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Influences of motor contexts on the semantic processing of action-related language

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Abstract The contribution of the sensory–motor system to the semantic processing of language stimuli is still controversial. To address the issue, the present article focuses on the impact of motor contexts (i.e., comprehenders' motor behaviors, motor-training experiences, and motor expertise) on the semantic processing of action-related language and reviews the relevant behavioral and neuroimaging findings. The existing evidence shows that although motor contexts can influence the semantic processing of action-related concepts, the mechanism of the contextual influences is still far from clear. Future investigations will be needed to clarify (1) whether motor contexts only modulate activity in motor regions, (2) whether the contextual influences are specific to the semantic features of language stimuli, and (3) what factors can determine the facilitatory or inhibitory contextual influences on the semantic processing of action-related language.

Keywords Embodiment · Action-related language · Motor behaviors · Motor expertise · Motor training

Language comprehension used to be regarded as amodal and distinct from perception and action (Hauser, Chomsky, & Fitch, 2002), but increasing evidence has shown that sensory and motor regions involved in action and perception are activated during the semantic processing of language stimuli (e.g., Aziz-Zadeh & Damasio, 2008; Pulvermüller & Fadiga, 2010; Willems & Casasanto, 2011). For instance, premotor regions involved in body actions are also activated during the semantic processing of action-related language (e.g., Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Hauk, Johnsrude, & Pulvermüller, 2004; Raposo, Moss, Stamatakis, & Tyler, 2009; Tettamanti et al., 2005). Studies using neurophysiological methods (EEG, MEG, and TMS) have indicated that motor activity can be elicited early after stimulus presentation, and that stimulation on motor regions at early latencies can interfere with language task performance. Additionally, the effects are independent of the participants' attention (e.g., Hauk, Shtyrov, & Pulvermüller, 2008). These findings have been regarded as evidence supporting the view that the sensory–motor system may contribute to semantic processing during language comprehension (e.g., Barsalou, 1999, 2008; Gallese & Lakoff, 2005; Pulvermüller, 1999, 2001, 2005).

However, this conclusion is highly controversial (Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012). First, the motor activations elicited by listening to or reading action language stimuli have indicated substantial discrepancies (e.g., Fernandino & Iacoboni, 2010) and have been challenged by other studies (e.g., de Zubicaray, Postle, McMahon, Meredith, & Ashton, 2010; Postle, Ashton, McFarland, & de Zubicaray, 2013; Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008). Second, the involvement of the motor system is not automatic, but context-dependent (e.g., Willems & Casasanto, 2011). Factors such as task demands, familiarity, semantic features of the language stimuli, and sentential contexts can influence motor activity (e.g., Desai, Binder, Conant, Mano, & Seidenberg, 2011; Desai, Conant, Binder, Park, & Seidenberg, 2013; Raposo et al., 2009; Rüschemeyer, Brass, & Friederici, 2007; van Dam, van Dongen, Bekkering, & Rüschemeyer, 2012). For instance, van Dam et al. (2012) found that when participants listened to words denoting objects with both action and color features (e.g., *tennis ball*), the functional connectivity between auditory-processing areas and sensory and motor areas was modulated by task demands (i.e., focusing on visual features or motor features). This finding is consistent with neuropsychological studies that have shown that a dissociation may exist between action and

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object knowledge (Garcea, Dombovy, & Mahon, 2013; Negri, Lunardelli, Reverberi, Gigli, & Rumiati, 2007), and against the strong version of embodiment, which suggests an automatic and necessary involvement of the motor system in processing the semantics of manipulable objects. Theoretically, motor activity could reflect mental imagery induced by meaning access (Tomasino, Werner, Weiss, & Fink, 2007; but see Willems, Toni, Hagoort, & Casasanto, 2010) or the spread of activation from an abstract conceptual representation to the motor system (e.g., Mahon & Caramazza, 2008). Recent studies have also indicated that human action understanding is not based on higher-level motor processing (i.e., the mirror neuron system; Hickok, 2009; Toni, de Lange, Noordzij, & Hagoort, 2008). Overall, whether the motor system contributes to the semantic processing of action language is still far from clear. Furthermore, even though the motor system may make a contribution, the relevant mechanism is still unknown.

One way to clarify whether the sensory–motor system contributes to semantic processing would be to examine how sensory–motor contexts modulate semantic processing. If the sensory–motor system plays a role in semantic processing, then modifying activity in the sensory–motor system would cause changes in semantic processing at behavioral and neural levels. The present article aims to review the behavioral and neuroimaging evidence on the impact of motor contexts on the semantic processing of action verbs or sentences, of object words related to actions, and of sentences describing actions at an abstract level (see Table 1). Here, motor contexts include comprehenders' short-term motor experience (e.g., motor task performance prior to language comprehension, such as motor preparation, motor execution, and motor imagery), midterm motor experience (e.g., motor training before language comprehension tasks), and long-term motor experience (e.g., motor expertise gained before language comprehension performance in experiments). Terms such as "motor preparation," "motor execution," "motor imagery," "motor expertise," "motor training," "motor learning," and "semantic processing" were used to select articles for the review. The three groups of studies chosen relate to each other; that is, they all try to clarify the role of the motor system in the semantic processing of action language stimuli. Nevertheless, they focus on different issues, and thus are reviewed separately.

The present review focuses on the motor contexts formed before semantic processing of language stimuli, such as motor behaviors initiated prior to language comprehension task performance, motor training experience gained prior to performing a comprehension task, and motor expertise acquired by comprehenders before they read or listen to language stimuli in an experiment. In this way, it is possible to see how modifying the motor system affects the semantic processing of action language stimuli (Glenberg, Sato, & Cattaneo, 2008). The present review does not include studies about how language comprehension influences subsequent motor processing. The review also does not discuss the processing of co-speech gestures, since co-speech gestures are usually initiated during language production, and the relation between language comprehension and co-speech gesture comprehension is complicated (e.g., Andric & Small, 2012). For instance, understanding gestures strongly relies on semantic processing of language stimuli. However, this topic is important for investigation of the relation between language and action, and for reviews of the literature about gesture processing, I refer the reader to a number of excellent studies (e.g., Andric & Small, 2012; Gentilucci & Corballis, 2006; Goldin-Meadow, 2001, 2010; Goldin-Meadow & Alibali, 2013; Goldin-Meadow & Beilock, 2010; Willems & Hagoort, 2007).

Exploring how motor contexts influence the semantic processing of action-related language also can help reveal the cognitive and neural mechanisms of language processing in real-life situations. First, in daily life, people often comprehend language while performing some motor behaviors, such as listening to news while driving, or comprehending other people's speech while writing or typing. These motor behaviors might influence meaning extraction from word forms, and such influences have been ignored in the previous laboratory research. Second, each individual has unique experiences in motor observation and execution, and these individual differences might influence the semantic processing of language stimuli. Previous studies have investigated influences of individual differences on language processing, but the main focus is on individual differences in language-related capability and other cognitive capabilities. How individual differences in sensory and motor experiences influence language processing has not been examined until very recently. Third, people often learn to perform new actions in daily life, and the acquisition of new motor experiences could modulate their semantic processing of action concepts at behavioral and neural levels. Overall, investigating the impacts of motor behaviors, motor expertise, and motor training on the semantic processing of action language may help to clarify how language comprehension occurs in the ecological environment.

Influence of motor behaviors on the semantic processing of action-related language

If the sensory–motor system contributes to the semantic processing of action concepts, then changing the activation of the motor system via performing motor behaviors should influence the extraction of action meaning (Rüschemeyer, Lindemann, van Rooij, van Dam, & Bekkering, 2010). Several studies have tested this hypothesis at behavioral and neural levels. The motor behaviors examined in these studies

Table 1 Studies included in the present review

Studies	Behavior/training/ expertise	Language stimuli	Language tasks	Methods
Influence of motor behaviors on action language comprehension				
van Dam et al. (2010)	Motor preparation	Object words related to actions toward to or away from the body	Go/no-go lexical decision task	Behavioral method
van Elk et al. (2008)	Motor preparation	Body-part words related to motor preparation	Semantic judgment	ERP
Rüschemeyer et al. (2010)	Motor execution	Words about manipulable and unmanipulable objects	Lexical decision	Behavioral method
van Dam et al. (2013)	Motor execution	Object words related to different manual actions	Word recognition	Behavioral method
Papeo et al. (2012)	Motor imagery	Verbs about hand actions or mental states	Passive reading	fMRI
Influence of motor training on action language comprehension				
Glenberg et al. (2008)	Motor training of manual actions	Sentences about concrete and abstract transfer actions	Semantic judgment	Behavioral method
Locatell et al. (2012)	Motor training of manual actions	Sentence–picture pairs	Semantic judgment	Behavioral method
Influence of motor expertise on action language comprehension				
Beilock et al. (2008)	Motor expertise in playing ice-hokey	Sentences about hockey actions	Passive listening + post semantic test	fMRI
Lyons et al. (2010)	Motor expertise in playing hokey	Sentences about hockey actions, hokey nonactions, everyday actions, and everyday nonactions	Passive listening + post semantic test	fMRI
Tomasino et al. (2012)	Motor expertise in playing volleyball	Positive or negative sentences about possible or impossible volleyball-specific actions	Possibility judgment	Behavioral method
Tomasino et al. (2013)	Motor expertise in playing volleyball	Positive or negative sentences about possible or impossible volleyball-specific actions	Possibility judgment	fMRI

have included motor execution, motor preparation, and motor imagery. During an experiment, participants perform a motor task initiated before a language comprehension task. Using behavioral and neuroimaging techniques, researchers have investigated how these motor behaviors change the performance, the time course, and the brain activation of action language comprehension.

Van Dam, Rüschemeyer, Lindemann, and Bekkering (2010) investigated the influence of motor preparation on lexical–semantic processing. In this study, participants performed a go/no-go lexical decision task. In each experimental trial, they saw a pair of stimuli in which the first item was a word and the second could be a real word or a nonword. If the second word was a real word, it could describe an object related to an action toward the body (e.g., *telephone*) or an object related to an action away from the body (e.g., *hammer*). The first word could provide a semantic context emphasizing a dominant feature (e.g., *conversation–telephone*) or a non-dominant action feature (e.g., *adapter–telephone*) of the second word. The participants responded to the real word by pressing a button close to or away from their bodies. The results indicated a context-dependent action–sentence compatibility effect (e.g., Glenberg & Kaschak, 2002): Motor preparation facilitated the lexical decision when the action implied by the target word and the prepared hand action had the same direction (e.g., both were toward or away from the body). Furthermore, the facilitation effect was reliable only when the first word in each trial supported the dominant action feature of the target word. The authors claimed that motor preparation can facilitate lexical–semantic processing and that the facilitation effect is influenced by the congruency between the action features of motor preparation and the action features implied by the language stimuli.

Van Elk, van Schie, and Bekkering (2008) investigated the influence of motor preparation on the time course of action word comprehension. In each trial, participants saw an object picture (e.g., cup) presented on the screen and prepared to perform a meaningful action involving the object (e.g., bringing the cup to their mouth) or a meaningless action involving the object (e.g., bringing the cup to their eye). Subsequently, a word was presented on the screen, and participants decided whether the word described a body part or an animal. The presented body-part word could be either congruent (e.g., *mouth*) or incongruent (e.g., *ear*) with the goal of the prepared action. The results showed that when the action goals were meaningful, consistency between the action goals and the presented words elicited a smaller N400 than during the inconsistent condition. No such facilitation effect was found when the action goals were meaningless. The authors suggested that motor preparation can facilitate the semantic integration of action concepts when the action goals of the motor preparation and the action features in the language stimuli involve a common part of the neural motor system. It is interesting to see that motor preparation mainly reduced the difficulty of semantic processing (i.e., reducing the event-related potential [ERP] amplitude), but did not enhance the semantic processing speed (e.g., reducing the ERP latency).

Rüschemeyer, Lindemann, van Rooij, van Dam, and Bekkering (2010) showed that motor execution could influence language comprehension. Participants performed either an intentional action (e.g., using the right index finger to follow the edge of a raised disk fixed to the table) or a passive action (e.g., fixing the right index finger to a motorized rotating disk) while doing a lexical-decision task on words about manipulable objects (e.g., *cup*) or unmanipulable objects (e.g., *bookend*). The results showed that performing actions could facilitate lexical decisions for words denoting manipulable objects, but that such an effect was only observed when the participants performed the intentional actions. When the participants performed the passive actions, the facilitation effect was gone. The authors claimed that the execution of motor actions has a selective effect on the semantic processing of words. This finding is important, because the intentional and the passive actions had no obvious relevance to the words in the lexical-decision task. It is possible that the facilitation effect came from the intentional action goals—that is, the goal to manipulate fingers to perform the action. This action goal might be congruent with the action goals implied in the words about manipulable objects, and thus, performing the intentional actions could have facilitated the lexical–semantic processing of these words. If this is true, it implies that action-related semantic features can be represented in the motor system at an abstract level.

Van Dam, Rüschemeyer, Bekkering, and Lindemann (2013) further found that motor execution influences the formation and consolidation of persisting memory representations of a word's referent. In the study, participants learned words about objects associated with pressing actions (e.g., *piano*) or words about objects associated with twisting actions (e.g., *key*). After that, participants were asked to perform an intervening task requiring pressing or twisting responses. A subsequent word recognition task showed that participants could recognize the learned words better when the actions associated with the object words and the actions performed in the intervening task were consistent than when they were inconsistent. The authors suggested that a reactivation of motor codes can help to stabilize the memory traces of words after initial acquisition.

Besides motor preparation and execution, researchers have also studied how motor imagery could influence the semantic processing of action concepts. Papeo, Rumiati, Cecchetto, and Tomasino (2012) investigated the brain activation of comprehending hand action verbs and mental verbs after mental rotation based on a motor strategy (motor imagery condition) or a visuospatial strategy (visual imagery condition). In the motor imagery condition, participants decided whether each photograph described a left- or a right-hand action by imagining rotating their hands until the hands reached the positions of the hand stimuli in the photographs. In the visuospatial imagery condition, participants mentally visualized the object rotating and aligning with the midline of the screen and decided whether red markers on either arm of 3-D objects were to the left or the right of the screen midline. After that, participants passively read verbs about hand actions (e.g., *to grasp*) or mental states (e.g., *to love*). The results showed that verb reading following motor imagery elicited stronger activation in the left primary motor cortex, bilateral premotor cortex, and the right sensorimotor cortex, as compared with verb reading following visual imagery. Moreover, the effects were similar for the action verbs and the mental verbs. A region-of-interest (ROI) analysis showed that in the right postcentral gyrus, the action verbs elicited reduced activity as compared to the mental verbs after motor imagery. According to the authors, the enhanced motor activity in both action and mental verbs indicated that after motor imagery, participants might implicitly apply the strategy of relating each verb's meaning to one's own bodily action, even though the verb meaning was irrelevant to the action. The authors suggested that language-related motor activity was not entirely determined by the semantic features of language stimuli, and that a top-down factor from the motor imagery strategy could influence the semantic processing of the action-related language.

Together, the evidence above shows that motor behaviors initiated before language tasks can influence the performance and the brain activity of language comprehension. The semantic processing of action language and motor behaviors might recruit common motor programs conducted by the motor system. Most of the studies indicated a facilitation effect: At a behavioral level, the motor behaviors elicited a faster comprehension speed and a higher accuracy than did a non-motor-behavior condition (Rüschemeyer et al., 2010; van Dam et al., 2013; van Dam et al., 2010); at a neural level, motor behaviors change the brain activity during action language comprehension (Papeo et al., 2012; van Elk et al., 2008). However, the facilitation effect reflected by the brain activity results is still unclear. Papeo et al. found that, as compared with the visual imagery condition, the motor imagery condition elicited stronger premotor activation for both action and mental verbs. But the ROI results showed that in the right postcentral gyrus, the action verbs elicited weaker activity than did the mental verbs. It seems that motor imagery could enhance the involvement of premotor cortex while reducing the involvement of somatosensory cortex during action language comprehension.

Previous studies have shown that repetition priming can cause either suppression or enhancement of neural activity in the cerebral cortex, and various factors—such as stimulus features, attention, expectation, and explicit memory—can determine the effects (Segaert, Weber, de Lange, Petersson, & Hagoort, 2013). These factors might also have influenced the findings from studies using cross-domain priming paradigms to investigate how motor behaviors influence action language comprehension. In addition, differences between motor preparation/execution and motor imagery might cause different influences on action language comprehension.

Influence of motor training on the semantic processing of action-related language

If the sensory–motor system plays a role in language comprehension, then modifying the motor system in terms of use-induced motor plasticity might change the semantic processing of a trained action. Several studies have tested this hypothesis using motor-training paradigms.

Glenberg et al. (2008) investigated whether the training of manual actions could influence the semantic processing of concrete and abstract action concepts. Participants moved beans with their right hands toward or away from their bodies 600 times, and then performed a semantic judgment task on sentences describing the transfer of concrete objects (e.g., *Mark deals you the cards*) or abstract quantities (e.g., *Anna delegates the responsibilities to you*) toward or away from their bodies. Reaction time results indicated an interaction between the direction of the bean movement and the direction of the described transfer in both types of sentences: When the two directions were consistent, the semantic judgment became slower. The authors concluded that moving beans with the right hand 600 times could induce short-term plastic changes in the cortical representation of the left inferior frontal and parietal regions that play roles in action language comprehension. Thus, motor training can modulate subsequent language comprehension performance.

Locatelli, Gatti, and Tettamanti (2012) investigated whether motor training could improve the conceptual processing of trained actions. They trained participants to learn complex manual actions and measured their behavioral performance on a semantic judgment task before and after the motor training. The sentence–picture pairs used in the semantic task were either semantically related or unrelated to the trained manual actions. The results of the semantic task showed that for both the related and unrelated sentence–picture pairs, the reaction times significantly decreased after the motor training, indicating more efficient comprehension performance. Furthermore, when the increased usage of target lexicon items during training was controlled, the reaction times for the related sentence–picture pairs decreased more than did those for the unrelated sentence–picture pairs. The authors suggested that motor training can improve the semantic processing of trained actions.

The studies above provide important evidence about experience-dependent processing of motor concepts, and they imply that the motor system could play a role in action language comprehension. Glenberg et al. (2008) interpreted the way that motor training influences the comprehension of action concepts. According to their view, motor training can induce short-term plastic changes in the cortical representation of actions in regions related to action execution. For instance, moving 600 beans with the right hand could reorganize the cortical representation of actions in the left inferior frontal and parietal regions important for manual action planning and execution. These regions are also involved in the semantic processing of action concepts at concrete and abstract levels, and thus the cortical reorganization in these regions changes the comprehension performance. In a word, use-induced motor plasticity modulates action language comprehension. Another possibility is that the influence of motor training on subsequent semantic processing comes from memory. The language comprehension task after motor training could be like a memory task requiring recognition of the trained actions. For instance, in Locatelli et al. (2012), participants performed a sentence–picture judgment task before and after motor training. The short sentences contained verbs relating to the trained actions, and thus when participants performed the semantic task after the motor training, they might recall the learned actions or the training situations. It is possible that the sentence stimuli induced the retrieval of episodic memory, which could facilitate the semantic judgment. If this is the case, then the observed facilitation effect from training (e.g., decreased reaction times in the semantic judgment task) might indicate that the motor training actually improved a post semantic judgment, rather than the motor simulation in an early lexical–semantic stage. However, this view cannot explain the results of Glenberg et al. (2008). That study showed that motor training also influenced the comprehension of abstract transfer actions. In that study, the abstract sentence meaning and the training situations were not directly related, and thus participants could not use episodic memory about the motor training to help them understand the sentences. Nevertheless, it is hard to make a clear conclusion on the basis of behavioral results, and further investigation using techniques with high temporal resolution might help to clarify how motor training influences motor simulation during the semantic processing of action concepts.

Influence of motor expertise on the semantic processing of action-related language

If the sensory–motor system contributes to the semantic processing of language stimuli, then individual differences in motor experience will cause differences in brain responses and behavioral performance in the semantic processing of action language. One possibility is that motor expertise in a certain domain could facilitate the semantic processing of language stimuli related to the specific domain. So far, several studies have tested this hypothesis.

Beilock, Lyons, Mattarella-Micke, Nusbaum, and Small (2008) investigated how motor expertise modulated brain activity during action sentence comprehension. Ice-hockey players and fans with strong experiences in playing and observing hockey games, as well as novices without such experiences, passively listened to sentences about hockey actions (e.g., *The hockey player finished the shot*) during scanning. After that, they performed a sentence–picture matching task outside of the scanner. The behavioral results showed that an action-match effect for the hockey sentences was only found for the ice-hockey players and fans. The brain results showed that processing hockey action sentences activated the left dorsal premotor cortex and the right dorsal primary sensory–motor cortex. A mediation analysis showed that hockey experience facilitated hockey sentence comprehension by increasing the activity in the left dorsal premotor cortex and decreasing the activity in bilateral sensory–motor cortex. An ROI analysis indicated that the ice-hockey players showed a positive correlation between activity in the left dorsal premotor cortex and their behavioral performance, whereas the fans showed positive correlations in bilateral dorsal premotor cortex. The novices did not indicate such effects; instead, they showed negative correlation effects in bilateral primary sensory–motor cortex. The authors suggested that motor experience could facilitate action language comprehension by enhancing the involvement of brain regions in action planning and implementation. Additionally, the experiences of performing and observing specific actions could facilitate comprehension differently.

Lyons et al. (2010) further found that the facilitation effect of motor expertise on action sentence comprehension was reliable only when the language described the specific actions. In their study, hockey players and novices comprehended sentences about hockey actions, hockey nonactions (e.g., *The hockey player enjoyed victory*), everyday actions (e.g., *The individual brushed this hair*), and everyday nonactions (e.g., *The individual earned the acclaim*). As compared with the novices, the hockey players showed stronger activation in the pars orbitalis of the left inferior frontal gyrus (IFG), the pars triangularis of the left IFG, and the left caudate for hockey sentences. The hockey players also showed stronger activity in the left dorsal premotor cortex and the anterior pars triangularis of the left IFG for hockey action sentences, and stronger activation in the right caudate anterior pars triangularis of the left IFG for hockey nonaction sentences. The authors suggested that personal experience can modulate the semantic processing of language stimuli relating to specific personal experiences.

Tomasino, Guatto, Rumiati, and Fabbro (2012) explored how the influence of motor expertise on action language comprehension is modulated by other factors. In their study, volleyball athletes, fans, and novices performed a possibility judgment on sentences about possible (e.g., *Cut shot!*) or impossible (e.g., *Jump roll!*) volleyball-specific actions. Additionally, the sentential context could be either negative (e.g., *Don't shank!*) or positive (e.g., *Jump serve!*). Previous studies had shown that a negative context can modulate brain activity in action language comprehension (Tettamanti et al., 2008; Tomasino, Weiss, & Fink, 2010). The new results showed that the impact of motor expertise was influenced by both the language contexts and motor feasibility. The volleyball athletes and fans took longer to process sentences about possible actions in the negative context than in the positive context, suggesting a difficulty in inhibiting motor simulation during sentence comprehension. No such effect was found in the action-impossible sentences. For the novices, the language context effects were similar on the reaction times for the possible and impossible action sentences. Moreover, a graded effect pattern in the comprehension performance was found in the three groups: The athletes showed higher accuracies and shorter reaction times than did the fans, and they were both more accurate than the novices. The authors claimed that on the one hand, motor expertise might influence action language comprehension by increasing the efficiency of conducting motor simulation during comprehension; on the other hand, the influence of motor expertise could be modulated by contextual factors and not totally stimulus-dependent.

Tomasino, Maieron, Guatto, Fabbro, and Rumiati (2013) used the same paradigm to examine whether activity in the motor system and functional connectivity between the cognitive and motor systems are influenced by motor expertise. Their results showed that, as compared with novices, experts showed decreased activity in the left primary motor cortex hand area (M1) and left premotor cortex when reading sentences about impossible actions in positive contexts. In addition, experts also showed increases of connectivity between motor areas (i.e., M1 and premotor) and visual areas (i.e., calcarine gyrus and fusiform gyrus) when possible actions were presented as positive commands. The authors suggested that motor activation with respect to action language stimuli is not automatic, and that the neural activity triggered by motor simulation is modulated by motor expertise, action feasibility, and context.

Together, the evidence above shows that motor expertise can modulate action language comprehension. One interpretation of the influence is that experience in forming and retrieving complex action plans can enrich semantic representation in the motor system (Lyons et al., 2010). When the semantic representation becomes deeper or more specific, the motor activation becomes stronger. This might imply an increased contribution of the motor system to action language comprehension. Nevertheless, motor expertise does not always influence semantic processing. When comprehension requires the inhibition of motor simulation, such as in negative contexts, high efficiency in conducting motor simulation could cause inhibitory influences.

One unsolved issue is whether motor expertise influences motor processing and semantic processing in the same way. Both Beilock et al. (2008) and Lyons et al. (2010) showed that motor expertise impacts action sentence comprehension by increasing activation in the regions involved in action planning and execution. This is different from findings about how motor expertise influences motor planning and imagery. Milton, Solodkin, Hlustík, and Small (2007) indicated that, as compared with novices, golf experts showed a more focused brain network during preshot routine preparation. The network included the superior parietal lobule (SPL), the dorsal lateral premotor area, and the occipital area. The novices, in contrast, showed a much wider network, including the posterior cingulate, the basal ganglia, and the amygdala–forebrain complex, all regions that had not been found in the experts. The authors suggested that during motor planning, experts can develop a focused and efficient organization of the task-related brain network, whereas novices might not be able to inhibit irrelevant information effectively. These results imply that the motor system can contribute to motor processing and semantic processing differently.

Discussion

The role of the sensory–motor system in language comprehension is still controversial. Although numerous studies have reported motor activation in action language comprehension (for reviews, see Aziz-Zadeh & Damasio, 2008; Pulvermüller & Fadiga, 2010) and have shown that motor activation occurs in early time windows during lexical–semantic processing (for a review, see Hauk et al., 2008), it is still unclear whether the motor system makes a functional contribution to action language comprehension. One possible way to address the issue would be to investigate how motor contexts modulate the semantic processing of action-related language. The present review suggests that comprehenders' motor behaviors, motor expertise, and motor-training experiences can modulate their semantic processing at behavioral and neural levels. These findings imply a role of the sensory–motor system in language comprehension, and suggest that language comprehension can be shaped by interactions between the body and the environment.

Pulvermüller (2005) claimed that cortical functions are served by distributed functional systems formed during learning, and that neuronal connections exist both within and between the systems. According to this view, word meaning is represented in a distributed functional network allowing fast and automatic activations across cortical regions. The distributed network was formed during word acquisition, during which neurons related to word-form processing and neurons related to the referred sensory–motor processing were frequently coactivated, thus strengthening their mutual connections (Pulvermüller, 2001, 2005). This network might be controlled by a central semantic component that can manage the dynamic functional links between different cortical regions. The central semantic component is supposed to be in the IFG, which is important for the semantic binding of different information (Rizzolatti & Craighero, 2004).

On the basis of our literature review of the influences of motor behaviors, motor expertise, and motor training on the semantic processing of action-related language, three questions about how motor contexts influence the network for word comprehension need to be answered (for the sake of simplicity, here I only discuss the contextual influence on action verb comprehension): (1) whether motor contexts only modulate activity in motor regions, (2) whether the contextual influences are specific to the semantic features of language stimuli, and (3) what factors can determine facilitatory or inhibitory contextual influences on the semantic processing of action-related language.

Do motor contexts only modulate activity in motor regions? Previous studies have indicated that motor contexts can influence the brain network for action language comprehension by directly modulating the activity of the motor system. By increasing or decreasing the activity of the involved motor regions, motor contexts can change the speed and the strength of the activations from word form to the referred motor process. For instance, when a motor behavior is initiated prior to action verb comprehension, the brain regions involved in this specific motor program are activated. Because these motor regions are functionally connected with regions of word-form processing to represent action verb meaning, preactivation in the motor regions can facilitate the activation of the whole network. At a behavioral level, motor behavior can facilitate semantic processing by increasing accuracy and decreasing reaction times during language comprehension tasks (e.g., Rüschemeyer et al., 2010; van Dam et al., 2010). At a neural level, motor behavior can influence the time course of network activation (e.g., van Elk et al., 2008) and the activity pattern of the motor regions (e.g., Papeo et al., 2012). Similarly, motor expertise influences language comprehension by directly modulating activity in motor regions (e.g., Beilock et al., 2008; Lyons et al., 2010). As we mentioned, motor expertise is gained through intensive practice with forming and retrieving complex action plans. Long-term practice can enrich the specific motor representation, and thus make the motor activation stronger (Lyons et al., 2010). This might facilitate the activation of the whole network for action verb comprehension. Motor training is supposed to change the cortical organization of the motor regions involved in the trained actions (Glenberg et al., 2008). These regions are also involved in the semantic processing of language about the specific actions, and thus the cortical reorganization can influence the brain activity for action language comprehension.

However, some studies have indicated that motor contexts can also modulate activity in brain regions outside premotor and motor cortex. For instance, Lyons et al. (2010) reported that motor expertise could change activity in the left IFG during action language comprehension. As compared with novices, hockey players showed stronger activations in the left IFG (BA 47) for general hockey sentences, and stronger activity in a more dorsal area in the left IFG for hockey action sentences, as compared with the novices. The authors suggested that motor expertise could change the depth of semantic processing in the left IFG. This might imply that influences of motor contexts can also modulate activity in the central semantic component (Pulvermüller, 2005). By changing the activity in IFG, motor contexts can modulate connections between the regions involved in word-form processing and motor processing.

Tomasino and Rumiati (2013) discussed the question of whether motor representation during action verb and sentence comprehension is bottom-up (i.e., specific to action-related language stimuli) or top-down (i.e., specific to the motor strategies adopted during task performance). Similarly, the modulation of IFG activity might suggest that motor contexts could influence semantic processing in a top-down manner. Some researchers have suggested that motor training exerts top-down contextual influences on language processing. For instance, Sato et al. (2011) suggested that motor training could influence top-down decisions or categorization processes during speech perception. In that study, participants performed lip or tongue movements for 10 min to induce changes in the corticomotor control of the orofacial musculature. After the motor training, participants underwent a forced two-choice auditory syllable decision task between /pa/ and /da/ syllables. The results showed that the motor training influenced the beta score for the signal detection significantly, but not the *d*-prime. The beta score indexes possible response bias, whereas *d*-prime indicates the ability to distinguish between the two syllables. Thus, the results suggested that the motor system contributes to high-level processes in speech categorization. It might be true that the motor system can also contribute to high-level processes in language comprehension, and thus that motor contexts could modulate activity not only in motor regions, but also in the regions involved in goal-directed control functions (O'Reilly, 2010). This issue needs to be clarified in further investigations.

Are the influences of motor contexts selective? The second question that needs to be answered is whether the impacts of motor contexts on language comprehension are selective—that is, whether the motor contexts need to share some common features with the language concepts. If motor contexts directly modulate activity in the motor system, then the contextual influences could be selective. The current evidence shows that when motor contexts and language stimuli have common features, facilitation effects may be found. For instance, behavioral and ERP findings have shown that motor preparation and execution can facilitate language comprehension only when the action information in these behaviors is congruent with the action information implied by the language stimuli (van Dam et al., 2013; van Dam et al., 2010; van Elk et al., 2008), even when the congruency is at an abstract level (Rüschemeyer et al., 2010). This is consistent with the idea that the specificity of semantic features is reflected in the motor system (van Dam et al., 2010). Similarly, Beilock et al. (2008) and Lyons et al. (2010) indicated that hockey expertise influences the comprehension of sentences about hockey, but not the semantic processing of sentences about daily actions. This also indicates the specificity of contextual influences.

On the other hand, if motor contexts influence semantic processing in a top-down manner, then the contextual influences might not be selective. For instance, Papeo et al. (2012) showed that motor imagery before the comprehension task changed the brain activity for both the action verbs and mental verbs. The authors suggested that the motor context in which the words are encountered prevails over the intrinsic semantic features of the language stimuli. Glenberg et al. (2008) showed that motor training moving beans changed the comprehension of sentences about both concrete and abstract transfers. Whether congruency between motor contexts and language stimuli is necessary for the emergence of contextual influences needs further investigation.

What factors determine the facilitatory and inhibitory influences of motor contexts? The third question that needs to be answered is what factors might determine the facilitatory and inhibitory influences of motor contexts on the semantic processing of action concepts. Previous studies have shown that this depends on the type of motor context.

For a motor task context, the factor is time. According to Boulenger et al. (2006) and Rüschemeyer et al. (2010), the temporal relation between action execution and semantic processing is a key factor in determining the inhibitory or facilitatory influences of motor behaviors on action language comprehension. If the motor behaviors are initiated at the same time as semantic processing, they could elicit an inhibitory effect. If the motor behaviors are initiated before semantic processing, they could cause a facilitatory effect. This view is supported by Rüschemeyer et al. (2010), van Dam et al. (2013), van Dam et al. (2010), and van Elk et al. (2008); in all of these studies, motor behaviors were initiated before the language tasks, and these behaviors facilitated language comprehension. Whether motor behaviors initiated at the same time as or later than the language comprehension performance would have inhibitory influences needs further investigation.

For a motor expertise context, whether semantic processing requires motor simulation could be a key factor that determines facilitatory or inhibitory influences. If motor expertise can help the comprehender conduct motor simulation more efficiently, then it would facilitate comprehension when the semantic processing of concepts requires conducting motor simulation. This idea has been supported by Beilock et al. (2008) and Lyons et al. (2010). However, when language comprehension requires the inhibition of motor simulation, such as in negative contexts, high efficiency in conducting motor simulation could hinder comprehension (Tomasino et al., 2012). This might also be true in the comprehension of figurative actions, such as metaphoric actions (e.g., *grasp the idea*) or idiomatic actions (e.g., *kick the bucket*). In such figurative expressions, the motor component of the verb is not required, or actually should be inhibited, and a more abstract meaning needs to be built. Thus, high efficiency of motor simulation might cause difficulty in comprehension, since it directly contributes to the motor component of the verb. This means that novices might have more efficient semantic processing of figurative actions than athletes and fans do. This view needs to be tested in future studies.

For a motor-training context, the factors determining the facilitatory or inhibitory influence might relate to training intensity. Glenberg et al. (2008) discussed several factors that could cause the inhibition effect. The first factor is fatigue. Repeating actions many times may cause peripheral fatigue in the effector (e.g., moving 600 beans in one direction induced muscle fatigue in the hand). The fatigue reflects that the central nervous system has failed to drive the motoneurons adequately (Gandevia, 2001). This failure could cause a loss of specificity to one action and decreased efficiency of comprehension of the relevant action language. Another factor might be the automaticity of the trained actions. When action performance becomes automatic, activity in the action-specific controllers is down-regulated, and this can cause a loss of specificity to one action (Wu, Kansaku, & Hallett, 2004). The third factor is the tuning of the action controllers to the motor task. Intensive motor training could increase the tuning while causing a concomitant loss of responsiveness to sentence processing (Glenberg et al., 2008). In a word, the intensity of motor training might determine how action language comprehension is modulated.

Conclusion The present article has reviewed findings related to the influences of comprehenders' motor behaviors, motor expertise, and motor-training experiences on their action language comprehension. The evidence shows that motor contexts can modulate comprehension at behavioral and neural levels. Further investigations will be required to clarify whether the motor contexts could influence action language comprehension in a top-down manner, whether the contextual influences are specific to the semantic features of language stimuli, and what factors can determine the facilitatory or inhibitory contextual influences on language comprehension.

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