

## Neuromagnetic hand and foot motor sources recruited during action verb processing



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### ABSTRACT

The current study investigated sensorimotor involvement in the processing of verbs describing actions performed with the hands, feet, or no body part. Actual movements were used to identify neuromagnetic sources for hand and foot actions. These sources constrained the analysis of verb processing. While hand and foot sources picked up activation in all three verb conditions, peak amplitudes showed an interaction of source and verb condition at 200 ms after word onset, thereby reflecting effector-specificity. Specifically, hand verbs elicited significantly higher peak amplitudes than foot verbs in hand sources. Our results are in line with theories of embodied cognition that assume an involvement of sensorimotor areas in early stages of lexico-semantic processing, even for single words without a semantic or motor task.

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### 1. Introduction

Embodied cognition theories postulate that concepts and their linguistic tokens are represented in modality-specific brain areas. Relevant modalities and neuronal networks associated with a certain concept are determined by the neuronal assemblies involved in originally acquiring the respective item of semantic knowledge (Pulvermüller, 2005; Barsalou, 2008). For action-related concepts and language, the relevant modalities include the sensorimotor domain. Consequently, their representations are assumed to engage sensorimotor areas of the brain, action execution networks, and the putative mirror neuron system (Gallese & Lakoff, 2005; Pulvermüller, 2005). Empirical studies addressed a number of questions about sensorimotor activation in language processing. These include where exactly language is processed in the sensorimotor system, whether sensorimotor activation occurs in a time window relevant for lexical-semantic processing, and whether it is crucial for language processing or epiphenomenal.

Evidence for sensorimotor involvement in action-related language processing stems from behavioural, neuroimaging, electrophysiological, neuropsychological and brain stimulation studies. For instance, verbs referring to actions performed with the mouth (*to lick*), the hands (*to pick*) or the feet (*to kick*) were shown to elicit blood-oxygenation-level-dependent (BOLD) activity in cortical

areas also involved in executing actions with the mouth, hands, and feet (Hauk & Pulvermüller, 2004). Similar results of somatotopy in bilateral or left-lateralized premotor and primary motor areas have been reported using functional magnetic resonance imaging (fMRI) both for single action verbs (Rüschmeyer, Brass, & Friederici, 2007; Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008; Willems, Toni, Hagoort, & Casasanto, 2010b; Hauk & Pulvermüller, 2011) and phrases or sentences (Tettamanti et al., 2005; Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Boulenger, Hauk, & Pulvermüller, 2009). Language processing was shown to occur in cortical regions representing action execution (Hauk & Pulvermüller, 2004, 2011; Boulenger et al., 2009) or observation (Aziz-Zadeh et al., 2006), despite some concerns about the precise location and functional overlap of motor and language functions (Postle, McMahon, Ashton, Meredith, & Zubicaray, 2008).

Somatotopically distributed neurophysiological responses were described using electroencephalography (EEG) and magnetoencephalography (MEG) for action verbs (Pulvermüller, Härle, & Hummel, 2001; Shtyrov, Hauk, & Pulvermüller, 2004; Hauk, Johnsrude, & Pulvermüller, 2004; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005a) and for literal as well as idiomatic sentences (Boulenger, Shtyrov, & Pulvermüller, 2012). These neurophysiological studies highlight the time course of embodied language processing, pinning down sensorimotor effects as early as 150–350 ms (Pulvermüller et al., 2005a; Boulenger et al., 2012). This implies that activations are part of lexical-semantic processing and do not reflect late motor imagery. Still, it is under debate in what respect motor activation during language processing is causal or merely reflects an epiphenomenon.

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Evidence for a functionally relevant relationship comes from studies showing that verb processing can interfere with concurrent motor tasks and vice versa (Glover, Rosenbaum, Graham, & Dixon, 2004; Boulenger et al., 2006; Zwaan & Taylor, 2006; Nazir et al., 2008; Shebani & Pulvermüller, 2013), while one study reported an unspecific dual task interference not related to verb semantics (Postle, Ashton, McFarland, & Zubizaray, 2013). Interestingly, readiness potentials of movements in EEG can be reduced even by subliminal presentation of hand action verbs (Boulenger et al., 2008). A causal involvement of the sensorimotor system in action related language processing may also be inferred from neuropsychological studies describing selective impairments for action verb processing following left premotor lesions (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001). Despite contradictory evidence (Kemmerer, Miller, Macpherson, Huber, & Tranel, 2013), Parkinson's disease (PD) as an example of movement disorders has also been associated with deficient action verb processing both in explicit and implicit semantic tasks (Fernandino et al., 2012). Moreover, impairments in PD may be sensitive to the degree of verbs' motion content (Herrera, Rodríguez-Ferreiro, & Cuetos, 2012). A direct causal link for sensorimotor processing of verbs can also be inferred from a study showing that transcranial magnetic stimulation (TMS) of the sensorimotor cortex could facilitate response latencies for verbs (Pulvermüller, Shtyrov, & Ilmoniemi, 2005b). Moreover, single TMS pulses during body part specific verb processing reduced motor evoked potentials (MEP) recorded from the respective effector (Buccino et al., 2005).

While this growing body of evidence amounts to a generally coherent picture of an involvement of the sensorimotor system in language processing, there are some open questions. Due to constraints depending on the methodological and design specifications, it is possible to address a combination of research aspects while necessarily having to ignore other issues. For instance, contrasting action-related versus abstract language or action verb versus object noun processing (Rüschmeyer et al., 2007; Boulenger et al., 2008) may produce results that could be explained by other factors apart from the action-relatedness, e.g. concreteness or grammatical class. Within the class of nouns, however, motor system activation in fMRI was found when participants named tools in comparison to animals (Martin, Wiggs, Ungerleider, & Haxby, 1996) and even somatotopically in the tongue area for food nouns and in the finger area for tool nouns (Carota, Moseley, & Pulvermüller, 2012). Findings from fMRI (e.g. Hauk & Pulvermüller, 2004; Tettamanti et al., 2005; Rüschmeyer et al., 2007; Desai, Binder, Conant, & Seidenberg, 2010; Aziz-Zadeh et al., 2006) based on the slowly developing BOLD response can hardly differentiate between lexical processing and later motor imagery, despite attempts to circumvent precisely this issue by contrasting explicit imagery and lexical decision tasks (Willemis, Hagoort, & Casasanto, 2010a). In turn, electrophysiological investigations (Pulvermüller et al., 2001; Shtyrov et al., 2004) provide important results pointing towards an early involvement of sensorimotor areas in language processing, but sometimes lack the spatial resolution to allow conclusions about the precise location of effector-specific language processing. Studies describing interactions of language processing and motor tasks (Boulenger et al., 2006; Buccino et al., 2005; Pulvermüller, 2005) cannot address the question whether sensorimotor activations would also arise in purely cognitive situations as a universal principle or are a product of motor task requirements. Related to accounts focusing on the task requirements provoking embodied language effects, accumulating evidence describes modulations of sensorimotor language processing depending on the linguistic context in which the language material was presented (Aravena et al., 2012; Schuil, Smits, & Zwaan, 2013). For instance, motor system activations seem sensitive to manipulations of affirmative versus negated

phrases (Tomasino, Weiss, & Fink, 2010). Still, it is not clear whether context elicits or only modulates embodied cognition. Finally, detecting somatotopy for standardised locations on group level (Hauk & Pulvermüller, 2004) loses out on information about individual persons' language processing and also about spatial specificity compared to action execution systems.

The current study aimed at estimating the contribution of individually specific motor sources to verb processing across time. More specifically, we investigated whether neuromagnetic equivalent current dipole (ECD) sources derived from actual hand and foot movements explained activation when silently reading single action verbs related to hand, foot or non-body actions while brain activations were recorded using MEG. ECDs for two distinct neuromagnetic fields accompanying voluntary movements were modelled: the motor field (MF) peaking around movement onset, and the movement evoked field (MEF) with a maximum shortly after movement onset (e.g. Cheyne & Weinberg, 1989; Kristeva, Cheyne, & Deecke, 1991). The neuromagnetic sources generating these two fields can be well separated for different effectors, such as the hands and feet (Kristeva-Feige et al., 1994). The MF, located in primary motor cortex with an anterior dipole orientation, is assumed to represent activity directly related to motor commands of a movement. Contrary, the MEF, located in postcentral sensory cortex with a posterior orientation, is attributed to sensory feedback evoked by a movement (for both MF and MEF, see Cheyne & Weinberg, 1989; Kristeva-Feige et al., 1994; Biermann-Ruben et al., 2012). When transferring these sources to silent single verb reading, we expected higher amplitudes for verbs of the matching effector compared to the other conditions in a time window around 200 ms (see Pulvermüller et al., 2001). Hand verbs were assumed to selectively activate hand motor areas and foot verbs to selectively activate foot motor areas, while non-body verbs should be non-selective for motor regions.

## 2. Material and methods

### 2.1. Participants

Fifteen healthy subjects (8 female, mean age = 22.1 years, SD = 1.8) took part in the experiment. All subjects had normal or corrected-to-normal vision, were native monolingual speakers of German and did not study linguistics. No participant had any neurological or psychiatric disorder nor took medication. Furthermore, right-handedness (Oldfield, 1971) and right-footedness (Ehrenstein & Arnold-Schulz-Gahmen, 1997) was ensured. All participants gave written informed consent prior to taking part in the experiment and received financial reimbursement. The study is in line with the Declaration of Helsinki and was approved by the ethics committee of the Medical Faculty at Heinrich-Heine-University, Düsseldorf (study number 3400).

### 2.2. Stimulus material

The stimulus set consisted of 144 action verbs describing hand actions (H), e.g. *greifen* (to grasp), foot actions (F), e.g. *gehen* (to walk), and actions in which no body part was involved (N), e.g. *raten* (to guess). All verbs were bisyllabic and always presented in their infinitive German form. Suitable stimuli were selected according to a successive multidimensional matching procedure. First, 30 participants (monolingual speakers of German, mean age = 29.7 years, SD = 6.8) stated which body part they habitually used to perform the actions described by 339 verbs that were a priori chosen as candidates for the target categories of H, F and N action verbs. Possible answers were "hands/arms", "feet/legs", "the whole body uniformly", "mouth/face", "no body part" and

"I don't know", including categories not used in the main experiment ("mouth/face", "whole body") to prevent forced choices of inaccurate answers. Verbs found to describe actions of the hands, feet, or no body part by at least 80% of the subjects, respectively, were further considered for the sets of H, F and N. For a high proportion of verbs, a typical pattern of results was seen where ratings were split between the categories "feet/legs" and "whole body". This is likely due to locomotion verbs such as *to run* being rated as "whole body" by some participants who focused on the body's change of location and the accompanying movements (of, for instance, arms and torso) rather than only on the movements of the lower extremity. Therefore, for the F category, verbs were also included if the sum of "feet/legs" and "whole body" was at least 80% as long as the majority of these was "feet/legs". The remaining 219 H, F and N verbs were rated again ( $n=30$ , mean age = 28.8, SD = 6.4) to assess the verbs' familiarity and imageability on 4-point rating scales. In addition to the mean familiarity and imageability derived from the rating studies, word length in letters and word frequency class (Leipzig Corpora Collection, LCC, Biemann, Heyer, Quasthoff, & Richter, 2007, available at <http://wortschatz.uni-leipzig.de>) were used to define suitably matched groups of stimuli, resulting in 48 verbs per condition (see supplementary Table 1). While familiarity did not differ between groups (analysis of variance (ANOVA),  $p = .547$ ) residual differences were found for other measures (ANOVA, all  $p < .010$ ). More precisely, according to pairwise tests, N verbs were on average 0.8 letters longer than H ( $t(94) = 3.09$ ,  $p = .003$ ) and F ( $t(94) = 2.70$ ,  $p = .008$ ), less imageable than H ( $t(94) = 23.33$ ,  $p < .001$ ) and F ( $t(94) = 18.08$ ,  $p < .001$ ), and more frequent than H ( $t(94) = 4.59$ ,  $p < .001$ ) and F ( $t(94) = 2.79$ ,  $p = .006$ ). Importantly, H and F conditions showed no significant differences for the above parameters (all  $p > .130$ ). From the verb material rejected during the matching procedure 18 filler verbs were selected, six from each condition. Additionally, 18 phonotactically legal pseudowords were created by reassembling first and second syllables of the stimulus verbs. For this, all first and second syllable occurrences in the data set were counted. Pseudoverb endings (for German, typically '-en', '-ern' or '-eln') as well as initial letters of first and second syllables were selected so that their relative frequencies in the set broadly resembled the endings and letter frequencies in the main data set in order to avoid introducing a processing bias.

### 2.3. Procedure

Before the measurement bipolar peripheral electrodes were attached to the subjects' skin to record vertical and horizontal electrooculogram (EOG) as well as electromyogram (EMG) of extensor digitorum communis (EDC) muscles of both arms and tibialis anterior (TA) muscles of both legs. Additionally, four head position indicator (HPI) coils were applied to the scalp. HPI coil location was digitized (Polhemus Isotrak, Colchester, Vermont, USA) for coregistration with anatomical MRI images. Participants were then comfortably seated in the magnetically shielded room.

During the language paradigm, stimuli were projected in black letters onto a light grey screen with a visual angle of  $3.4^\circ$  horizontally by  $0.7^\circ$  vertically, on average. The experimental procedure is shown in Fig. 1. Presentation 14.9 software (Neurobehavioral Systems, Albany, California, USA) was used. Verbs were presented for 500 ms followed by a central fixation cross displayed for 2000 ms. After that, for silent reading trials (80% of the whole experiment), the pictogram of an eye signalled 2000 ms for eye blinks. During an intertrial interval jittered from 900 to 1100 ms the fixation cross was presented again. Lexical decision trials (20% of the whole experiment) consisted of 500 ms presentation of the filler or pseudoverb and the subsequent fixation cross displayed for 2000 ms. During this time, silent

reading and lexical decision trials were indistinguishable. Then the response prompt was shown for 1500 ms. It consisted of a central horizontal arrow pointing either to the right or to the left side of the screen, where target locations were marked by crosses. Participants were instructed to perform a saccade following the arrow's direction if the preceding stimulus was a real word and to the opposite if it was a pseudoverb. Arrow directions were counterbalanced. The eye pictogram then indicated 1000 ms time for eye blinks followed by the intertrial interval.

The experiment included four blocks of about 8 min each and a short practice block at the beginning. Stimulus presentation was pseudorandomized with block 1 and 2 containing the first occurrence of all stimuli, block 3 and 4 the second occurrence, randomized within the two repetitions.

After the language paradigm participants performed a movement paradigm consisting of alternating hand movements and alternating foot movements. The arms rested on a table in front of the body while the legs were supported by cushions of the MEG chair. Styrofoam ear plugs were used to minimise evoked potentials due to auditory movement feedback. In the hand movement condition, participants were instructed to briskly raise and immediately after drop their hands alternately every two seconds. The same task was executed with the feet in the foot movement condition. Hand and foot movements were recorded for five minutes each. The order of task execution was counterbalanced across subjects.

### 2.4. Neurophysiological data acquisition

MEG recordings were performed using a 306 channel Neuromag MEG system with 204 planar gradiometers and 102 magnetometers (Elekta Neuromag, Helsinki, Finland) located at University Hospital Düsseldorf. Sampling rate during all experiments was 1000 Hz with an online bandpass filter of 0.03–330 Hz. All further analyses were performed offline. Acquisition of anatomical MRI images was performed in a separate session one to two weeks after the MEG session with a 3 T magnetom machine (Siemens, Erlangen, Germany).

### 2.5. Data processing

MEG, EOG, EMG and MRI data were analysed offline using software packages by Elekta Neuromag (Graph, Xfit, Xplotter, MriLab).

Continuously recorded MEG signals from the 204 planar gradiometers were bandpass filtered from 0.1 to 100 Hz and segmented for further analyses. For each paradigm, trials containing sensor jumps and eye movements were rejected. The eye blink rejection threshold was adjusted individually by visual inspection of individual EOG traces. For the language paradigm, epochs with EMG power exceeding an individually adjusted threshold indicating muscle tension (defined in the movement paradigm, see next paragraph) were discarded as well.

For the movement paradigm, data epochs were averaged from –2000 to 500 ms with respect to movement onset as defined by rectified EMG. Thresholds were defined per subject and adjusted individually by visual inspection to capture the earliest deviation from resting activation level. Eye blinks in the time window of –1500 to 200 ms led to the exclusion of the respective trial. Excessive eye blinking caused an insufficient number of valid trials in 11 subjects. In these cases, signal-space projection method (SSP, Uusitalo & Ilmoniemi, 1997) was used to remove the field patterns associated with eye blinks from the MEG data, returning cleaned signal traces.

Trials in the language paradigm were defined from –500 to 2000 ms with respect to word onset and averaged for the three experimental conditions. EOG rejection span was set at –100 to

500 ms. Blink-SSP was performed for data from the 11 subjects for whom this had also been applied to the movement paradigm.

Anatomical MRI images were transferred into Talairach Space by anterior and posterior commissure (AC–PC) alignment. Spherical conductor models for the modelling of equivalent current dipoles were fitted to the individual anatomy guaranteeing an optimal fit to the curvature of the sensorimotor cortex (compare Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993).

## 2.6. Dipole modelling

To identify ECDs related to movements of each limb, an MEG channel selection was chosen which covered the sensorimotor cortex presumed to control the respective limb. For each hand, this included 10 dorsolateral fronto-parietal sensor pairs in the contralateral hemisphere, as depicted in Fig. 2A. For the feet, 9 dorsomedial fronto-parietal sensor pairs were selected, including 3 central channels to either side of the midline and the 3 adjacent contralateral channels (Fig. 2B). This takes into account the fact that the anatomical correlate of the foot representation may reach into the longitudinal fissure. If sensors neighbouring the selected channels prominently captured movement-associated evoked activity – due to individual head position in the MEG system – they were included for dipole modelling. For the movement paradigm, data were baseline corrected from –1500 to –1400 ms. Dipole fitting followed well-established procedure (Hämäläinen et al., 1993; Salmelin, Schnitzler, Schmitz, & Freund, 2000; Biermann-Ruben et al., 2012). Event related responses of possible MF and MEF for each effector were visually inspected for times of approximate peaks. For the 20 ms before and after these time points automated dynamic dipole fitting was used to identify the single ECD with the maximal goodness of fit (GOF). Only GOF values above 60% were accepted.

This resulted in a maximum of eight ECDs per subject, i.e., 2 effectors (hand, foot)  $\times$  2 sides (right, left)  $\times$  2 components (MF, MEF). These ECDs were then transferred to the language paradigm and used to explain neuromagnetic activity during verb processing. Amplitude peaks exceeding baseline activity by at least one standard deviation were considered for further analyses.

## 2.7. Statistical analysis

Peak latencies and amplitudes of the MF and MEF dipoles in the language paradigm were entered into an analysis of variance (ANOVA) with the factors verb condition (H, F, N), effector (hand, foot) and laterality (left, right). Planned comparisons were carried out to directly compare peak activations in the H and F conditions for hand and foot sources by means of one-tailed paired *t*-tests, because higher amplitudes of H than F in the hand sources and higher amplitudes of F than H in the foot sources were expected. Post-hoc comparisons of other effects were Bonferroni corrected.

# 3. Results

## 3.1. Behavioural

The accuracy of lexical decision responses varied between 77.8% and 97.2% (Mean = 89.4%, SD = 6.2%). This confirms participants' attention throughout the experiment.

## 3.2. Evoked responses

Whole head views of root mean square evoked responses are shown in Fig. 3. For the movement task, Fig. 3A overlays the two conditions of left hand and right foot movement, also

representative for the other two mirrored tasks. Responses for the hand movement include more lateral channels and for the foot movement more medial channels, with the maximum response in the contralateral hemisphere for each task. Note that before movement onset as identified by EMG traces, activity levels rise to a peak which represents the MF, followed by the large peak of the MEF after EMG onset. For the verb paradigm, evoked responses are shown collapsed over all conditions in Fig. 3B. Large responses related to the visual stimulus can be seen in posterior channels and smaller activations in centromedial and contralateral channels, with a slightly longer latency than the visual responses. Note also the absence of any overt movement as shown by the EMG traces for all four limbs.

## 3.3. Location of motoric dipole sources

MF sources could be modelled in all participants, albeit not for each limb. Hand MF could be identified in 10 (left hand) to 11 (right hand) subjects with GOF values between 60.1% and 95.8%. Foot MF was evident in 12 (left foot) to 13 (right foot) participants with GOF 64.6–94.2%. MEF dipole sources were obtained for all participants and for each effector, except for one subject (left foot). GOF values ranged from 63.8% to 98.6%. Since for one subject an anatomical MRI could not be obtained dipoles for this subject were projected into a template brain. Hand movement ECDs were generally located more laterally than foot movement ECDs, in line with the somatotopic organisation of the sensorimotor cortex. MFs on average originated more anteriorly than MEFs, with opposite orientation indicating opposite direction of current flow. In a few cases, foot movement ECDs were located ipsi- rather than contralaterally, which can be attributed to the medial representation of legs and feet in both primary motor and primary sensory cortex (compare Endo, Kato, Kizuka, Masuda, & Takeda, 2004) in combination with limitations of the spatial resolution of MEG.

## 3.4. Transfer of sources into the language paradigm

ECD information from the four movement conditions was imported into the verb paradigm. To prohibit dipole interaction all dipoles were used separately to explain the measured signal for the corresponding channels of interest (see Fig. 2). MEF sources did not show activation exceeding baseline consistently across subjects and were therefore discarded from further analyses. In contrast, MF sources were active during processing of all verb conditions, with a peak on average at 194 ms (SD = 33 ms) after word onset distributed evenly across effectors and sides. Grandaverage time courses of MF activations during the language paradigm are shown in Fig. 4.

For the four MF sources in the three verb conditions, individual peak amplitudes and latencies were extracted for statistical comparisons. In the ANOVA, both missing (no MF source or no activation exceeding one SD in the verb paradigm) and outlier values ( $\pm 2$  SD of group mean) were replaced using mean imputation from the respective group average. For each source, between 9 and 13 out of 15 subjects provided a value, 10.92 on average.

While no main effects were found, the interaction of verb condition by effector was significant ( $F(2;28) = 4.081$ ,  $p = .028$ ). Peak amplitudes of the MF hand and foot sources (averaged across hemispheres) are shown in Fig. 5. According to the main hypothesis of higher amplitudes for effector-related compared to unrelated action verbs, we directly contrasted peak amplitudes of hand and foot MF sources in hand and foot verb conditions: In the hand MF source, amplitudes for hand verbs were larger than for foot verbs ( $t(14) = 2.529$ ,  $p = .012$ ; one-tailed). In the foot MF source, the contrast marginally failed to reach significance



( $t(14) = -1.737$ ,  $p = .052$ ; one-tailed) despite numerically larger amplitudes for foot than for hand verbs (see Fig. 5).

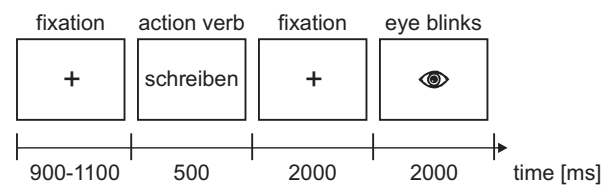
The analysis of MF peak latencies revealed a  $p$ -value of  $p = .057$  for the main effect of side ( $F(1;14) = 4.259$ ) due to a tendency towards shorter latencies for right limb sources, as well as a significant interaction of side by effector ( $F(2;28) = 12.569$ ,  $p = .003$ ), see Fig. 6. Bonferroni corrected multiple comparisons show this interaction to be driven by shorter latencies for right hand sources than left hand sources ( $t(14) = -5.000$ ,  $p < .001$ ). No influence of verb condition was found (all other  $p > .139$ ).

#### 4. Discussion

The current study shows that individually specific hand and foot motor dipole sources are preferentially involved in single action verb processing when verbs refer to the respective body part, in the time window of lexico-semantic access. It is conceivable that the effect is due to differences in the semantic content of the verbs, i.e., the characteristics of the actions described, including the body part involved in it (Pulvermüller, 2005). For each participant, we derived motor dipole sources using a simple movement task. These sources can be assumed to be functionally relevant for the respective movement of the hand or the foot. Instead of interpreting activation topographies and time courses for the raw signal during language processing, we transferred the motor source information, i.e. location and orientation of the dipole, into the verb paradigm as a “source of interest” analysis. We found that at about 200 ms after word onset, verb conditions elicited differential activation in the MF motor sources, constituting a somatotopic effect of verb processing. Crucially, this difference was found for the processing of a set of single words without linguistic context. Moreover, since no overt semantic task nor any hand or foot motor response was required, embodiment effects can be detected with low levels of semantic processing requirements in a purely cognitive task. While evidence is accumulating that linguistic context modulates sensorimotor activations in language processing tasks (Tomasino et al., 2010; Aravena et al., 2012; Schuil et al., 2013), an involvement of sensorimotor networks may at the same time be a universal processing principle also found in context-free environments as a response of access to semantics of, for instance, bare verbs (Hauk et al., 2004; Rüschemeyer et al., 2007; Kemmerer et al., 2008; Willems et al., 2010b). Our results favour a view of embodied cognition where semantic knowledge can be accessed by processing of single action verbs and thereby recruits motor areas, strongly enough to be detected by MEG. Hence, this is in line with the strong claim of embodiment theories that sensorimotor activation occurs automatically – and possibly necessarily – during verb processing (Pulvermüller et al., 2005b; Boulenger et al., 2008; Rüschemeyer, Lindemann, van Elk, & Bekkering, 2009). This is also in accordance with neuropsychological findings (Bak et al., 2001; Fernandino et al., 2012; Herrera et al., 2012). Beyond that, embodied cognition can unequivocally be influenced and modified by factors like attention, linguistic context, and task.

Interestingly, while MF dipole sources were sensitive to verb processing, MEF sources were not. This may be due to MF sources originating in precentral, primary motor areas (Kristeva-Feige et al., 1994), while MEF sources are typically located in postcentral sensory areas (Oishi, Kameyama, Fukuda, Tsuchiya, & Kondo, 2004). Consistently, the involvement of primary motor or premotor cortex in action language processing was shown in neuroimaging studies (Hauk & Pulvermüller, 2004; Rüschemeyer et al., 2007; Aziz-Zadeh et al., 2006; Kemmerer et al., 2008; Boulenger et al., 2012). MEF sources being attributed to sensory feedback of one's own movements (Cheyne & Weinberg, 1989) do not seem to be recruited for single verb processing.

#### 80% silent reading



#### 20% lexical decision

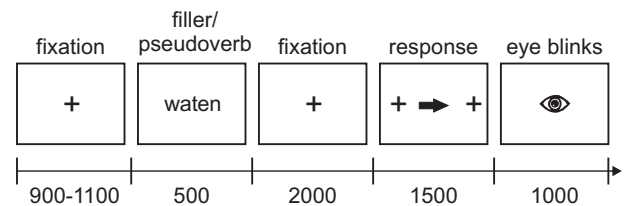


Fig. 1. Experimental procedure for the language paradigm. Until the response prompt stimulus, presentation times were identical for silent reading and lexical decision trials.

Our results could imply that the same specific neuron populations involved in movement execution are also active when processing verbs that describe actions including a similar movement. Admittedly, the simple hand and foot movement task is less complex than the actions described by the verbs. Nevertheless, a concerted recruitment of the motor neuron populations involved in motor acts that are part of a complex action may be an informative functional mechanism for the motor system to contribute to language processing; for instance as a means of embodied simulation (Barsalou, 2008). Therefore, using simple basic hand and foot motor acts as a proxy seems feasible for the current research question (for a theoretical account of verb semantics concerning action templates, see Kemmerer & Gonzalez-Castillo, 2010).

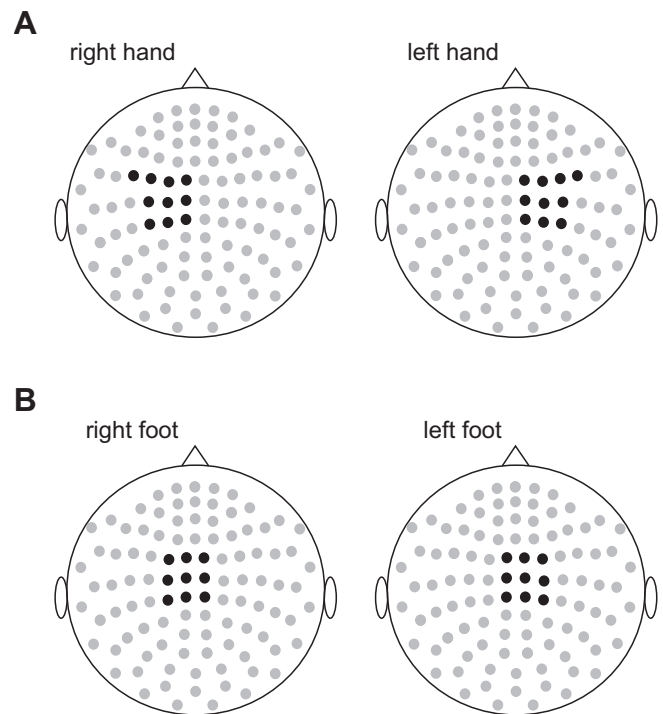
When directly comparing verb conditions for hand sources, hand verbs indeed elicited higher amplitudes than foot verbs. This suggests a stronger involvement of hand-specific motor regions in processing language related to actions that recruit the same motor regions. The inverse comparison in foot sources was marginally significant. This mirrors findings obtained by Boulenger et al. (2012), who, in a similar time window during hand and foot action sentence processing, observed a significant difference for hand regions, but only a numerical difference for foot regions. Possibly, true differences in our study were masked by anatomical issues regarding the representation of the feet/legs. First, hand regions are massively overrepresented in both the sensory and the motor homunculus, with the foot/leg representation smaller in total (Aziz-Zadeh & Damasio, 2008). Second, the signal quality from the foot region may be reduced when it is located medially in the intrahemispheric sulcus with cortical layers deviating from the optimal orientation for MEG (Hämäläinen et al., 1993). This problem is exacerbated when inverse source modelling relies on forward volume conducting models intended to maximise sensitivity on the surface of a smooth sphere.

The activation pattern picked up by both hand and foot motor sources showed general non-zero activity and a peak at around 200 ms in all conditions. This implies that embodied cognition is not an all-or-nothing response, but rather a relative and graded sensitivity of the motor system to action relatedness of language. In fact, most studies described a pattern of results where not only the relevant conditions exclusively activated regions of interest,

but where the other, less related conditions also led to positive signal change (Hauk & Pulvermüller, 2004; Aziz-Zadeh et al., 2006). Curiously, neuronal activation for the processing of non-body related verbs was also picked up by the motor dipole sources, with a peak around the same latency as the other verb conditions. This may imply the involvement of motor dipole sources in abstract verb processing. Alternatively, it could be related to another neuronal process not originating in the area exactly around the dipole, but nevertheless located and oriented in a way for which all MF dipoles were sensitive, for instance a deeper medial region. Such a source may be located in the cingulate cortex, which has been described to be involved in abstract word processing (Tettamanti et al., 2005; Vigliocco et al., 2013), in prefrontal areas (D'Esposito et al., 1997; Binder, Westbury, McKiernan, Possing, & Medler, 2005; Rodríguez-Ferreiro, Gennari, Davies, & Cuetos, 2011; Moseley, Carota, Hauk, Mohr, & Pulvermüller, 2012) or also subcortically in the thalamus (Friederici, Opitz, & Cramon, 2000). Examples for some sensorimotor activation for abstract language processing also exist (Rüschmeyer et al., 2007; Desai et al., 2010). In an fMRI study, Moseley et al. (2012) found activity in cortical motor regions when processing abstract emotion words. Interestingly, this activation was as strong as for mouth-related verbs in the mouth area and as strong as for arm-related verbs in the arm area, with the non-corresponding action verbs eliciting lower activation than corresponding and abstract verbs. Abstract words in general have been proposed to have a stronger valence than concrete words and often can be classified as emotion words (Kousta, Vigliocco, Vinson, Andrews, & Del Campo, 2011). This emotionality may be the basis for their grounding in sensorimotor systems as emotions can be experienced by and expressed with your body (Moseley et al., 2012). Our set of non-body verbs was not explicitly tested for its emotional valence, but it is conceivable that for verbs like *to hate* or *to honour*, the same mechanisms as described for Moseley et al.'s abstract emotion verbs apply. Similarly, Moseley et al. (2012) described emotion verbs with sensorimotor links such as *to huff* which are also associated with motor system activations. Again, a subset of our non-body verbs may fall into this category. More precisely, even though we acquired ratings where 80% of participants stated that no body part was required for the global meaning of these action verbs, this doesn't exclude the possibility that during the MEG experiment subjects activated more sensorimotor readings of some verbs. Even if not overtly polysemous, verbs can still inherently comprise different readings that are more abstract or more concrete, for instance *to grieve*, *to improve* or *to defy*. Taken together, this can explain why on average we saw true motor activation during the processing of non-body verbs in our study.

Which of the explanations best fits our pattern of results – or if, in fact, several or all do – remains elusive. Crucially, no difference between hand and foot sources could be observed for non-body verbs in the current study, indicating a uniform activation of a – possibly nearby – source not sensitive to action content modulations.

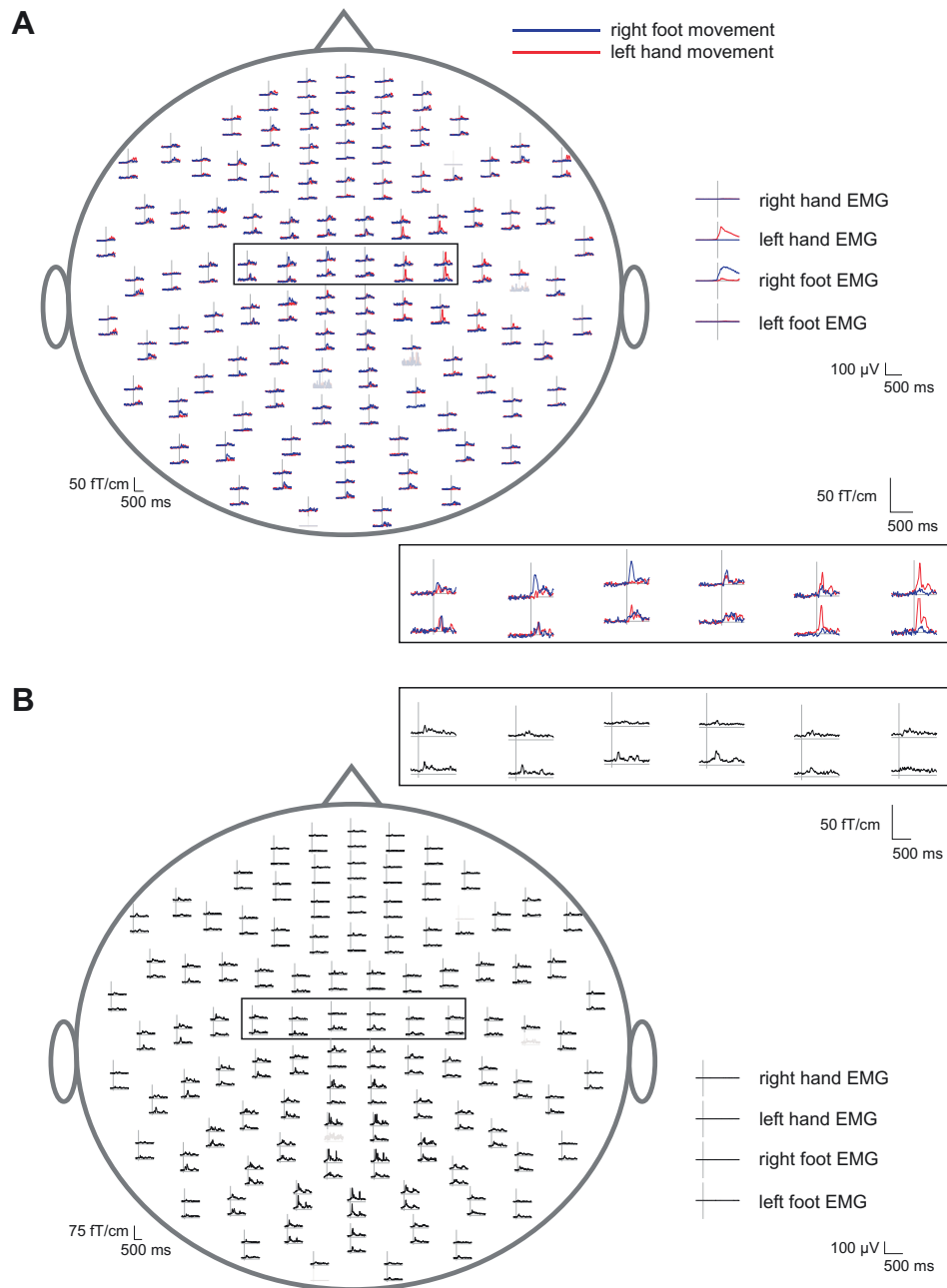
Importantly, we found somatotopic motor system activations on the basis of individually specific movement execution sources. This suggests that embodied cognition recruits not only motor neurons located in the premotor cortex (e.g., Aziz-Zadeh et al., 2006; Willems et al., 2010b) or even nodes in larger scale action networks including the parietal cortex (van Dam, Rüschmeyer, & Bekkering, 2010), but also distinctly in the primary motor cortex (compare also Hauk & Pulvermüller, 2004; Rüschmeyer et al., 2007). Indeed, evidence for an involvement of the primary motor cortex in action verb processing was found using TMS (Buccino et al., 2005; Repetto, Colombo, Cipresso, & Riva, 2013). A theoretical account of a distributed neuronal network comprising premotor, primary motor and other regions being involved in action



**Fig. 2.** MEG channel selection for dipole fitting of MF and MEF. Selected channels are indicated by a black dot, other channels are shown in grey. Each dot represents one pair of orthogonal gradiometer sensors, i.e., 102 channel locations are depicted for the 204 gradiometers. (A) Hand movements (B) foot movements

execution, observation and language processing has been described (Gallese, 2008). In this framework, the distinguishing factors between action execution and access to action knowledge include inhibitory processes preventing motor output while allowing activation of distinctly motor related neuronal populations. Therefore, the primary motor cortex is a likely candidate for an embodied cognition network. Note, however, that while it is conceivable to attribute MF sources to the primary motor cortex, the dipole transfer method cannot provide perfectly accurate information about the location of neuromagnetic activations during language processing. It is possible that sources during action execution and verb processing for each limb are not identical, but nevertheless positioned and oriented in a way that activation is differentially picked up by the execution sources. For instance, if verb processing activation extended to premotor locations anterior to the execution foci, we would still see a similar pattern of results because hand verb sources would still be preferentially detected by hand execution sources and vice versa for foot verbs. Note also that a similar hypothesis can be assumed for the activation found for non-body verbs, as outlined above.

Unfortunately, the downside of investigating individual overlap of motor and language networks is that results rely on the identification of sources for each individual subject. This has previously been shown to be especially challenging for the MF while fitting of the MEF has a higher probability of success (Kristeva-Feige et al., 1994; Endo et al., 2004) and a higher goodness of fit (Biermann-Ruben et al., 2012). Indeed, if there were participants for whom we could not identify an ECD source, it was generally for one of the MFs. Moreover, there are other issues which may have led to a poor signal quality in some participants where only a small number of ECDs could be fitted. For instance, the individual folding of the cortex or the head position of the participant within the MEG device may have exacerbated source analysis. Nevertheless, we obtained MF sources for some or all of the four



**Fig. 3.** Grandaverage root mean square evoked responses during the movement task and the verb paradigm in the 204 planar gradiometers. Top view, left is left, anterior is up. Bad channels are semi-transparently masked. (A) Movement task. An enlarged selection of sensorimotor channels is shown separately in the box at the bottom.  $n = 14$  with one subject excluded due to large artefacts on frontal sensors. (B) Verb task, collapsed over all three conditions. An enlarged selection of sensorimotor channels is shown separately in the box at the top.

movement conditions in each subject, on the basis of which we analysed verb processing and found somatotopy to play a role.

The present results do not indicate any differences between hemispheres for the amplitude of somatotopic motor activation during language processing. The question whether the left, generally language-dominant hemisphere is more strongly activated in action verb processing or whether both motor cortices contribute was directly addressed by comparing left- and right-handers during processing of uni- and bimanual verbs, with mixed results (Willems et al., 2010a; Hauk & Pulvermüller, 2011). One study claims body-specific motor involvement (Willems et al., 2010a) while the other stresses the specific role

of the left hemisphere even for bimanual verbs regardless of handedness (Hauk & Pulvermüller, 2011). While not specifically controlling stimulus material for this issue in the present study, a large proportion of hand verbs and virtually all of the foot verbs were bimanual or bipedal, respectively. It is conceivable that this also led to bilateral motor recruitment. This suggests that embodied cognition may use a mechanism of action simulation recruiting bilateral regions involved in action execution. However, we found a significant latency effect implying an earlier involvement of right hand motor sources than left hand sources, regardless of the language material. This could be due to an earlier responsiveness of the left lateral precentral cortex than the

corresponding right hemispheric regions for language processes. Differences in latencies of neuronal as well as overt motor responses have been hypothesised and empirically described in a network model attributing them to spatial distance from the left inferior frontal language areas, with a larger distance for feet than hand motor cortex (Pulvermüller, Härle, & Hummel, 2000, 2001). In the context of our results, right hand motor sources, being spatially closer to left temporal and inferior frontal language areas than left hand motor sources, may be faster in picking up language processing activity. Furthermore, there may be a special role for left hemispheric hand areas linking motor and communication functions, both for gestural and linguistic communication (Gallese, 2008).

An interesting proposal regarding the relative contributions to conceptual processing across time by core linguistic and modality-specific simulation areas has been put forward by the language and situated simulation (LASS) framework (Barsalou, Santos, Simmons, & Wilson, 2008). Here, understanding of meaning is assumed to first be dominated by linguistic processing, such as word form and statistical linguistic information. Simulations can arise simultaneously but only develop their full extent later in time. What is meant by early and late in this respect has been described in an fMRI study (Simmons, Hamann, Harenski, Hu, & Barsalou, 2008), where in a property generation task linguistic processing prevailed for the first 7.5 s of a trial while simulations dominated in the latter 7.5 s. This view may reconcile classical and embodied views of language processing and has successfully been linked to language processing on the sentence level, where integration processes occurring with a delay of several seconds seem feasible (Boulenger et al., 2009). The latency of the evoked responses described in the present study of about 200 ms after the onset of a single verb is similar to previous electrophysiological results (Pulvermüller et al., 2001). This component may reflect the first detectable activation of simulation systems, even though the linguistic system can be strongly involved in processing and dominate behavioural output (Simmons et al., 2008). Possibly, early phase-locked simulation activation has a minimum latency, following primary perceptual processing, which can be pinned down at 150–200 ms (Pulvermüller et al., 2001; Boulenger et al., 2012). After this, processing becomes more diverse and dependent on stimulus and task characteristics, resulting in simulation activation that

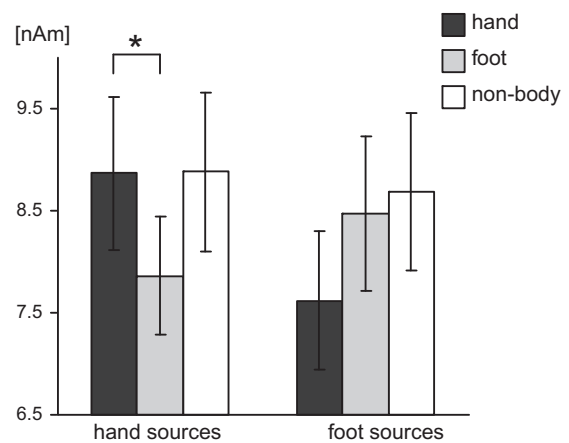


Fig. 5. Mean peak amplitudes for MF hand and foot sources in the three verb conditions, averaged across hemispheres. Error bars show SEM. \* =  $p < .05$

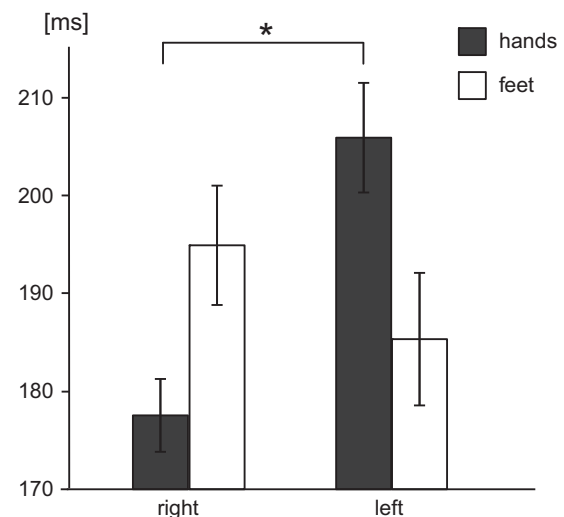


Fig. 6. Peak latencies for hand and foot MF sources, averaged across the three verb conditions. Note that right limb sources correspond to left hemispheric ECDs and vice versa. \* =  $p < .008$  (according to Bonferroni correction).

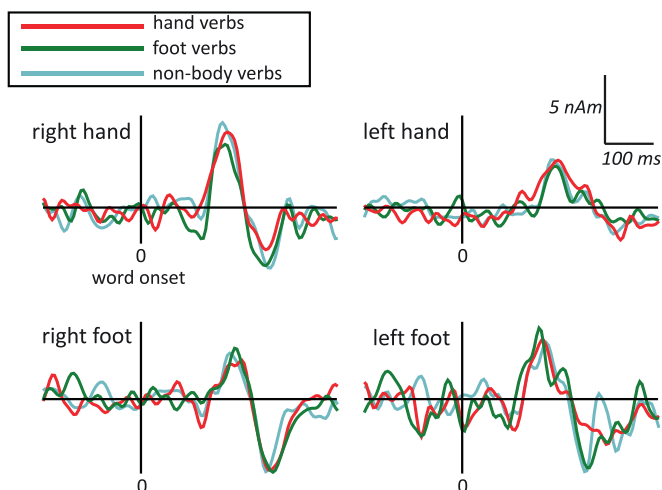


Fig. 4. Grandaverage time course of MF dipole activation during the verb processing paradigm for the three conditions (hand, foot, non-body verbs). Data from all subjects for which MF could be fitted for the respective effector are included. Baseline correction was applied from –200 ms until word onset.

is building up across time but nevertheless smeared in averaged evoked responses as it is no longer phase-locked to the stimulus. Thus there would not only be simulation activation differing from baseline around 200 ms, but even a peak as seen in the current results and previous studies, implying fluctuations in activation level following the 150–350 ms range (Pulvermüller et al., 2005a; Boulenger et al., 2012). A direct test of the LASS theory should incorporate an appropriate behavioural task – as opposed to our speeded silent reading paradigm – and possibly larger chunks of language such as sentences.

Current results are in line with an embodied cognition theory which assumes semantic knowledge to be grounded in modality-specific, sensorimotor, brain areas (Barsalou, 2008; Pulvermüller, 2005). The early, somatotopic activation of presumably primary motor areas described here complements and combines previous findings from neuroimaging (Hauk & Pulvermüller, 2004) and electrophysiology (Pulvermüller et al., 2001; Boulenger et al., 2012). Importantly, processing single verbs bare of context and without semantic or motor tasks was sufficient to elicit early effector-specific motor activations.



## Acknowledgments

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## Appendix A. stimulus characteristics

Table 1.

**Table 1**  
Stimuli in each of the three experimental conditions.

Condition	German	English	Frequency	Familiarity	Imageability	Letters
H	angeln	to fish	3.37	3.50	15	6
H	basteln	to tinker	3.67	3.60	13	7
H	binden	to tie	3.47	3.50	12	6
H	boxen	to box	3.40	3.47	12	5
H	buddeln	to dig	3.07	3.40	16	7
H	falten	to fold	3.50	3.73	15	6
H	fassen	to grab	3.57	3.43	11	6
H	feilen	to file	3.17	3.47	14	6
H	flechten	to plait	3.00	3.50	16	8
H	fuchteln	to wave	2.76	3.10	18	8
H	greifen	to grasp	3.90	3.90	10	7
H	häkeln	to crochet	2.97	3.33	19	6
H	kehren	to sweep	3.13	3.40	12	6
H	klatschen	to clap	3.77	3.77	13	9
H	kneifen	to pinch	3.47	3.57	16	7
H	kneten	to knead	3.47	3.70	17	6
H	knoten	to knot	3.23	3.57	19	6
H	melken	to milk	3.20	3.37	16	6
H	nähen	to sew	3.47	3.70	15	5
H	paddeln	to paddle	3.10	3.60	16	7
H	pelln	to peel	2.90	3.30	18	6
H	pflücken	to pick	3.30	3.77	15	8
H	rubbeln	to scour	3.10	3.43	18	7
H	rütteln	to shake	3.27	3.37	13	7
H	schälen	to peel	3.60	3.60	15	7
H	scheuern	to rub	2.90	3.33	18	8
H	schlagen	to beat	3.73	3.77	10	8
H	schleifen	to whet	3.17	3.20	14	9
H	schleudern	to hurl	3.23	3.23	15	10
H	schneidern	to tailor	3.10	3.20	16	10
H	schnipsen	to flick	3.03	3.70	19	9
H	schnitzen	to carve	3.17	3.50	17	9
H	schnüren	to lace	3.17	3.17	14	8
H	schreiben	to write	4.00	4.00	9	9
H	schrubben	to scrub	3.13	3.47	17	9
H	spitzen	to sharpen	2.83	2.97	14	7
H	stapeln	to pile	3.43	3.60	13	7
H	stochern	to stoke	2.90	3.13	17	8
H	stopfen	to stuff	3.27	2.90	13	7
H	stricken	to knit	3.33	3.40	15	8
H	stupsen	to nudge	3.07	3.27	19	7
H	tippen	to tap	3.50	3.40	14	6
H	trommeln	to drum	3.43	3.69	15	8
H	wedeln	to waggle	2.70	3.07	16	6
H	wickeln	to wrap	3.27	3.37	15	7
H	winken	to wave	3.63	3.87	13	6
H	zerren	to drag	3.00	3.33	14	6
H	zupfen	to pluck	3.10	3.07	16	6
<b>H</b>	<b>Mean</b>		<b>3.27</b>	<b>3.45</b>	<b>14.94</b>	<b>7.15</b>
<b>H</b>	<b>±SD</b>		<b>±0.29</b>	<b>±0.25</b>	<b>±2.45</b>	<b>±1.25</b>
F	eilen	to hurry	3.37	3.33	14	5
F	fliehen	to flee	3.60	3.37	12	7
F	flitzen	to dash	3.10	3.21	15	7
F	flüchten	to escape	3.63	3.20	12	8
F	folgen	to follow	3.70	3.40	9	6
F	gehen	to walk	3.97	3.93	6	5
F	grätschen	to straddle	2.57	2.80	17	9
F	hasten	to rush	2.77	2.87	16	6
F	hinken	to limp	3.10	3.40	15	6
F	hocken	to squat	3.40	3.53	14	6
F	hoppeln	to lollop	2.77	2.93	17	7
F	hopsen	to skip	2.72	3.33	17	6
F	humpeln	to hobble	3.23	3.37	17	7
F	hüpfen	to hop	3.63	3.77	14	6
F	joggen	to jog	3.83	3.87	15	6

(continued on next page)

Table 1 (continued)

Condition	German	English	Frequency	Familiarity	Imageability	Letters
F	kicken	to kick	2.97	3.33	14	6
F	knien	to kneel	3.40	3.72	16	5
F	latschen	to traipse	2.80	3.13	18	8
F	laufen	to run	4.00	3.90	8	6
F	radeln	to cycle	3.57	3.70	15	6
F	rasen	to rush	3.50	3.24	13	5
F	rennen	to run	3.90	4.00	12	6
F	scharren	to scrabble	2.40	2.93	16	8
F	schleichen	to creep	3.53	3.57	14	10
F	schlendern	to saunter	3.13	3.23	14	10
F	schlittern	to slither	2.73	3.27	16	10
F	schlurfen	to scuffle	2.80	3.20	17	9
F	schreiten	to stride	2.90	2.87	14	9
F	skaten	to skate	2.97	3.47	17	6
F	springen	to jump	3.97	3.90	11	8
F	sprinten	to sprint	3.30	3.60	16	8
F	spurten	to spurt	2.67	2.97	17	7
F	stampfen	to stomp	3.10	3.30	15	8
F	stapfen	to trudge	2.93	3.00	16	7
F	stehen	to stand	3.93	3.90	6	6
F	steigen	to climb	3.60	3.33	8	7
F	steppen	to tap-dance	2.47	2.73	17	7
F	stolpern	to stumble	3.60	3.67	14	8
F	strampeln	to struggle	3.07	3.40	16	9
F	stürmen	to storm	3.23	2.93	12	7
F	tänzeln	to prance	2.83	3.03	17	7
F	torkeln	to stagger	2.70	3.43	17	7
F	trampeln	to trample	3.17	3.47	16	8
F	treten	to kick	3.87	3.77	9	6
F	trotten	to trot	2.47	2.87	16	7
F	wandern	to hike	3.73	3.90	12	7
F	watscheln	to waddle	2.47	2.87	17	9
F	wippen	to seesaw	3	3.23	16	6
<b>F</b>	<b>Mean</b>		<b>3.21</b>	<b>3.36</b>	<b>14.21</b>	<b>7.08</b>
<b>F</b>	<b>±SD</b>		<b>±0.47</b>	<b>±0.35</b>	<b>±3.05</b>	<b>±1.35</b>
N	achten	to respect	3.33	2.07	10	6
N	ähneln	to resemble	3.47	2.03	13	6
N	ahnen	to suspect	3.27	2.20	12	5
N	angsten	to fear	2.70	2.20	12	6
N	bessern	to improve	3.17	1.93	14	7
N	büffeln	to swot	3.00	2.86	16	7
N	bürgen	to vouch	2.67	1.80	16	6
N	büßen	to atone	2.73	1.70	14	5
N	denken	to think	3.93	2.47	9	6
N	dulden	to tolerate	3.10	2.23	13	6
N	ehren	to honour	3.20	2.27	13	5
N	eignen	to suit	3.17	1.73	13	6
N	folgern	to conclude	3.47	2.10	15	7
N	fügen	to comply	2.80	1.67	13	5
N	glauben	to believe	3.90	2.17	9	7
N	gönnen	to grant	3.43	2.10	12	6
N	grämen	to grieve	2.03	1.87	16	6
N	grübeln	to brood	3.37	2.50	15	7
N	hadern	to quarrel with	2.47	1.83	15	6
N	hassen	to hate	3.77	2.47	14	6
N	herrschen	to govern	3.37	2.57	12	9
N	hoffen	to hope	3.87	2.20	9	6
N	irren	to err	3.37	2.17	14	5
N	meinen	to mean	3.87	2.17	8	6
N	meistern	to master	3.13	1.80	12	8
N	merken	to notice	3.90	2.20	11	6
N	mogeln	to cheat	3.27	2.30	17	6
N	mögen	to like	3.97	2.41	10	5
N	plagen	to afflict	2.93	2.10	13	6
N	planen	to plan	3.83	2.47	10	6
N	raten	to guess	3.73	2.31	11	5
N	schätzen	to estimate	3.70	2.17	10	8
N	schulden	to owe	3.37	1.90	15	8
N	schummeln	to cheat	3.27	2.50	17	9
N	sehnen	to yearn	3.07	2.23	14	6
N	sinnen	to ponder	2.17	1.70	17	6
N	streben	to aspire	3.27	2.23	12	7
N	täuschen	to fool	3.50	2.20	13	8
N	trauen	to trust	3.53	2.20	11	6

Table 1 (continued)

Condition	German	English	Frequency	Familiarity	Imageability	Letters
N	träumen	to dream	3.80	3.00	11	7
N	trotzen	to defy	2.90	2.10	14	7
N	wagen	to dare	3.37	2.00	11	5
N	werten	to assess	3.20	1.90	12	6
N	wissen	to know	3.90	2.27	7	6
N	wundern	to marvel	3.80	2.43	12	7
N	wünschen	to wish	3.90	2.30	10	8
N	zaudern	to tarry	1.97	1.77	17	7
N	zweifeln	to doubt	3.77	2.47	12	8
N	<b>Mean</b>		<b>3.31</b>	<b>2.17</b>	<b>12.63</b>	<b>6.42</b>
N	<b>±SD</b>		<b>±0.50</b>	<b>±0.29</b>	<b>±2.48</b>	<b>±1.05</b>

## References

- Aravena, P., Delevoeye-Turrell, Y., Deprez, V., Cheylus, A., Paulignan, Y., Frak, V., et al. (2012). Grip force reveals the context sensitivity of language-induced motor activity during "action words" processing: Evidence from sentential negation. *PLoS One*, 7, e50287.
- Aziz-Zadeh, L., & Damasio, A. (2008). Embodied semantics for actions: Findings from functional brain imaging. *Journal of Physiology Paris*, 102, 35–39.
- Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology*, 16, 1818–1823.
- Bak, T. H., O'Donovan, D. G., Xuereb, J. H., Boniface, S., & Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease-dementia-aphasia syndrome. *Brain*, 124, 103–120.
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review Psychology*, 59, 617–645.
- Barsalou, L. W., Santos, A., Simmons, W. K., & Wilson, C. D. (2008). Language and simulation in conceptual processing. In M. d. Vega, A. Glenberg, & A. Graesser (Eds.), *Symbols and embodiment debates on meaning and cognition* (pp. 245–284). Oxford University Press.
- Biemann, C., Heyer, G., Quasthoff, U., & Richter, M. (2007). The Leipzig Corpora Collection – Monolingual corpora of standard size. In *Proceedings of corpus linguistics 2007*. Birmingham, UK.
- Biermann-Ruben, K., Miller, A., Franzkowiak, S., Finis, J., Pollok, B., Wach, C., et al. (2012). Increased sensory feedback in Tourette syndrome. *Neuroimage*, 63, 119–125.
- Binder, J. R., Westbury, C. F., McKiernan, K. A., Possing, E. T., & Medler, D. A. (2005). Distinct brain systems for processing concrete and abstract concepts. *Journal of Cognitive Neuroscience*, 17, 905–917.
- Boulenger, V., Hauk, O., & Pulvermüller, F. (2009). Grasping ideas with the motor system: Semantic somatotopy in idiom comprehension. *Cerebral Cortex*, 19, 1905–1914.
- Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M., & Nazir, T. A. (2006). Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *Journal of Cognitive Neuroscience*, 18, 1607–1615.
- Boulenger, V., Shtyrov, Y., & Pulvermüller, F. (2012). When do you grasp the idea? MEG evidence for instantaneous idiom understanding. *Neuroimage*, 59, 3502–3513.
- Boulenger, V., Silber, B. Y., Roy, A. C., Paulignan, Y., Jeannerod, M., & Nazir, T. A. (2008). Subliminal display of action words interferes with motor planning: A combined EEG and kinematic study. *Journal of Physiology Paris*, 102, 130–136.
- Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Brain Research, Cognitive Brain Research*, 24, 355–363.
- Carota, F., Moseley, R., & Pulvermüller, F. (2012). Body-part-specific representations of semantic noun categories. *Journal of Cognitive Neuroscience*, 24, 1492–1509.
- Cheyne, D., & Weinberg, H. (1989). Neuromagnetic fields accompanying unilateral finger movements: Pre-movement and movement-evoked fields. *Experimental Brain Research*, 78, 604–612.
- van Dam, W. O., Rüschmeyer, S. A., & Bekkering, H. (2010). How specifically are action verbs represented in the neural motor system: An fMRI study. *Neuroimage*, 53, 1318–1325.
- Desai, R. H., Binder, J. R., Conant, L. L., & Seidenberg, M. S. (2010). Activation of sensory-motor areas in sentence comprehension. *Cerebral Cortex*, 20, 468–478.
- D'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. J., et al. (1997). A functional MRI study of mental image generation. *Neuropsychologia*, 35, 725–730.
- Ehrenstein, W. H., & Arnold-Schulz-Gahmen, B. E. (1997). Auge, Ohr, Hand und Fuß: Bestimmung des individuellen Lateralitätsprofils. Dortmund: Institut für Arbeitsforschung.
- Endo, H., Kato, Y., Kizuka, T., Masuda, T., & Takeda, T. (2004). Bilateral cerebral activity for unilateral foot movement revealed by whole-head magnetoencephalography. *Somatosensory Motor Research*, 21, 33–43.
- Fernandino, L., Conant, L. L., Binder, J. R., Blindauer, K., Hiner, B., Spangler, K., et al. (2012). Parkinson's disease disrupts both automatic and controlled processing of action verbs. *Brain and Language*, 51, 1510–1517.
- Friederici, A. D., Opitz, B., & Cramon, D. Y. v. (2000). Segregating semantic and syntactic aspects of processing in the human brain: An fMRI investigation of different word types. *Cerebral Cortex*, 10, 698–705.
- Gallese, V. (2008). Mirror neurons and the social nature of language: The neural exploitation hypothesis. *Society for Neuroscience*, 3, 317–333.
- Gallese, V., & Lakoff, G. (2005). The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology*, 22, 455–479.
- Glover, S., Rosenbaum, D. A., Graham, J., & Dixon, P. (2004). Grasping the meaning of words. *Experimental Brain Research*, 154, 103–108.
- Hämäläinen, M., Hari, R., Ilmoniemi, R., Knuutila, J., & Lounasmaa, O. (1993). Magnetoencephalography – Theory, instrumentation, and applications to noninvasive studies of the working human brain. *Reviews of Modern Physics*, 65, 413–497.
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41, 301–307.
- Hauk, O., & Pulvermüller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping*, 21, 191–201.
- Hauk, O., & Pulvermüller, F. (2011). The lateralization of motor cortex activation to action-words. *Frontiers in Human Neuroscience*, 5, 149.
- Herrera, E., Rodríguez-Ferreiro, J., & Cuetos, F. (2012). The effect of motion content in action naming by Parkinson's disease patients. *Cortex*, 48, 900–904.
- Kemmerer, D., Castillo, J. G., Talavage, T., Patterson, S., & Wiley, C. (2008). Neuroanatomical distribution of five semantic components of verbs: Evidence from fMRI. *Brain and Language*, 107, 16–43.
- Kemmerer, D., & Gonzalez-Castillo, J. (2010). The Two-Level Theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system. *Brain and Language*, 112, 54–76.
- Kemmerer, D., Miller, L., Macpherson, M. K., Huber, J., & Tranel, D. (2013). An investigation of semantic similarity judgments about action and non-action verbs in Parkinson's disease: Implications for the Embodied Cognition Framework. *Frontiers in Human Neuroscience*, 7, 146.
- Kousta, S.-T., Vigliocco, G., Vinson, D. P., Andrews, M., & Del Campo, E. (2011). The representation of abstract words: Why emotion matters. *Journal of Experimental Psychology – General*, 140, 14–34.
- Kristeva, R., Cheyne, D., & Deecke, L. (1991). Neuromagnetic fields accompanying unilateral and bilateral voluntary movements: Topography and analysis of cortical sources. *Electroencephalography and Clinical Neurophysiology*, 81, 284–298.
- Kristeva-Feige, R., Walter, H., Lütkenhöner, B., Hampson, S., Ross, B., Knorr, U., et al. (1994). A neuromagnetic study of the functional organization of the sensorimotor cortex. *European Journal of Neuroscience*, 6, 632–639.
- Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, 379, 649–652.
- Moseley, R., Carota, F., Hauk, O., Mohr, B., & Pulvermüller, F. (2012). A role for the motor system in binding abstract emotional meaning. *Cerebral Cortex*, 22, 1634–1647.
- Nazir, T. A., Boulenger, V., Roy, A., Silber, B., Jeannerod, M., & Paulignan, Y. (2008). Language-induced motor perturbations during the execution of a reaching movement. *Quarterly Journal of Experimental Psychology (Hove)*, 61, 933–943.
- Oishi, M., Kameyama, S., Fukuda, M., Tsuchiya, K., & Kondo, T. (2004). Cortical activation in area 3b related to finger movement: An MEG study. *Neuroreport*, 15, 57–62.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9, 97–113.
- Postle, N., Ashton, R., McFarland, K., & Zubicaray, G. I. d. (2013). No specific role for the manual motor system in processing the meanings of words related to the hand. *Frontiers in Human Neuroscience*, 7, 11.
- Postle, N., McMahon, K. L., Ashton, R., Meredith, M., & Zubicaray, G. I. d. (2008). Action word meaning representations in cytoarchitecturally defined primary and premotor cortices. *Neuroimage*, 43, 634–644.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6, 576–582.

- Pulvermüller, F., Härle, M., & Hummel, F. (2000). Neurophysiological distinction of verb categories. *Neuroreport*, 11, 2789–2793.
- Pulvermüller, F., Härle, M., & Hummel, F. (2001). Walking or talking? Behavioral and neurophysiological correlates of action verb processing. *Brain and Language*, 78, 143–168.
- Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005a). Functional links between motor and language systems. *European Journal of Neuroscience*, 21, 793–797.
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005b). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, 17, 884–892.
- Repetto, C., Colombo, B., Cipresso, P., & Riva, G. (2013). The effects of rTMS over the primary motor cortex: The link between action and language. *Neuropsychologia*, 51, 8–13.
- Rodríguez-Ferreiro, J., Gennari, S. P., Davies, R., & Cuetos, F. (2011). Neural correlates of abstract verb processing. *Journal of Cognitive Neuroscience*, 23, 106–118.
- Rüschmeyer, S.-A., Brass, M., & Friederici, A. D. (2007). Comprehending prehending: Neural correlates of processing verbs with motor stems. *Journal of Cognitive Neuroscience*, 19, 855–865.
- Rüschmeyer, S.-A., Lindemann, O., van Elk, M., & Bekkering, H. (2009). Embodied cognition: The interplay between automatic resonance and selection-for-action mechanisms. *European Journal of Social Psychology*, 39, 1180–1187.
- Salmelin, R., Schnitzler, A., Schmitz, F., & Freund, H. J. (2000). Single word reading in developmental stutterers and fluent speakers. *Brain*, 123(Pt 6), 1184–1202.
- Schuil, K. D. I., Smits, M., & Zwaan, R. A. (2013). Sentential context modulates the involvement of the motor cortex in action language processing: An fMRI study. *Frontiers in Human Neuroscience*, 7, 100.
- Shebani, Z., & Pulvermüller, F. (2013). Moving the hands and feet specifically impairs working memory for arm- and leg-related action words. *Cortex*, 49, 222–231.
- Shtyrov, Y., Hauk, O., & Pulvermüller, F. (2004). Distributed neuronal networks for encoding category-specific semantic information: The mismatch negativity to action words. *European Journal of Neuroscience*, 19, 1083–1092.
- Simmons, W. K., Hamann, S. B., Harenski, C. L., Hu, X. P., & Barsalou, L. W. (2008). fMRI evidence for word association and situated simulation in conceptual processing. *Journal of Physiology Paris*, 102, 106–119.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, 17, 273–281.
- Tomasino, B., Weiss, P. H., & Fink, G. R. (2010). To move or not to move: Imperatives modulate action-related verb processing in the motor system. *Neuroscience*, 169, 246–258.
- Uusitalo, M. A., & Ilmoniemi, R. J. (1997). Signal-space projection method for separating MEG or EEG into components. *Medical and Biological Engineering and Computing*, 35, 135–140.
- Vigliocco, G., Kousta, S.-T., Della Rosa, P. A., Vinson, D. P., Tettamanti, M., Devlin, J. T., et al. (2013). The neural representation of abstract words: The role of emotion. *Cerebral Cortex*. epub ahead of print, <http://dx.doi.org/10.1093/cercor/bht025>.
- Willems, R. M., Hagoort, P., & Casasanto, D. (2010a). Body-specific representations of action verbs: Neural evidence from right- and left-handers. *Psychological Science*, 21, 67–74.
- Willems, R. M., Toni, I., Hagoort, P., & Casasanto, D. (2010b). Neural dissociations between action verb understanding and motor imagery. *Journal of Cognitive Neuroscience*, 22, 2387–2400.
- Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: Motor resonance in language comprehension. *Journal of Experimental Psychology – General*, 135, 1–11.