



Research report

Moving the hands and feet specifically impairs working memory for arm- and leg-related action words

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ABSTRACT

Language and action systems of the human brain are functionally interwoven. Speaking about actions and understanding action-related speech sparks the motor system of the human brain and, conversely, motor system activation has an influence on the comprehension of action words and sentences. Although previous research has shown that motor systems *become* active when we understand language, a major question still remains whether these motor system activations are *necessary* for processing action words. We here report that rhythmic movements of either the hands or the feet lead to a differential *impairment* of working memory for concordant arm- and leg-related action words, with hand/arm movements predominantly impairing working memory for words used to speak about arm actions and foot/leg movements primarily impairing leg-related word memory. The resulting cross-over double dissociation demonstrates that body part specific and meaning-related processing resources in specific cortical motor systems are shared between overt movements and working memory for action-related words, thus documenting a genuine motor locus of semantic meaning.

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1. Introduction

Embodied semantic theories have long claimed that language understanding and memory depend on links between linguistic brain systems and sensorimotor domains (Barsalou, 1999; Lakoff, 1987; Pulvermüller, 1999; Pulvermüller and Fadiga, 2010; Rizzolatti and Craighero, 2004). Neuroimaging and behavioural evidence for motor cortex activation in the comprehension of language provides partial support for such models. The meaning of language materials including words, phrases, concrete, and even abstract figurative sentences, was found to be manifest in motor systems activation, as

documented by functional magnetic resonance imaging (fMRI), electroencephalography (EEG), magnetoencephalography (MEG), transcranial magnetic stimulation (TMS)-elicited motor activity and action execution performance (Boulenger et al., 2006, 2009; Buccino et al., 2005; Fadiga et al., 2002; Glenberg et al., 2008a; Hauk et al., 2004; Shtyrov et al., 2004; Pulvermüller et al., 2005b; Fischer and Zwaan, 2008; D'Ausilio et al., 2009; Dalla Volta et al., 2009). For example, the passive reading of action words with specific body part relationship led to semantic-somatotopic activity, with face-related action words, such as “talk”, strongly activating inferior-frontocentral areas close to the motor representation of the face and

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articulators, arm-related action words, such as “grasp”, sparking areas also activated during finger movements, and leg words, such as “walk”, igniting the cortical leg region also active during foot movements (e.g., Hauk et al., 2004; Kemmerer and Gonzalez-Castillo, 2010). The reverse link, from motor to language systems, was shown to be effective in TMS studies in which magnetic pulses were injected in different parts of the motor system, thereby modulating the processing of arm and leg words differentially (Pulvermüller et al., 2005a), in investigations of the effects of action execution on the processing of language (Glenberg and Kaschak, 2002; Glenberg et al., 2008a) and by patient work (Bak et al., 2001; Boulenger et al., 2008; Cotelli et al., 2006; Damasio and Tranel, 1993; Kemmerer et al., in press; Neininger and Pulvermüller, 2003). For example, repeatedly moving beans either towards or away from the body later modulated the processing of “towards” or “away” sentences (Glenberg et al., 2008a) and specific impairments of action words, compared with matched nouns, were present in patients with motor neuron disease (Bak et al., 2001). However, apart from general issues regarding the interpretation and generality of the reported data (for detailed discussion, see Section 4.3), these results do not unambiguously document a necessary role of motor system functionality for processing action-related language. The behavioural results in healthy people are manifest specifically in the slowing of one type of sentence processing relative to that of other types of sentences, thus showing that linguistic-semantic processes are still possible, albeit modulated. The clinical studies document profound action verb deficits relative to noun control words in stroke patients with lesioned motor regions and patients with motor neuron disease and Parkinson’s disease, but most of these studies suffer from linguistic caveats, especially the multiple psycholinguistic differences between verbs and nouns (in word frequency, syntactic function, imageability, etc., see Bird et al., 2000), which make it impossible to uniquely attribute noun/verb dissociations to semantic factors. In essence, the available evidence does not prove a necessary role of motor systems for semantic language processing. Following a widely accepted inference scheme in neuropsychology (Shallice, 1988), such necessary role can be demonstrated if functional changes in different subparts of the cortex lead to specific processing impairments at the cognitive level taking the form of a *cross-over double dissociation*. In our case, functional changes in different parts of the motor system would be hypothesised to have a differential and damaging effect on the processing of specific subclasses of action words, such that changing the function of one part of the motor system leads to a relative impairment of word class A, but functional change in a different part of the motor system relatively impairs word class B.

We here target working memory processes and ask whether movements of part of the body impair the memory for concordant action words. It is well known that speaking or repetitive articulation of syllables impairs working memory for speech and language stimuli (Baddeley, 1992, 2003). This finding led cognitive scientists to state that verbal working memory and syllable repetition draw upon the same processing resource, called the phonological or articulatory loop. In a neurobiological theory of working memory (Fuster, 1995), the phonological loop is implemented as a network of left-perisylvian neuronal

circuits linking word production and perception circuits with each other (Pulvermüller, 1999); activity in these regions is seen in verbal memory tasks (D’Esposito, 2007; Fuster, 2009). Indeed, left-lateralised perisylvian circuits develop consequent upon articulation of novel word forms (Pulvermüller et al., in press). Syllable articulation and verbal working memory seem to engage the same left-perisylvian areas, thus explaining articulatory suppression of word-related memory processes. In addition to their left-perisylvian phonological loop component (grey neuron ensembles in Fig. 1a), memory circuits for action words are envisaged to link with semantic networks in other parts of the motor system, located laterally for arm words and dorsally in the case of leg words (Fig. 1a, b for theory and neuroimaging data). In this neurobiological perspective, lexicosemantic circuits include an articulatory–phonological perisylvian component, and extend into arm and leg motor cortex if the represented word is semantically related to actions typically involving these extremities. In this model, complex motor movement control and motor schema-based action-word memory compete for the same neuronal resources – therefore predicting that movements of the arms impair the memory for arm words most strongly, whereas leg movements most severely impair leg-word memory. To test these novel predictions, we investigated the ability of human subjects to memorize matched arm and leg words while performing continuous and demanding rhythmic movements of different parts of the body.

2. Materials and methods

2.1. Participants

Fifteen monolingual, native speakers of English (8 males) aged 18–30 (mean = 20.4, standard deviation – SD = 3.2) took part in the experiment. All reported normal vision and hearing and had no history of neurological or psychiatric illness. All participants were also right-handed with an average laterality quotient (Oldfield, 1971) of 80.5% (SD = 23.6) and reported no immediate left-handed family members (parents or siblings). All gave their informed, written consent prior to their participation and were reimbursed for their time. Ethics permission for the study was obtained from the Cambridge Psychology Research Ethics Committee.

2.2. Material

The lexical stimuli used in the experiment consisted of 72 words, 36 arm-related action verbs (e.g., *clap, braid, grab*) and 36 leg-related action verbs (e.g., *step, kick, hop*). Lexical stimuli were matched for psycholinguistic variables including number of letters, number of phonemes, standardized lexical frequency, lemma frequency, letter bigram frequency and letter trigram frequency. Further matching was done for the variables grammatical ambiguity, valence, arousal, imageability, visual relatedness, body relatedness and general action relatedness as revealed by semantic ratings performed on each word by a set of subjects not involved in the behavioural experiment reported here (Table 1). The two word groups differed significantly on semantic arm- [5.46 (standard

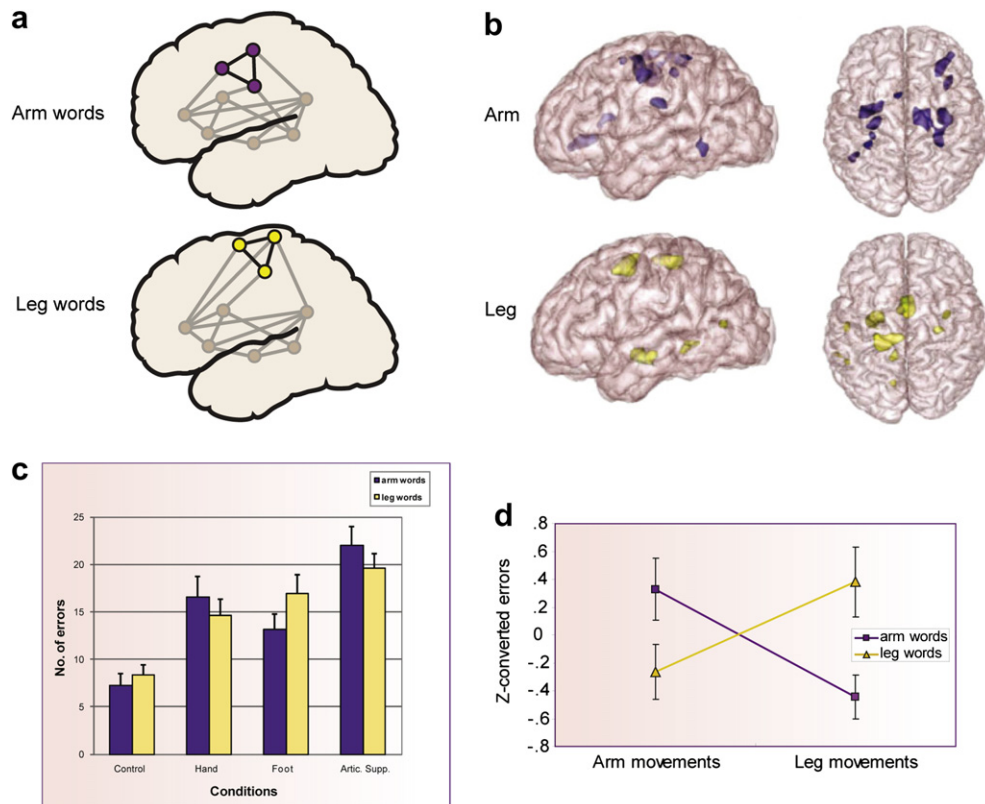


Fig. 1 – Theory and data on interaction between motor and language systems. (a) Cortical circuits for arm- and leg-related words as proposed by the semantic somatotopy model. Links between words and their meaning-related action concepts are realized by connections between articulatory-loop circuits in the perisylvian language cortex (shown in grey) and semantic circuits in the motor system. Semantic circuits of words related to action schemes typically involving the arms (shown in purple) and legs (shown in yellow) are organised by neuronal ensembles in somatotopically organised sections of the motor and premotor cortex. **(b)** Brain activation revealed by functional MRI during a silent word reading task confirms that understanding arm-related action words (such as “grasp” or “peel”; shown in purple) and leg-related action words (such as “step” or “kick”; shown in yellow) indeed activate motor and premotor cortex in a semantic-somatotopic manner. **(c)** Average errors on arm and leg words and s.e.m. in the four conditions (rest/control, hand movement, foot movement and articulation) of the working memory task. **(d)** z-normalised average errors and s.e.m. in the hand and foot motor conditions. Arm movements led to reduced memory performance for arm words in comparison to leg words, while with leg movements, memory performance dropped more sharply for leg words relative to arm words. This result demonstrates a crucial role of motor systems for action-word memory (see [Discussion](#)). Part b is reproduced, with permission, from Pulvermüller et al. *Hum Brain Mapp* 2009. Copyright © 2009 Wiley-Liss, Inc.

error = .14) vs 1.92 (.12)] and leg-relatedness [2.28 (.13) vs 5.58 (.22)], as assessed by further semantic ratings. Two pseudo-randomized stimulus sequences were used in the experiment, counterbalanced across subjects.

2.3. Procedure

There were two specific interference conditions in the experiment in which hand or foot motor movements were required. A control condition, during which no movement had to be performed (rest), was added to provide information about verbal working memory performance without motor interference, and, in addition, an articulatory suppression condition was run. In each of the four conditions (control/rest, hand movement, foot movement, articulation), a fixation point was presented alone in the centre of the screen for 3 sec.

The fixation point was then replaced with 4 words presented serially. The words in each trial were either all arm-related action words or all leg-related action words. Each word was presented for 100 msec. The stimulus onset asynchrony (SOA) of two subsequent stimuli was 500 msec (2 words per second). Stimulus presentation was followed by a 6 sec memory period during which subjects were required to retain the four words in memory in the order in which they were presented. After this delay, a beep prompted subjects to repeat the words they saw on screen. Testing of pilot subjects had confirmed that, without motor movements, the memory task led to occasional errors (errors in ca. 30% of the trials).

Subjects received different instructions in the four conditions. In the control/rest condition, subjects were asked to wait silently while keeping the words in memory during the delay until they heard the beep prompting them to repeat the

Table 1 – Means and standard errors of psycholinguistic properties for arm and leg words.

Psycholinguistic feature	Arm words		Leg words	
	Mean	(SE)	Mean	(SE)
Number of letters	4.47	(.15)	4.61	(.13)
Number of phonemes	3.75	(.13)	3.92	(.15)
Word frequency	218.5	(50.6)	227.6	(48.9)
Lemma frequency	534.4	(90.0)	574.9	(108.7)
Bigram frequency	29885	(2703)	33575	(2913)
Trigram frequency	3211	(423)	3045	(346)
Grammatical ambiguity	1.92	(.05)	1.94	(.04)
Valence	3.66	(.14)	3.99	(.15)
Arousal	3.04	(.14)	3.12	(.18)
Imageability	4.55	(.12)	4.56	(.15)
Visual relatedness	4.38	(.17)	4.13	(.17)
Body relatedness	3.67	(.17)	3.75	(.14)
Action relatedness	5.06	(.15)	5.26	(.17)

words in the order they had been presented on screen. In the articulatory condition, subjects were required to repeat the syllable [bla] continuously and at an even pace (approximately 2 words per second) while keeping the words in memory during the 6 sec delay. Sufficient time was provided for subjects to practice the paced syllable articulation during a practice memory block before starting the experiment. In the other two conditions, in addition to retaining the words in memory, subjects were required to perform a continuous rhythmic motor task (motor tapping of hands or feet) throughout the 6 sec delay. In these motor conditions, subjects were instructed to “tap their hands/feet” using a motor sequence which is known as a drumming exercise called the single paradiddle (RLRRLRL, etc.). As this exercise is difficult, even for musicians not experienced with drumming, subjects were given ample opportunity for practice before the memory experiment was started. Subjects first practiced the pattern on its own and very slowly. Secondly, the motor task was made more challenging by increasing speed, up to the highest beat frequency subjects could maintain without errors. Using a metronome and gradually increasing beat frequency, each subject’s individual “frequency limit” was determined separately for arm and foot paradiddles. Subjects started at 100 beats per minute, gradually increasing the frequency by 10 beats per minute until they could no longer maintain the pace without making errors in the pattern. Each subject’s arm/leg frequency threshold was defined as the highest pace at which error-free performance could be maintained for 20 sec. Once confident, they then performed a practice block in order to practice paradiddles while doing the memory task (using words other than the ones included in the experiment). Subjects did not start the experiment until they were comfortable with the pace and motor tasks, and they and the experimenter were satisfied that they understood the instructions. Average speed for hand and foot tapping of paradiddles was 155 (s.e.m. 5.97) and 152.5 (s.e.m. 5.79) beats per minute, respectively (difference n.s.).

The conditions were run as separate blocks with twenty-four trials in each block, twelve arm-word trials and twelve leg-word trials. Trial presentation was self-paced; subjects initiated each trial by pressing the space bar of a computer

keyboard before them. Stimulus items were presented in a different random order in each trial, with the full set of 72 words being presented twice in all conditions. Arm- and leg-word trials were randomized within each block with the constraint that not more than three trials of the same word category appeared consecutively. The order of the blocks was counterbalanced across subjects using a Latin-square design. Clear written and verbal instructions were given to all subjects prior to each block as well as ample opportunity for practice. Subjects did not begin each block until they and the experimenter were satisfied that they understood the instructions. Subjects were encouraged to take breaks between blocks and indeed within blocks if needed.

2.4. Statistical analysis

Number of errors, including omission, addition, replacement and transposition/shift errors, obtained in the four conditions (hand tapping, foot tapping, control, articulatory) and two word categories (arm vs leg words) were obtained for each participant and condition and submitted to statistical analysis. Note that such evaluation, including transposition/shift errors, is the standard in working memory research (Baddeley, 2003). To test differences in arm- and leg-word memory between the conditions, two-way repeated measures Analyses of Variance (ANOVAs) (Word Type \times Condition) and subsequent Planned Comparison F-tests were conducted on raw results and z-scores calculated for each subject individually and entered into an overall ANOVA. z-transformed values (adjusted to a mean of 0 and an SD of 1) were calculated on a subject-by-subject basis for the critical conditions, arm- and leg-movement interference, to reduce between-subject variability in performance and the possible contribution of occasional outliers. All tests used were two-tailed.

3. Results

In the basic working memory task, series of written words were shown on a screen and subjects successfully repeated these series verbally after a delay. Errors were consistently present but low (averaging 7.8 errors over 24 trials), showing that the task was demanding but achievable. No difference in the general level of performance was found between word types (7.2 and 8.3 errors for arm and leg words, respectively; difference n.s.). ANOVA (4 Conditions \times 2 Word Categories) performed on cumulative numbers of errors revealed a significant main effect of Condition [$F(3, 42) = 23.77$, $MSE = 43.4$, $p < .0001$] and a significant interaction effect between the factors Condition and Word Category [$F(3, 42) = 7.64$, $p < .0004$]. Planned comparison tests revealed no significant word category difference in the control condition [$F(1, 14) = 1.7$, $MSE = 24.13$, Cohen’s $d = .25$, $p = .21$]. However, with rhythmic foot/leg movements, memory performance dropped more sharply for leg than for arm words [16.9 vs 13.1 errors; $F(1, 14) = 7.97$, $MSE = 48.0$, Cohen’s $d = .55$, $p = .014$], whereas a trend towards reduced arm-word memory performance relative to that for leg words was seen with rhythmic hand/arm movements [16.5 vs 14.6 errors; $F(1, 14) = 3.83$, $MSE = 57.4$, Cohen’s $d = .26$, $p = .07$]. A further near significant word

category difference was found in the articulatory suppression condition [$F(1, 14) = 3.63$, $MSE = 47.1$, Cohen's $d = .35$, $p = .08$; Fig. 1c]. However, when this condition was excluded in a 3×2 analysis, effects of condition [$F(2, 28) = 14.94$, $MSE = 42.2$, $p < .0001$] and general interaction [$F(2, 28) = 10.68$, $p < .0004$] remained highly significant.

Most importantly, directly addressing the main hypothesis motivating this study, a 2×2 analysis (Word Type \times Moving Body Part) revealed that when subjects engaged in performing this rhythmic motor pattern with either their hands or feet, errors in memory performance increased and a significant interaction effect was found [$F(1, 14) = 12.67$, $MSE = 20.9$, Cohen's $d = 1.25$, $p = .003$] while no significant effect of condition was found in this case ($F < 1$), documenting a differential influence of movement type on word type performance. Normalised z-transformed data confirmed this significant Word Type \times Moving Body Part Interaction [$F(1, 14) = 25.49$, $MSE = .92$, Cohen's $d = 1.48$, $p < .0002$; Fig. 1d]. For the z-transformed data, in which the contribution of outliers and between-subject variance is reduced, t-tests now also revealed fully significant word category differences in both critical movement interference conditions, for hand/arm movements [more errors for arm words $F(1, 14) = 5.65$, $MSE = .67$, Cohen's $d = .73$, $p < .032$] and foot/leg movements [more errors for leg words, $F(1, 14) = 11.26$, $MSE = .66$, Cohen's $d = 1.0$, $p < .0047$].

Apart from overall errors, the different error types were calculated and averaged separately (see Table 2). Most errors were omissions (47%) and replacements (41%). A smaller fraction of the errors (12%) were transposition or shift errors. When transposition/shift errors were removed from the analysis, the Word Type \times Moving Body Part interaction effect was confirmed for the comparison of arm/leg words in the hand/foot movement conditions [$F(1, 14) = 14.77$, $MSE = 16.64$, Cohen's $d = 1.1$, $p < .002$]. Replacement errors on their own, but not the other two error types evaluated separately, further confirmed this interaction [$F(1, 14) = 4.8$, $MSE = 9.77$, Cohen's $d = .73$, $p = .046$].

4. Discussion

In this study, we report a differential memory deficit for arm- and leg-related action words brought about by complex-sequential movement performance involving different parts of the body, the hands and arms versus the feet and legs. More errors in recollecting arm-related action words than leg-related action words were seen after subjects had to move their hands and arms according to a complex rhythmic

drumming exercise; the reverse effect, more errors on leg- than arm-related words, was seen when subjects moved their feet and legs during the memory interval. Following an inference scheme well-established in neuropsychological research, this pattern of results demonstrates that sensorimotor brain systems exert *inhibitory causal effects* on action-word memory and that these effects are specific to semantic word type and (sub-) area of sensorimotor cortex. Note (i) that pre-existing evidence documents that overlapping sensorimotor areas are active during body movements and the processing of concordant action words (see, for example, Hauk et al., 2004; Kemmerer and Gonzalez-Castillo, 2010) and (ii) that sensorimotor areas are the only loci in cortex that distinguish locally between body part representations (Rizzolatti and Craighero, 2004). Therefore, the observed specific memory degradation for arm-related action words by complex rhythmic arm movements and the corresponding specific memory impairment for leg-related action words during complex leg movements can be attributed to the sensorimotor system, implying a causal inhibitory effect of this system on working memory for specific semantic categories of action-related words.

It may be argued that the massive increase in the number of errors observed with motor movements (to 15.6 in arm and 15.0 in the leg-movement condition, difference n.s.) relative to the baseline task may be related to the engagement of the motor system, but may also, in part, depend on more general processing resources such as the attentional demands of the dual task. A similar point can, of course, be raised with respect to the even more substantial articulatory suppression effect observed. While this is a valid point, our main argument is based on the specifically increased memory impairments seen for action-word subtypes with performance of concordant movements. This differential effect, and the more general degradation, emerged in a task where the executed movements were demanding in the sense that they had to be practiced before and were executed at performance limit. Using a pattern of jazz drumming, subjects had to perform single paradiddles (RLRRLRL, etc.) continuously at the highest constant speed they could afford. Interference was predicted as this unusual motor pattern (musicians were excluded from the experiment) is incompatible with the typical actions related to the action words used in the study (e.g., *grasp*, *walk*). In the articulatory interference condition, syllable repetition was not particularly demanding, but, possibly due to the engagement of both articulatory-motor and acoustic-auditory circuits immanent to the perisylvian articulatory–phonological loop, the well-known strong

Table 2 – Average and SD (in brackets) of each error type in the four experimental conditions: the control/rest condition and the conditions with motor interference, by hand movements, foot movements and articulation.

Type of error	Control		Hand motor		Foot motor		Articulatory		Total
	Arm	Leg	Arm	Leg	Arm	Leg	Arm	Leg	
Omission	2.6 (2.06)	2.8 (3.30)	8.07 (5.59)	6.73 (5.64)	6.46 (4.32)	7.33 (6.31)	12.07 (6.75)	10.1 (5.16)	56.1
Replacement	3.67 (3.75)	4.46 (3.38)	6.07 (4.5)	5.93 (4.92)	5.53 (2.77)	7.7 (4.43)	7.53 (3.50)	7.13 (4.32)	48
Transposition/shift	.93 (1.16)	1.07 (.96)	2.4 (1.72)	1.93 (1.53)	1.13 (1.36)	1.9 (1.87)	2.4 (2.06)	2.4 (2.26)	14.2
Total	7.2 (4.97)	8.3 (4.19)	16.5 (8.39)	14.6 (6.66)	13.1 (6.23)	16.9 (7.56)	22 (7.69)	19.6 (5.91)	118.3

suppression effect on working memory performance could be replicated (Baddeley, 2003).

4.1. *The motor system's role in verbal working memory: just inhibitory or necessary?*

One may ask whether our data allow for a conclusion on the necessity of sensorimotor arm and leg representations for the processing of semantically congruent word types. In the cognitive psychological literature, the crucial observation of articulatory suppression of verbal working memory performance has been used, with good reason, to argue that the two processes, syllable articulation and verbal working memory, share processing resources, namely the mechanism called the phonological or articulatory loop (Baddeley, 1992, 2003). This common mechanism is thus considered necessary for both processes. Using the same inference scheme, our present results support that body movements and working memory for action-related words share processing resources. Within the semantic somatotopy framework (Pulvermüller, 2001, 2005), these common processing resources are the motor mirror systems that include sensorimotor neuronal circuits specific to body parts (Buccino et al., 2001). Such action-perception circuits are included in the neuronal devices underlying action-word processing and are, therefore, the substrate of action-word working memory (Pulvermüller and Fadiga, 2010). Together with circuit parts of the articulatory–phonological loop, which characterise all words, the action-semantic mirror circuits carry working memory processes for action-related words specifically (cf. model in Fig. 1a). Therefore, when demanding and continuous complex-sequential rhythmic arm movements are carried out during the working verbal memory task, movement-related activation in the sensorimotor cortex is co-present with activity of semantic memory networks that are part of the distributed circuits underpinning action-word processing. As the complex motor schemes that are part of the semantic networks of the action words (e.g., grasping, writing) are incompatible with the complex drumming pattern executed, the respective motor circuits may compete with each other, possibly due to local cortical inhibition (for a formal model see Garagnani et al., 2008; Garagnani and Pulvermüller, 2011). The limitation of processing resources underlying the differential interference effects observed would accordingly result from local inhibition between overlapping or adjacent memory and motor circuits within sensorimotor cortex. This explains the word-category-specific degradation of verbal working memory during arm and leg movements. The explanation of the articulatory interference follows the same rationale, but based on closely adjacent or overlapping articulatory–phonological perisylvian circuits. The trend toward a word category difference for arm words in the articulatory condition can also be explained in similar terms. The increased number of errors on arm words compared to leg words may result from ‘overspill’ activation in the face/articulator motor cortex reaching into the adjacent arm motor cortex. Because repeated syllable articulation engages mouth motor representations, activation in the face/articulator motor cortex may have extended into the adjacent arm motor cortex and,

again by way of local cortical inhibition, led to reduced performance on arm-word memory relative to that for leg words.

As the present results show that engaging the motor system can degrade working memory for action words, they also support the position that the sensorimotor system shares processing resources with these verbal working memory processes, which, therefore, in the healthy functional brain, can be considered to be necessary for action-word memory. Note that specific inhibitory causal effects are commonly used to infer necessity – as, for example, in the neuropsychological lesion literature, where double dissociations in behavioural performance originating in different areas are considered the strongest evidence for a differential localisation of functions in these areas (Shallice, 1988). Although not all brain models of cognition share assumptions about a modular organisation of brain and cognition, the inference on the necessity of specific neuronal systems for the cognitive processes affected by a double dissociation is shared by different cognition-and-brain models (Hinton and Shallice, 1991; Plaut and Shallice, 1993; Pulvermüller and Preissl, 1991; Pulvermüller and Fadiga, 2010; D’Ausilio et al., 2009). Following this well-established neuropsychological inference scheme, our present data support the necessity of sensorimotor areas of the upper and lower extremities for arm- and leg-word processing.

Our present results agree with clinical neuropsychological work relating motor system impairments to difficulties in processing action-related language (see Introduction, e.g., Bak et al., 2001, 2006; Boulenger et al., 2008; Cotelli et al., 2006; Damasio and Tranel, 1993; Kemmerer et al., in press; Neiningner and Pulvermüller, 2003; Tranel et al., 2003), although we note that not all patient studies agree that deficits in action word and concept processing follow lesions to motor cortex (see Arevalo et al., in press; Kalenine et al., 2010). A significant number of patient studies showed a link between deficits for action verbs – as compared with control nouns – after lesion of the cortical and subcortical motor system; however, most of these studies are difficult to interpret because of the multiple differences between nouns and verbs, which cannot be attributed to action semantics exclusively (Kemmerer et al., in press; Pulvermüller et al., 2010). In the present study, well controlled word groups were used that were matched for a range of psycholinguistic variables, including length, word frequency, bi- and trigram frequency, imageability, and general strength of action relatedness (Table 1). The sole psycholinguistic feature these word groups differed in substantially and significantly was their semantic relationship to body movements preferentially performed with the hands/arms or feet/legs. This semantic dissociation was validated using semantic ratings performed by an independent set of subjects. Therefore, this present study is the first to demonstrate processing impairments critically depending on the meaning of action words as a result of motor system engagement.

4.2. *Motor–language influences are bidirectional and can be facilitatory or inhibitory*

Over and above the results of earlier behavioural work, our present results show that an impairment of arm- or leg-word

processing can be induced, in the healthy brain, by engaging the motor system in complex motor schemes. Previous behavioural and TMS studies in healthy subjects have shown facilitation or inhibition effects both of motor systems activity on language processing (see for example, Glenberg et al., 2008a; D'Ausilio et al., 2009; Pulvermüller et al., 2005a) and in the reverse direction, from language processes on motor excitability or performance (Boulenger et al., 2006; Buccino et al., 2005; Sato et al., 2008; Glenberg et al., 2008b; Dalla Volta et al., 2009; Fadiga et al., 2002). As of yet, we do not fully understand what influences the sign of the effect (facilitation or interference) of motor–language interaction. One behavioural study managed to successfully influence the sign of the effect by manipulating the timing of action language interference in a motor task involving a reaching movement (Boulenger et al., 2006), reporting that action-word processing can facilitate or hinder motor behaviour depending on the temporal relationship between motor and linguistic processes. Further research may clarify whether additional features, for example TMS stimulation strength, the sequential nature of motor performance and/or the similarity between word-related action scheme and to-be-performed motor activity, co-determine the sign of the interaction effect.

In contrast with earlier reports, our present study did not reveal influences of verbal working memory on rhythmic body movement. Performance errors or obvious rhythm violations were very rare and did not support differences between conditions. However, in our opinion, this null effect should not receive a strong interpretation. We note that word category effects on motor system activity are not always revealed by crude behavioural measures (such as response times, Buccino et al., 2005) and may require the use of TMS to the motor cortex (Fadiga et al., 2002) or application of fine-grained kinematic measures (Boulenger et al., 2006; Dalla Volta et al., 2009). Redesigning our present experiment to allow, in addition to linguistic monitoring, the probing of motor systems, for example by using TMS-elicited EMG responses, would not have been possible without putting in danger the main aim of this study, the investigation of motor processes on word-category-specific verbal working memory. As language-to-motor effects are well-established in the literature, the present experiment, which was not set up to test such functional influences, cannot provide evidence against their existence.

4.3. Is there a semantic role of the motor system?

Recent papers have called into question findings about semantic somatotopy and, especially, whether the motor system serves a genuinely semantic role (see, for example, Tomasino et al., 2007, 2008; Willems et al., 2010; Arevalo et al., in press; Postle et al., 2008). Postle and colleagues reported numerically enhanced activation to face words in face motor ROIs and to leg words in leg motor regions of interest (ROIs), but no statistically significant differences (Postle et al., 2008). However, given the consistency of a good number of studies of semantic somatotopy using event-related fMRI (for review, see Kemmerer and Gonzalez-Castillo, 2010; Pulvermüller and Fadiga, 2010), it appears that the blocked design favoured by Postle and colleagues might not be optimal for

revealing semantic somatotopy. Tomasino replicated semantic somatotopy to action words presented in an imagery task but not in a phonological task (Tomasino et al., 2007). These authors also found effects of transcranial magnetic stimulation of motor cortex on single action-word processing in an imagery task, but when subjects had to indicate the time they had finished word reading or the frequency of occurrence of word stimuli, such effects were absent (Tomasino et al., 2008). Based on such task dependence, the authors conjecture that post-comprehension imagery phenomenon, rather than the automatic simulation of motor schemes immanent to action-word comprehension itself, might be reflected by motor systems activation to words. On the other hand, it is possible that phonological judgements enhance phonologically-related activity in the motor system (Pulvermüller et al., 2006), which overlays and may therefore mask semantic somatotopy, and that the latency of silent reading or frequency judgement are not sensitive enough to reveal effects of motor systems stimulation. Task differences in motor systems activation to action words were also reported between a lexical decision and an explicit action simulation task (Willems et al., 2010), but in that study, unfortunately, subjects had to press buttons in one of the tasks versus open and close their eyes in the other, thus confounding task-related motor systems activation by response mode. Several other studies were able to document semantic-somatotopic activation in the sensorimotor cortex in a range of tasks (lexical decision, passive reading, passive listening, semantic judgement), languages (English, Finnish, German, Italian) and with multiple methods (fMRI, EEG, MEG, TMS) (Pulvermüller et al., 2001, 2005b, 2009; Hauk et al., 2004; Hauk and Pulvermüller, 2004; Shtyrov et al., 2004; Boulenger et al., 2009; Raposo et al., 2009; Kemmerer et al., 2008; Tettamanti et al., 2005; van Elk et al., 2010; Aziz-Zadeh et al., 2006), especially at early latencies (150–250 msec), thus arguing that semantic somatotopy indexes a fast, early process of motor scheme simulation immanent to the language comprehension process, rather than a subsequent, post-comprehension, epiphenomenal process such as imagery (for review, see Pulvermüller, 2005; Pulvermüller and Fadiga, 2010; Kiefer and Pulvermüller, in press).

Still, even after acknowledging the evidence for associative links between motor systems and lexical circuits in perisylvian cortex, such association could be questioned with respect to its relevance to semantics (Mahon and Caramazza, 2008; Hickok, 2010). It is well known that behaviourist theories explaining meaning in terms of association are too limited to account for the wide range of facets of semantics, especially combinatorial aspects (Alston, 1969). Over and above semantic links with sensorimotor systems, brain mechanisms for other facets of semantics, including combinatorial processes, have been worked out in detail (Pulvermüller, 1999, 2003, in press; Kemmerer and Gonzalez-Castillo, 2010). In fact, neuroimaging evidence demonstrating modulation of motor systems activation by context (Tomasino et al., 2010; Tettamanti et al., 2008; van Elk et al., 2010) and reactivation of motor circuits with disambiguation of idiomatic action sentences (Boulenger et al., 2009) provide strong arguments that such activity serves a semantic role rather than representing “just” word-evoked

association. We hasten to add that this is not to deny that association between words and the objects and actions they are typically used to speak about is a relevant mechanism. In fact, any neurobiologically realistic theory needs to acknowledge the cortex' function as an associative memory (for discussion, see [Braitenberg and Schüz, 1998](#)) and, in the case of word–world relationships, associative learning provides a crucial mechanism for important types of semantic learning, especially for referential and interaction-based meaning ([Pulvermüller, in press](#)). If words are presented in sentence contexts, these semantic circuits interact with other networks dedicated to combinatorial processing, yielding priming and activity modulation of the lexicosemantic circuits (for discussion, see [Pulvermüller, 2003](#)).

Rather than looking at word perception and recognition, we here investigated working memory processes simultaneous with complex body movements. An obvious advantage of this paradigm is that continuous processes can be titrated to a level where performance is difficult, both in the motor and the linguistic domains. After ample pre-experimenting, we chose a working memory setup where a good number of errors were made (~30% of the trials) and a complex motor task at a speed at which individual subjects were just able to maintain error-free rhythmic performance. Therefore, our conclusions on a movement-elicited category-specific impairment of semantic working memory in healthy subjects are based on the application of a strictly controlled dual task paradigm in which both motor and working memory systems are under high demand. In this dual task context, performance on the demanding working memory task would have dropped substantially and unspecifically if subjects had engaged in epiphenomenal cognitive activity such as imagining motor activities or scenes. Imagery would not have been useful for making the fine-grained conceptual distinctions required to accurately replicate the verbal stimuli in the memory task. For example, imagining a walking person is unhelpful in distinguishing between potentially relevant stimuli such as “go”, “walk”, “stroll”, “hike”, “ambulate”, “wander”, “pace”, etc. Our tasks forced subject to focus on rehearsing action words; sensorimotor activation necessary for body movements therefore interfered with lexicosemantic memory processes, rather than with processes unrelated to verbal working memory *per se*. The present results could not be explained by a symbolic semantic system without recurring to the motor system as a critical contributor to semantic-category-specific processing (for discussion of such “disembodied” models, see [Hickok, 2010](#); [Mahon and Caramazza, 2008](#)). This argues against a disembodied proposal and in favour of critical functional links between linguistic and action-semantic systems of the human brain (for review, see [Pulvermüller and Fadiga, 2010](#); [Kiefer and Pulvermüller, in press](#); [Jeannerod, 2006](#)).

5. Conclusions

It had been suggested that sensorimotor brain systems are not necessary for action-word processing. However, the semantically specific working memory impairment for arm- and leg-related action words we report here during complex motor

movements involving the hands and feet indicates that both motor movements and semantic memory for action words rely on overlapping and closely interfering processing resources, thus supporting a vital function of cortical motor systems for action-word understanding and memory.

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Appendix Lexical stimuli

Arm words	Leg words
Peel	Hop
Bash	Stomp
Chop	Limp
Clap	Skip
Scratch	Stamp
Skim	Scuff
Grab	Leap
Scrub	Crawl
Grip	Jog
Click	Roam
Tug	Glide
Grate	Flit
Carve	Hike
Braid	Plod
Wipe	Stride
Stir	Mount
Hack	Stray
Delve	Tread
Rub	Kick
Bind	Wade
Seize	Creep
Dunk	Kneel
File	Pace
Stab	Sprint
Whip	Stroll
Switch	Roll
Scrape	Flee
Clean	Step
Dig	Slide
Grasp	Slip
Lift	Climb
Fold	Inch
Scoop	Skate
Nip	Trudge
Pat	Strut
Wash	Dance

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