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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.

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 (Rüschemeyer, 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, & Zubicaray, 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 (Rüschemeyer 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; Rüschemeyer 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 (Willems, 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 seperated 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