with either their right index or middle finger. Before the formal experiment, each participant completed a practice run outside the scanner with additional stimuli; the procedure of this run was identical to that of the formal experiment.

Acquisition and Analysis of Magnetic Resonance Imaging Data

Structural and fMRI data were collected with a 3-T Siemens Trio Tim scanner (Erlangen, Germany) at the Beijing Normal University MRI Center. A T2*-weighted gradient EPI sequence was applied to acquire BOLD signals (repetition time = 2000 msec; echo time = 30 msec; flip angle = 90°; matrix size = 64 × 64; 33 slices; voxel size = 3.125 mm × 3.125 mm × 4 mm). A high-resolution 3-D structural data set was acquired with a 3D MPRAGE sequence in the sagittal plane (repetition time = 2530 msec; echo time = 3.39 msec; flip angle = 7°; matrix size = 256 × 256; 128 slices; voxel size = 1.33 mm × 1 mm × 1 mm).

fMRI data were preprocessed using Statistical Parametric Mapping software (SPM8; www.fil.ion.ucl.ac.uk/spm/) and the advanced edition of DPARSF V2.1 (Yan & Zang, 2010). The first five volumes (10 sec) of each functional run were discarded for signal equilibrium. Slicing timing and 3-D head motion correction were then performed, and a mean functional image was obtained for each participant. Specifically, functional runs were first realigned with one another by aligning the first scan from each run to the first scan of the first run. Subsequently, the images within each run were aligned to the first image of the run. No participant exhibited head motion of >3 mm maximum translation or 3° rotation throughout the experiments. To normalize functional images, the structural image of each participant was coregistered to the mean functional image and then subsequently segmented. The parameters obtained in the segmentation were used to normalize the functional images of each participant onto the Montreal Neurological Institute (MNI) space. The functional images were resampled to 3-mm isotropic voxels and spatially smoothened using a 6-mm FWHM Gaussian kernel.

Statistical analyses were conducted according to two-level, mixed-effects models. At the first level, a general linear model was applied to explore the fixed effect within each subject. Trial types and the onsets of the delayed responses were modeled as regressors and were convolved with a standard hemodynamic response function. Six head motion parameters obtained by head motion correction were also included as nuisance regressors. The default value of the high-pass filter (128 sec) was included to remove confounding influences on the BOLD signal, such as physiological noise from cardiac and respiratory cycles. The subsequent second-level random effects analyses were performed using a whole-brain mask and a small volume mask comprising the left BA 4 and BA 6 areas (corresponding to motor and premotor cortex) of the Brodmann template in the MRIcron software (www.mccauslandcenter.sc.edu/mricro/mricro/mricro.html). In the whole-brain analysis, we focused on the contrast between character and pseudocharacter conditions; previous studies using the lexical decision task have obtained consistent results for this contrast, and their results can serve as a criterion for the reliability of our data. In the small volume correction analysis, we focused on the potential radical effects in characters and pseudocharacters. To be consistent with de Zubicaray et al. (2013), we first examined the contrasts "hand radical character versus water radical character" and "hand radical pseudocharacter versus water radical pseudocharacter" using within-subject t test. After that, a full factorial random-effects model was used to further examine the "lexicality (character/pseudocharacter) × radical (hand/water)" interaction. In all analyses, the false positive rate was always controlled at $\alpha < 0.05$ using REST AlphaSim (REST version 1.8; www.restfmri.net; Song et al., 2011), a Monte Carlo simulation program similar to AlphaSim in AFNI (afni.nimh.nih.gov). The individual voxel threshold probability was set as $p < .001$ and $p < .01$ in the whole-brain analysis and in the small volume correction analysis, respectively. The results of the whole-brain and small volume correction analyses were shown using the Brainnet Viewer software (Xia, Wang, & He, 2013).

To determine the relationship between the results of this study and the findings of de Zubicaray et al. (2013), we conducted further ROI analyses. Two ROIs were set on the basis of peak voxels of the verb-specific clusters reported by de Zubicaray et al. (2013). Given that the activation clusters reported by de Zubicaray et al. (2013) are relatively small (17 voxels and 30 voxels), we defined our ROIs as small spheres with a 6-mm diameter centered in the reported MNI coordinates (left lateral precentral gyrus = −54 −2 42; left medial precentral gyrus = −4 14 50).

Supplemental Behavioral Experiment

We took extra caution to exclude the possibility that potential null results in the fMRI task associated with pseudocharacters were due to little processing or attention on these stimuli. Given that the RT data of the delayed response task in the fMRI experiment are negligible, we carried out an additional behavioral experiment without the delay outside the scanner with a new set of participants. Considering that a direct comparison between characters and pseudocharacters may be confounded by the response-type difference ("true" vs. "false"), we added noncharacters in the behavioral study. The pseudo- and noncharacters are two types of frequently used false characters in studies of Chinese character recognition: pseudocharacters comprise radicals positioned legally (i.e., positioned where they may appear in real characters), and noncharacters comprise radicals positioned illegally. Previous studies have shown that noncharacters can easily be rejected, whereas pseudocharacters are likely to be misperceived as real characters (Ho, Ng, & Ng, 2003; Peng, Li, & Yang, 1997; Cheng & Huang, 1995). Longer RT and/or higher error rates of pseudocharacters than those of noncharacters would indicate that the pseudocharacters are processed at least to some degree.

Twenty healthy undergraduate and graduate students (12 women; mean age = 23.6 years, *SD* = 1.7 years) participated in the experiment. In addition to the four conditions used in the fMRI experiment, two noncharacter conditions (a hand radical one and a water radical one) were included. The character and pseudocharacter items were identical to those used in the fMRI experiment. The noncharacters were produced by transforming the positions of the radicals of the pseudocharacters (see Figure 1 for examples of our stimuli). The experiment consisted of three runs containing 84 trials each, 14 for each of the six conditions. In each trial, a white fixation was presented at the center of the screen for 500 msec, followed by the appearance of a target character/pseudocharacter/noncharacter that remained on the screen until the response. Subsequently, a blank screen was presented for 1000 msec. Participants were instructed to perform a lexical decision task by pressing one of two response buttons. Each participant received a different random order of targets. In the analyses of RT, trials in which participants made an erroneous response were excluded. We also excluded trials with RTs that were shorter than 100 msec or over three standard deviations from the mean RT (calculated separately for each condition for each participant) from the analyses.

RESULTS

Behavioral Results

Mean percent accuracy and RT for each condition are shown in Table 2. In the fMRI experiment, accuracy and RT data were collected while the participants performed their tasks in the scanner. We compared the different conditions by using the within-subject paired *t* test. The accuracy of the character conditions was significantly higher than that of the pseudocharacter conditions [mean accuracy (*SD*): character, 96.3% (3.6%); pseudocharacter, 86.8% (9.5%); $t(19) = 3.90$, $p < .001$]. The accuracy of the water radical pseudocharacter condition was significantly lower than that of the hand radical pseudocharacter condition [mean accuracy (*SD*): hand radical, 90.7% (8.3%); water radical, 83.0% (12.4%); $t(19) = 3.71$, $p = .001$]. This difference might be caused by the fact that, across all Chinese characters, there are more low-frequency water radical characters than low-frequency hand radical characters (number of characters with frequency lower than 1 per million: water radical: 77, hand radical: 38; Chinese Linguistic Data Consortium, 2003), which could make it more difficult to identify a water radical pseudocharacter. The RT data were negligible because of the use of a delayed response task, so they were not considered in the fMRI experiment.

In the supplemental behavioral experiment, the RT of the pseudocharacter condition was significantly longer than that of the two other conditions [mean RT (*SD*): pseudocharacter, 938 msec (262 msec); character, 653 msec (108 msec); noncharacter, 567 msec (90 msec); pseudocharacter vs. character: $t(19) = 6.15$, $p < .001$; pseudocharacter vs. noncharacter: $t(19) = 7.98$, $p < .001$], and the accuracy of the pseudocharacter condition was significantly lower than that of the two other conditions [mean accuracy (*SD*): pseudocharacter, 79.9% (16.6%); character, 94.7% (5.6%); noncharacter, 99.6% (0.7%); character vs. pseudocharacter: $t(19) = 3.65$, $p = .002$; noncharacter vs. pseudocharacter: $t(19) = 3.78$, $p = .001$]. Moreover, replicating the data pattern of the fMRI experiment, the accuracy of the water radical pseudocharacter condition was significantly lower than that of the hand radical pseudocharacter condition [mean accuracy (*SD*): hand radical, 84.3% (12.6%); water radical, 75.6% (21.9%); $t(19) = 2.95$, $p = .008$], and the RT of the water radical pseudocharacter condition was significantly longer than that of the hand radical pseudocharacter condition [mean RT (*SD*): hand radical, 909 msec (254 msec); water radical, 966 msec (280 msec); $t(19) = 2.59$, $p = .018$].

fMRI Results

Whole-brain Analyses

The results of the whole-brain analysis are shown in Table 3 and Figure 2. For the contrast "character >

Table 2. Mean Percent Accuracy and RT for Each Condition in the fMRI Experiment and in the Supplemental Behavioral Experiment

	Character		*Pseudocharacter*		*Noncharacter*	
	Hand Radical	*Water Radical*	*Hand Radical*	*Water Radical*	*Hand Radical*	*Water Radical*
The fMRI Experiment						
Accuracy (%)	96.4 (4.5)	96.2 (4.2)	90.7 (8.3)	83.0 (12.4)	–	–
RT (msec)	641 (126)	647 (101)	652 (137)	671 (124)	–	–
The Supplemental Behavioral Experiment						
Accuracy (%)	95.5 (4.4)	93.9 (8.6)	84.3 (12.6)	75.6 (21.9)	99.5 (1.0)	99.6 (0.9)
RT (msec)	661 (105)	646 (121)	909 (254)	966 (280)	574 (93)	561 (87)

*SD*s are included in parentheses.

Table 3. Results of Whole-brain fMRI Analysis

Contrast	*Anatomical Region*	*Cluster Size (Voxels)*	*MNI Coordinates (x, y, z)*			*Peak t Value*
Character > pseudocharacter	Right cingulate gyrus	157	3	−9	39	5.86
	Right inferior parietal lobule	101	60	−30	36	5.47
	Left superior temporal sulcus	74	−45	−54	27	5.22
Pseudocharacter > character	Right inferior occipital gyrus	429	30	−93	−6	9.92
	Left inferior occipital gyrus	375	−21	−96	−9	9.86
	Left superior frontal gyrus	173	−3	15	51	7.55
	Left fusiform gyrus	147	−45	−60	−9	7.92
	Left inferior frontal gyrus	143	−48	3	27	5.18
	Right inferior frontal gyrus	129	51	9	33	6.98
	Left claustrum	72	−24	21	0	6.66

pseudocharacter," significant activation was observed in the cingulate gyrus, right inferior parietal lobule, left posterior STS, and supramarginal gyrus. For the contrast "pseudocharacter > character," significant activation was observed in the bilateral medial frontal gyri, bilateral middle and inferior frontal gyri, left claustrum, bilateral inferior occipital gyri, and bilateral fusiform gyri. No radical effect was observed within or across character and pseudocharacter conditions.

The activation differences between character and pseudocharacter conditions replicate the findings of previous fMRI studies that used the lexical decision task (Cattinelli, Borghese, Gallucci, & Paulesu, 2013; Taylor, Rastle, & Davis, 2013; Thompson et al., 2007; Binder, Westbury, McKiernan, Possing, & Medler, 2005). It should be noted that inferior occipital activation is less frequently observed in studies of alphabetic word reading than in studies of Chinese reading. As reflected by cross-linguistic meta-analyses, Chinese word reading evokes stronger activation in the inferior occipital regions than alphabetic word reading, specifically in the right hemisphere (Bolger, Perfetti, & Schneider, 2005; Tan, Laird, Li, & Fox, 2005). The inferior occipital activation in reading might reflect generalized and nonlexical orthographic processing and is modulated by visual-spatial complexity and orthographic typicality of stimuli (Taylor et al., 2013; Bolger et al., 2005; Tan et al., 2005).

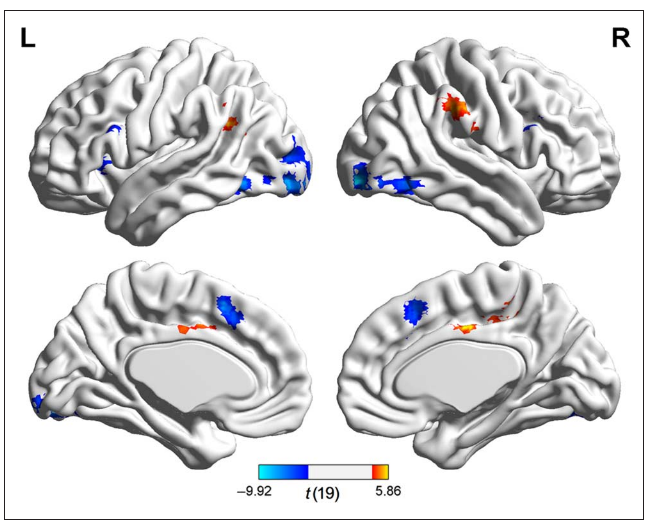

Figure 2. Results of the whole-brain analysis. The brain regions that showed stronger activation to character than to pseudocharacter are shown in warm color; the brain regions that showed stronger activation to pseudocharacter than to character are shown in cold color.

Small Volume Correction Analyses

Small volume correction analyses were conducted within a mask comprising the left BA 4 and BA 6 areas (see Figure 3A). For the contrast "hand radical character versus water radical character," a cluster showing significantly stronger activation to hand radical characters than that to water radical characters was observed in the left lateral precentral gyrus (peak coordinate: −57 −3 39; cluster size = 31 voxels; Figure 3B). No significant cluster was observed for the contrast "hand radical pseudocharacter versus water radical pseudocharacter." For the "lexicality × radical" interaction, a significant activation cluster was observed in the left lateral precentral gyrus (peak coordinate: −57 −3 42; cluster size: 16 voxels; see Figure 3C).

We conducted two sets of follow-up analyses based on the results of small volume correction analyses. First, we conducted ROI analyses to explore the activation patterns within the significant clusters observed in small volume correction analyses. We analyzed whether the left lateral precentral region that showed a significant "hand radical character > water radical character" effect also shows a trend toward preferring hand radical pseudocharacters to water radical pseudocharacters. No significant difference was found between the hand radical and water radical pseudocharacter conditions [mean beta-value (*SD*): hand radical, 1.94 (1.49); water radical, 2.03 (1.56); $t(19) < 1$]. We also analyzed the radical effect within

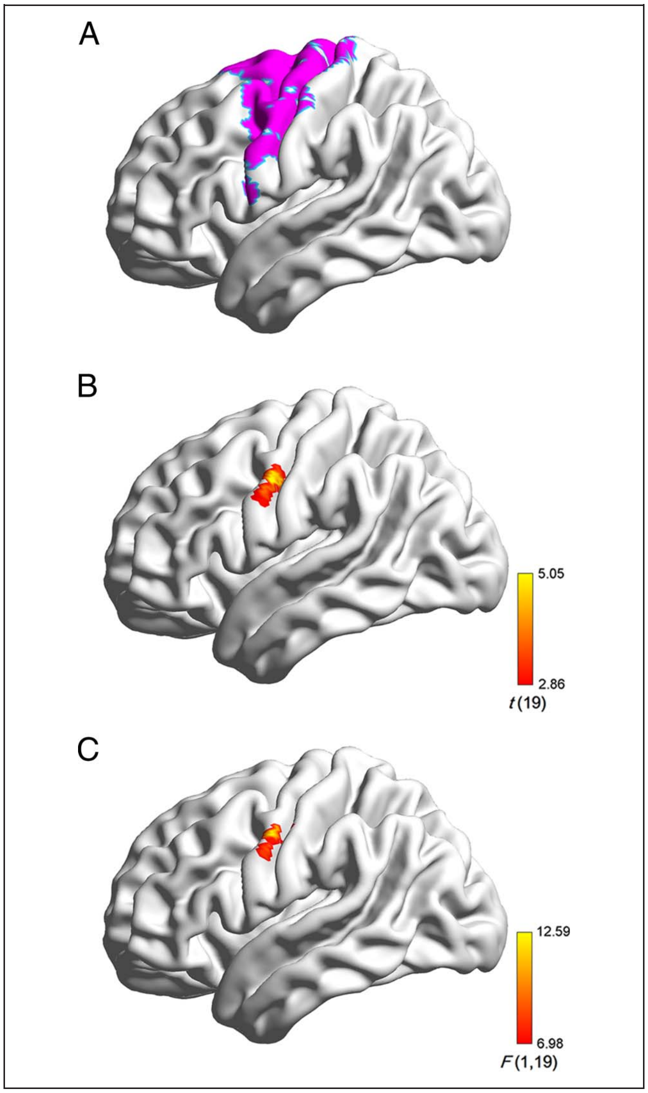

Figure 3. Results of the small volume correction analysis: (A) the mask used in the small volume correction analysis, (B) the brain region that showed stronger activation to hand radical characters than to water radical characters, and (C) the brain region that showed significant "lexicality × radical" interaction.

character conditions and within pseudocharacter conditions in the ROI showing a significant "lexicality × radical" interaction. We found a significant "hand radical > water radical" effect in character conditions [mean beta-value (*SD*): hand radical, 1.88 (1.43); water radical, 1.38 (1.45); $t(19) = 4.74$, $p < .001$], and no activation difference between pseudocharacter conditions [mean beta-value (*SD*): hand radical, 1.58 (1.53); water radical, 1.74 (1.65); $t(19) = 1.30$, $p = .208$] was observed. Therefore, the clusters identified in our small volume correction analyses consistently showed stronger activation to hand radical characters than water radical characters, and no activation difference was found between hand radical and water radical pseudocharacters.

Second, we examined the distances between the activation peaks observed in this study and those reported by previous related studies. The peak coordinates observed in this study (hand character > water character: −57 −3 39; "lexicality × radical" interaction: −57 −3 42) were less than two voxels away from the peak coordinate (−54 −2 42) reported by de Zubicaray et al. (2013), which indicated that the contrast between our character conditions successfully replicated the left lateral precentral activation reported by de Zubicaray et al. (2013). We further compared our peak coordinates to those reported by Buccino et al. (2001), a highly cited study that reported somatotopically organized activation in the premotor cortex during action observation. Buccino et al. (2001) used a three (mouth/hand/foot) by two (object-related/object-unrelated) design and reported six coordinates in the left premotor cortex. The distances from the six coordinates reported by Buccino et al. (2001) to the peak coordinate of our "hand character > water character" cluster are as follows (arranged from nearest to farthest): non-object-related hand action: 7.8 mm; object-related hand action: 8.2 mm; object-related mouth action: 8.7 mm; non-object-related mouth action: 14.5 mm; non-object-related foot action: 29.4 mm; object-related foot action: 37.8 mm. Meanwhile, the distances from the six coordinates reported by Buccino et al. (2001) to the peak coordinate of our "lexicality × radical" interaction cluster are as follows: object-related hand action: 6.1 mm; non-object-related hand action: 7.5 mm; object-related mouth action: 10.0 mm; non-object-related mouth action: 13.6 mm; non-object-related foot action: 27.0 mm; object-related foot action: 35.5 mm. Therefore, in terms of the somatotopic organization of the premotor cortex, our coordinates were nearest to the hand regions.

ROI Analysis on the Basis of the Results of de Zubicaray et al. (2013)

We conducted ROI analyses on the basis of the verb-specific activation of the left lateral and medial precentral gyrus that was reported by de Zubicaray et al. (2013). For the ROI located in the left lateral precentral gyrus, the hand radical character condition evoked stronger activation than the water radical character condition did [mean beta-value (*SD*): hand radical, 3.11 (1.69); water radical, 2.74 (1.86); $t(19) = 3.48$, $p = .003$]. There was no significant activation difference between the two pseudocharacter conditions [mean beta-value (*SD*): hand radical, 2.80 (1.69); water radical, 2.93 (1.66); $t(19) = 1.14$, $p = .268$]. The "lexicality × radical" interaction was significant [$F(1, 19) = 14.05$, $p = .001$]. Therefore, in this study, the verb preference of this region is clearly restricted to real characters (words).

For the ROI located in the left medial precentral gyrus, there was no significant difference in activation between the two character conditions [mean beta-value (*SD*): hand radical, 4.59 (3.24); water radical, 4.77 (3.20); $t(19) = 1.06$, $p = .302$], and the water radical pseudocharacter condition evoked stronger activation than the hand radical pseudocharacter condition did [mean beta-value (*SD*): hand radical, 5.73 (3.34); water radical, 6.23 (3.35); $t(19) = 2.20$, $p = .040$]. There was no significant "lexicality × radical" interaction [$F(1, 19) = 1.21$, $p = .285$]. The stronger activation observed in this region for the water radical pseudocharacter condition could be due to processing difficulty associated with the condition, which is reflected by the behavioral accuracy results. As suggested by de Zubicaray et al. (2013), the greater activity observed for verb-like stimuli in their study may reflect the relative difficulty of processing verbs compared to nouns. To evaluate this possibility, we compared the brain activation evoked by the character and pseudocharacter conditions. As expected, the pseudocharacter condition, which the behavioral data indicate to be more difficult, evoked significantly stronger activation than the character condition did [mean beta-value (*SD*): character, 4.68 (3.20); pseudocharacter, 5.98 (3.30); $t(19) = 7.35$, $p < .001$].

DISCUSSION

We examined whether a sublexical cue, called the hand radical, which strongly indicates the semantic feature "hand-related" and the grammatical class "verb," can modulate the activation of the motor system during word reading. We found that the left lateral precentral cortex showed stronger activation to hand radical characters than to the control characters; however, it showed no activation difference between hand radical and control pseudocharacters. These findings were confirmed by further analyses within ROIs defined by the activated regions observed in this study and de Zubicaray et al. (2013). Therefore, the hand radical characters referring to manual actions could elicit selective activation in the left lateral precentral cortex, but the hand radical alone could not do that.

The negative finding in the pseudocharacter conditions cannot be readily explained by the lack of processing of the stimuli. In the supplemental behavioral experiment, we showed that the mean RT of pseudocharacter trials was significantly longer than that of the character and noncharacter trials. In addition to our behavioral data, previous studies of Chinese character processing have indicated extensive sublexical processing of semantic radicals in pseudocharacter reading. The importance of sublexical processing of semantic radicals increases as the character familiarity decreases (Zhou et al., 2013; Shu & Anderson, 1997). For example, Zhou et al. (2013) examined the sublexical semantic processing of semantic radicals using a primed naming task, in which the target character is semantically related to the semantic radical embedded in a prime character, but not to the prime character itself. They found semantic priming effects from semantic radicals embedded in low-frequency prime characters and not from those embedded in high-frequency prime characters, indicating that semantic radicals evoke stronger semantic activations when embedded in unfamiliar characters. Therefore, the activations resulting from the sublexical processing of semantic radicals might be even stronger in the pseudocharacter conditions than those in the character ones.

With respect to the embodied and disembodied semantic theories mentioned in the Introduction, our findings have three aspects of implications. First, we provided evidence against Disembodied Explanation II, which assumes that the premotor cortex activation during action verb processing can be reduced to the processing of statistical regularities between sublexical features and grammatical classes (de Zubicaray et al., 2013). By contrast, we found that the premotor cortex activation elicited by Chinese characters referring to manual actions could not be explained by their sublexical feature strongly indicating the grammatical class "verb." Second, our results could be explained according to the embodied cognition hypothesis, and they are specifically in accordance with the Two-Level Theory of verb semantic representation (Kemmerer & Gonzalez-Castillo, 2010). The Two-Level Theory suggests that the premotor cortex subserves the "root-level" features of verb meaning that characterize individual verbs, but not the "template-level" features that are shared by all the verbs in a given class. Therefore, coinciding with our results, the Two-Level Theory predicts that the hand radical does not elicit the premotor cortex activation as action verbs do because the hand radical can indicate only "template-level" semantic features, but not "root-level" ones. Finally, our results could also be explained according to Disembodied Explanation I, which interprets the premotor cortex activation during verb processing as spreading activation from an amodal semantic system (Mahon, 2015). Our results indicated the triggering condition for the presumed spreading activation from the semantic system to the motor system: the spreading activation relies on the access of relative specific motor semantic content, such as the "root-level" features of verb meaning; by contrast, the effector information (e.g., hand-related) alone cannot trigger the spreading activation.

On the basis of the findings of this study, an important question to be addressed in future is how information in the motor system is organized and represented along fine-grained motor-semantic dimensions. Previous studies have proposed some coarse-grained factors that may affect the motor system activation during verb processing, including the effector information of action verbs (Wu, Mai, et al., 2013; Pulvermüller et al., 2012; Aziz-Zadeh et al., 2006; Tettamanti et al., 2005; Hauk et al., 2004), handness of the participants (Hauk & Pulvermüller, 2011; Willems, Hagoort, & Casasanto, 2010), and task demands (Tomasino, Weiss, & Fink, 2010; Tettamanti et al., 2008; Tomasino, Werner, Weiss, & Fink, 2007). However, studies focusing on these coarse-grained factors have obtained some inconsistent findings (e.g., Hauk & Pulvermüller, 2011; Willems et al., 2010). Our findings demonstrated that more fine-grained motor-semantic dimensions, such as the finger movement pattern of an action (Bartoli, Maffongelli, Jacono, & D'Ausilio, 2014), are warranted to be considered in future studies of verb semantic organization. Such dimensions may provide better explanations for the motor system activation during verb processing.

Our findings also provide new insight into a long-lasting debate about whether the brain activation differences between action verbs and nonaction nouns reflect semantic or grammatical difference between the two word categories (Crepaldi, Berlingeri, Paulesu, & Luzzatti, 2011; Vigliocco, Vinson, Druks, Barber, & Cappa, 2011). It has been found that the premotor cortex activation for action verbs could be better explained by the processing of action semantic information than by that of grammatical class information of words. For example, Saccuman et al. (2006) used a two (manipulable/nonmanipulable) by two (verb/noun) design to dissociate the brain activations reflecting the semantic classes "manipulable or not" from those reflecting grammatical classes "verb or noun." The left premotor cortex showed stronger activation to manipulable items than to nonmanipulable ones and no activation difference to verbs and nouns, favoring a semantic-based account. However, given that the sublexical features of stimuli were not controlled in those previous studies, whether the grammatical or semantic information accessed via sublexical processing can explain the premotor cortex activation during action verb processing is unclear. Our findings, together with evidence in the literature, collectively indicated that the grammatical class information, whether accessed via sublexical or whole word processing, is unlikely to evoke selective activation in the premotor cortex.

A final question that must be discussed is how to explain the discrepancies between our results and those of de Zubicaray et al. (2013). Two discrepancies were observed between the two studies. First, in the lateral precentral cortex, although we replicated the findings of de Zubicaray et al. (2013) in the character/word conditions, we did not observe the sublexical cuing effect that they observed in pseudocharacter/nonword conditions. This discrepancy has several possible reasons. A first possible reason is that the semantic information indicated by the sublexical cues is different between the two studies. The sublexical cues used in this study were consistent within each condition, and the mapping between sublexical cues and semantic features is highly specific. In contrast, the sublexical cues used by de Zubicaray et al. (2013) lacked this consistency. It is possible that some of these sublexical cues are shared by only a small group of words and indicate relative specific semantic features, resulting in word-like activation patterns. A second possible reason is related to the task difference between the two studies. de Zubicaray et al. (2013) used a grammatical judgment task to examine processing of words and nonwords. As mentioned in the Methods section, because nonwords do not belong to any grammatical class, the grammatical judgment task may implicitly encourage participants to associate a target nonword to its orthographic neighboring words. Therefore, the brain activation observed in the nonword trials may reflect not only nonword processing but also word processing. In contrast, this study used a lexical decision task, in which participants cannot benefit from associating target pseudocharacters to their orthographic neighboring characters when making their responses, meaning this potential confounding strategy was largely avoided. A third possible reason is related to the phonological properties of the sublexical cues. The sublexical cues manipulated by de Zubicaray et al. (2013) are both orthographic and phonological, but the sublexical cues manipulated in our present study had no phonological attribute associated with the whole characters. Therefore, if the sublexical effect observed by de Zubicaray et al. (2013) relies on the phonological representations, then it would explain why we did not observe the same effect in Chinese characters. These possible reasons should be examined in future studies.

Second, we did not replicate the findings of de Zubicaray et al. (2013) in the left medial precentral region; instead, we found that the activation level of the same region was modulated by processing difficulty. Actually, de Zubicaray et al. (2013) themselves have suggested that the greater activity observed for verb-like stimuli in their study may actually reflect the relative difficulty of processing verbs compared with nouns. Consistent with this, it has been found that activation of the left medial precentral gyrus is positively correlated with the length of RT across several kinds of cognitive tasks (Yarkoni, Barch, Gray, Conturo, & Braver, 2009), and studies using lexical decision tasks have also consistently found that pseudowords (typically more difficult) can evoke stronger activation than real words in this region (Cattinelli et al., 2013; Taylor et al., 2013; Thompson et al., 2007; Binder et al., 2005). Additionally, activation of this same region is observed in various types of working memory tasks (Owen, McMillan, Laird, & Bullmore, 2005). Therefore, it is quite likely that the observed activation difference in the left medial precentral gyrus is a reflection of processing demand, and not related to processing of grammatical class information.

In conclusion, by manipulating the sublexical cues embedded in Chinese characters and pseudocharacters, we found that verbs referring to specific manual actions evoked stronger activation in the premotor cortex than the control words, but their sublexical cue indicating effector and grammatical class information did not evoke any selective activation. Therefore, the premotor cortex activation observed during action verb processing did not simply reflect the widely shared effector or grammatical class information; rather, it relied on the access of more specific motor semantic content.

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