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Embodied semantics:
a neurophysiological perspective

Habilitationsschrift

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Vorgelegt von

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I. Zusammenfassung

Die in dieser Arbeit ausgewählten und berichteten Forschungsartikel befassen sich mit den neurophysiologischen Korrelaten der Konzeptrepräsentation und liefern Hinweise für den theoretischen Rahmen der verkörperten Kognition (*embodiment*). Demnach ist die Konzeptverarbeitung modalitätsspezifisch und rekrutiert sowohl motorische als auch sensorische kortikale Areale. Sensomotorische und auditive Hirnareale wurden in diesen Studien mit Neuroimaging-, Verhaltens- und Neuromodulationsmethoden gezielt untersucht. Insbesondere wurden neuronale Oszillationen, ereigniskorrelierte Felder und Aktivierungsquellen mit Hilfe der Magnetenzephalographie (MEG) untersucht, während einsprachige gesunde deutsche Studienteilnehmer Tätigkeitsverben verarbeiteten. Außerdem wurde die modulierende Rolle einer internen versus einer externen Perspektive auf die Aktion und die damit verbundene kortikale Rekrutierung untersucht. Die Automatizität der *embodied* Semantik und die Rolle der semantischen Verarbeitungstiefe wurden mit Hilfe eines Verhaltensparadigmas und transkranieller Gleichstromstimulation (tDCS) schlussendlich erforscht.

Die MEG-Studien zeigten eine somatotopische spezifische Aktivierung kortikaler motorischer Areale während der Verbverarbeitung in Abhängigkeit von dem durch das Aktionsverb dargestellten Körperteil. Die Ergebnisse der Verhaltens- und der tDCS-Studie wiesen auf eine Modulation dieser selektiven Rekrutierung von somatotopisch umschriebenen kortikalen Arealen durch die Tiefe der semantischen Verarbeitung hin. In Bezug auf die sensorische Modalität zeigte sich, dass der auditorische Kortex von der Relevanz akustischer Merkmale der von den Verben beschriebenen Aktionen beeinflusst wird. Schließlich wurde eine Sensibilität bestimmter Hirnareale für die/den Akteur:in einer durch Pronom-Verb-Paare ausgedrückten Handlung festgestellt. Insgesamt erwiesen sich neuronale Oszillationen in einem abgegrenzten Frequenzbereich als potenzielle neurophysiologische Marker für die kortikale Rekrutierung bei *embodied* Semantik.

Insgesamt deuten diese Befunde auf eine Beteiligung des motorischen und sensorischen Kortex an der Sprachverarbeitung hin. Die Ergebnisse zeigen außerdem eine Kontextabhängigkeit dieser Aktivierung sowohl von der Tiefe der semantischen Verarbeitung wie auch von der Perspektivenübernahme.

II.   Summary

The research articles selected and reported in this thesis deal with the neurophysiological correlates of concept representation and offer evidence for the theoretical framework of embodied cognition. According to this, concept processing is modality specific and recruits motor as well as sensory cortical areas. Sensorimotor and auditory brain areas were targeted in these studies using neuroimaging, behavioral, and neuromodulation methods. In particular, neuronal oscillations, event-related fields, and source of activation were inspected using magnetoencephalography (MEG) while German monolingual healthy participants processed action verbs. Further, the modulatory role of an internal versus external perspective on the action and the related cortical recruitment were addressed. The automaticity of embodied semantics and the role of semantic processing depth were finally inspected by means of a behavioral paradigm and transcranial direct current stimulation (tDCS).

The MEG studies revealed somatotopical specific engagement of cortical motor areas depending on the body-part involved in the action described by the verb. Findings of the behavioral and the tDCS study provided further evidence for the modulation of the selective recruitment of somatotopically circumscribed cortical motor areas by the depth of meaning processing. As for the sensory domain, activation of the auditory cortex was shown to be affected by the relevance of acoustic features of the action described by the verb. Moreover, specific brain areas were identified, that are sensitive to the agent of an action as expressed by pronoun-verb pairs. Overall, neuronal oscillations in a delimited frequency range emerged as potential neurophysiological marker of cortical recruitment accompanying embodied semantics.

Altogether, these findings point to the engagement of the motor and sensory cortex in language processing as well as to a context-dependence of this activation on action agency and on the depth of semantic processing.

III.   List of selected research articles

1. **Niccolai, V.**, Klepp, A., Weissler, H., Hoogenboom, N., Schnitzler, A., & Biermann-Ruben, K. (2014). Grasping hand verbs: Oscillatory beta and alpha correlates of action-word processing. *PloS One*, *9*(9), e108059. https://doi.org/10.1371/journal.pone.0108059

2. Klepp, A., Weissler, H., **Niccolai, V.**, Terhalle, A., Geisler, H., Schnitzler, A., & Biermann-Ruben, K. (2014). Neuromagnetic hand and foot motor sources recruited during action verb processing. *Brain and Language*, *128*(1), 41–52. https://doi.org/10.1016/j.bandl.2013.12.001

3. **Niccolai, V.**, Klepp, A., van Dijk, H., Schnitzler, A., & Biermann-Ruben, K. (2020). Auditory cortex sensitivity to the loudness attribute of verbs. *Brain and Language*, *202*, 104726. https://doi.org/10.1016/j.bandl.2019.104726

4. Röders, D., Klepp, A., Schnitzler, A., Biermann-Ruben, K., & **Niccolai, V**. (2022). Induced and Evoked Brain Activation Related to the Processing of Onomatopoetic Verbs. *Brain Sciences*, *12*(4). https://doi.org/10.3390/brainsci12040481

5. **Niccolai, V.**, Klepp, A., Schnitzler, A., & Biermann-Ruben, K. (2021). Neurophysiological mechanisms of perspective-taking: An MEG investigation of agency. *Social Neuroscience*, *16*(5), 584–593. https://doi.org/10.1080/17470919.2021.1974546

6. Klepp, A., **Niccolai, V.**, Sieksmeyer, J., Arnzen, S., Indefrey, P., Schnitzler, A., & Biermann-Ruben, K. (2017). Body-part specific interactions of action verb processing with motor behaviour. *Behavioural Brain Research*, *328*, 149–158. https://doi.org/10.1016/j.bbr.2017.04.002

7. **Niccolai, V.**, Klepp, A., Indefrey, P., Schnitzler, A., & Biermann-Ruben, K. (2017). Semantic discrimination impacts tDCS modulation of verb processing. *Scientific Reports*, *7*(1), 17162. https://doi.org/10.1038/s41598-017-17326-w

1. Introduction

1.1 The embodied cognition framework

In the attempt to answer the question how concepts are represented in the brain, the embodiment framework (Barsalou, 2008) distanced itself from an earlier perspective on language processing and thereby challenged the amodal approach (Fodor, 1985). According to the latter, word meanings are abstract, amodal, and separated from the sensorimotor as well as autobiographic experience of the subject. This perspective implies that concepts are symbolic entities disconnected from the related perception. The embodied perspective reestablished a link between the symbolic and the perceptually founded meaning of words. The turning point was the postulation that sensory, motor, and emotion neural systems are not only responsible for perception and motor processes, but they are also engaged by language understanding. Using Glenberg`s words (Glenberg, 2015), "our thoughts are based on bodily experiences, and our thoughts and behaviors are controlled by bodily and neural systems of perception, action, and emotion interacting with the physical and social environments". This was proposed to apply to any form of cognition independently from the concrete or abstract content of words and thoughts. The embodied approach thus upgraded and expanded the role of the body in linguistic representations, pointing to the implicit experiential aspects of words. *Simulation* of the content addressed by language, be it action, perception or emotion, was intended as a context-dependent reuse of sensorimotor processes (Barsalou, 1999; Ostarek & Bottini, 2021). The particular category of abstract concepts was proposed to be grounded in complex simulations of combined physical and introspective events: the differences between concrete and abstract word meanings was associated to the proportion and exact type of experiential and linguistic information from which they are derived (Meteyard et al., 2012). Here, the internal experience, also in form of affective associations, was suggested to play a critical role in learning abstract words. While a continuum from strongly embodied ("full simulation") to unembodied ("fully symbolic") theories exist (Meteyard et al., 2012), I will refer here to the embodied cognition framework as an umbrella term.

The neurophysiological mechanisms that enable embodied semantics were suggested to be mirror neurons and Hebbian association mechanisms. Mirror neurons, defined as a particular class of visuo-motor neurons, were originally localized in a portion of the ventral premotor cortex of monkeys and were found to be active both during movement execution and action observation (Rizzolatti et al., 2001). Mirror neurons were also suggested to inhibit the execution of a movement during action observation (Glenberg & Gallese, 2012). In the field of language understanding, this was interpreted as an action being understandable when its observation causes the motor system of the observer to „resonate". Some critic has however been advanced: although the existence of mirror neurons in

humans was suggested by studies based on single-cell recording (Mukamel et al., 2010) and on cytoarchitectonic homologies between the premotor cortex of monkeys and the Broca area (Glenberg & Gallese, 2012), their localization in the human brain is still not clear. Moreover, the exact link between mirror neurons and language processing has not been determined yet, thus leaving the question on the related mechanisms unanswered.

Hebbian mechanisms (Hebb, 1949) were suggested to enable embodied meaning representations in that frequent co-activation of neurons leads to formation of strongly connected neuron ensembles that implement associative memory (Pulvermüller, 1999). In the case of action words, which frequently occur with movements, this neural connection might relay on the co-activation of perisylvian cortices and motor areas in the frontal lobe; the latter would be activated accordingly to the somatotopical distribution of motor areas (Figure 1). The simultaneously active neurons belonging to a network would for example link the word´s sensory perception (temporal cortex) with the related articulatory program (inferior-frontal cortex) as well as a sensory or motor reference depending on the word category (Shtyrov et al., 2014). A neurocomputational attempt was done to model the cortical function based on Hebbian learning and simulate the time-line of linguistic understanding (Tomasello et al., 2017).
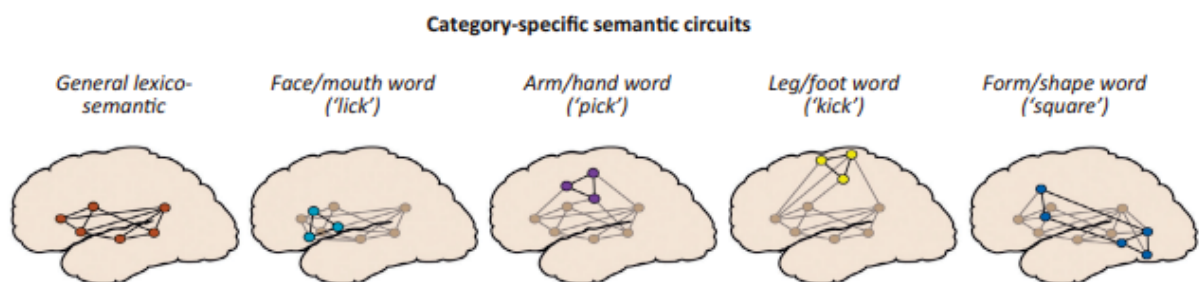
Figure 1. Model of general lexico-semantic circuits and referential-semantic circuits for four different semantic word types, as indicated above. Figure adapted and reproduced from Pulvermüller (2013), distributed under Creative Commons Attribution-NonCommercial-No Derivatives License (CC BY NC ND).

It is worth noting that while studies on embodiment in language have mainly addressed the processing of nouns (e.g., Carota et al., 2012) and verbs (for a review see Fischer & Zwaan, 2008), also pronouns (Brilmayer et al., 2019), adjectives (Gough et al., 2013), and adverbs (Sieksmeyer et al., 2021) have been shown to modulate sensorimotor cortical activation. In the following sections, I will concentrate on the embodiment of verbs, as this was the focus of my selected studies.

1.2 Behavioral evidence for *sensorimotor* embodied semantics

Behavioral experiments tackling embodiment in language processing show that motor resonance occurs during exposure to action-related words, these being nouns, verbs or adjectives (Fischer & Zwaan, 2008). Specifically, behavioral measures of verbal-motor interaction such as priming (facilitation) and interference effects consistently hint at shared brain resources between linguistic and motor processes (for a review see Garcia & Ibanez, 2016). The processing of hand-related action verbs for example was shown to affect the concurrent manual action (Boulenger et al., 2006; Dalla Volta et al., 2009; Nazir et al., 2008; Sato et al., 2008). Thereby, earlier or later delivery of the prompt affected the result of faster hand responses for hand- than for foot-related verbs. The stimulus-response delay, in particular the timing of the semantic decision task, abolished the priming effect (Garcia & Ibanez, 2016). Beyond the time lag between linguistic and motor processes, also the level of verbal processing as required by the task revealed to be crucial. Lexical versus semantic processing of words may differently affect the outcome of verbal-motor interaction. For lexical tasks a more superficial understanding of the word may suffice: typically, the participant is asked to distinguish between a word and a pseudoword (i.e., detection of erroneous letters), thus making unnecessary the processing of the meaning as it is the case for semantic tasks. Task requirement may thus play an important role in the amount or quality of action-related simulation and may modulate the engagement of cortical areas. This aspect is further discussed in section 1.6 at the light of literature evidence.

Another interesting effect supporting the link between verb processing and motor simulation is the Action-Sentence-Compatibility Effect (ACE). One version of the paradigm related to the ACE consists in the presentation of words that refer to an action with a specific direction (e.g., forward, like in "close the drawer"). When the movement required for responses is congruent with this body-related direction (e.g., the participant presses the button that is further away from him/her), reaction times are faster than when the direction described by the verb and that one of the movement are incongruent (Glenberg & Kaschak, 2002). The ACE effect was interpreted as an indicator of the fact that action simulation automatically accompanies linguistic verbal processing and that linguistic understanding may rely on this simulation process. Further, some kinematic variables such as movement force seem to modulate motor responses relatively to the content of linguistic stimuli (Buccino et al., 2005). These findings point to a conjunct function of cortical motor areas: on the one hand, the execution of motor processes and on the other hand the analysis of verbal content based on an implicit simulation of the related action.

1.3 Neural evidence for *sensorimotor* embodied semantics

Beyond or complementary to the behavioral approach, efforts have been also made to identify distinct neural correlates of sensorimotor simulation during the processing of body-related action verbs using neuroimaging and electrophysiological techniques. In the following sections, I address findings concerning concept representation emerging from different methodological approaches and I thereby introduce the techniques applied in my studies.

1.3.1. Neuroanatomical signatures

Through a localization approach it has been possible to determine which cortical areas are engaged by word processing beyond the core temporal language areas. Several studies targeted the sensorimotor cortex as a main area recruited while accessing the meaning of specific linguistic material. Functional magnetic resonance imaging (fMRI) studies showed that effector-specific cortical premotor and primary motor regions were for example activated by words or sentences referring to actions performed with different body parts (Aziz-Zadeh et al., 2006; Boulenger et al., 2009; Ge et al., 2018; Hauk et al., 2004; Hauk & Pulvermüller, 2004; Kemmerer et al., 2008; Rüschemeyer et al., 2007; Tettamanti et al., 2005; but see Postle et al., 2008). Beyond the motor components also sensory aspects of actions were shown to be embodied (see Binder & Desai, 2011 for a review); Figure 2).
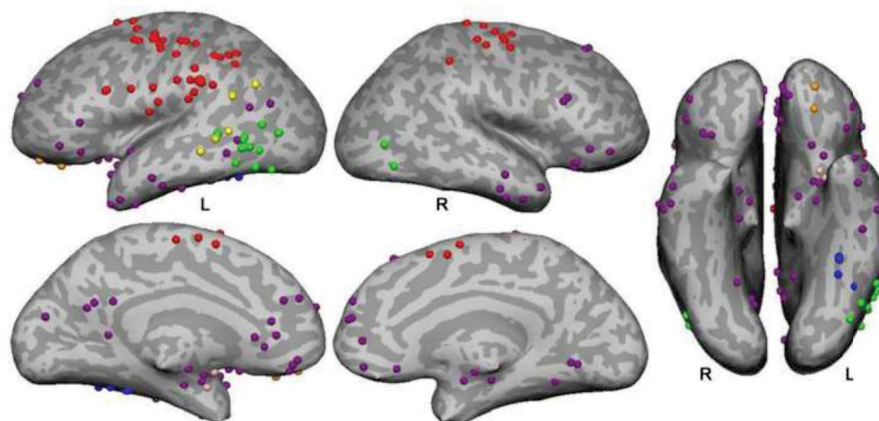

Figure 2. Modality-specific activation peaks during language comprehension: sites of peak activation from 38 imaging studies that examined modality-specific knowledge processing during language comprehension tasks. Peaks were mapped to a common spatial coordinate system and then to a representative brain surface. Red= primary and secondary sensorimotor regions in the posterior frontal and anterior parietal lobes; green= motion area in posterior inferolateral temporal regions; yellow= auditory area in superior temporal and temporoparietal regions; blue = color area in the fusiform gyrus; pink= olfactory areas (prepiriform cortex and amygdala); orange = gustatory area in the anterior orbital frontal cortex; purple = area involved in emotion, anterior temporal, medial and orbital prefrontal, and posterior cingulate regions. Figure from Binder & Desai (2011), reproduced with permission from Elsevier and Copyright Clearance Center.

For example, words referring to auditory experiences like "telephone" were shown to induce stronger activation in the auditory cortex compared to words denoting visual features like "moon" (Kiefer et al., 2008). Also the comprehension of concepts based on multimodal-based experiences like "playing" appears to be supported by different modality-specific networks (i.e., visual and action-related; van Dam et al., 2012).

1.3.2 Electrophysiological signatures

Another methodological approach also used in the field of embodied cognition consists in targeting electrophysiological activation patterns detected with electroencephalography (EEG) or magnetoencephalography (MEG). While EEG is sensitive to the neural current across radially oriented bands of synchronously activated pyramidal cells, MEG detects the magnetic field of tangentially oriented currents. In the following sections, I first introduce the functioning of MEG, which I applied in study 1 to 5 and then concentrate on the two different patterns of activation targeted in my studies: event-related fields (the magnetic equivalent of event-related potentials) and brain oscillations. I finally present evidence for these neurophysiological patterns of activation within the framework of embodied semantics.

1.3.2.1. Magnetoencephalography (MEG)

MEG is a non-invasive method that allows investigating brain electrophysiology and imaging. This is accomplished through the measurement of the magnetic field produced by the electrochemical current flows within and between neurons. Since the magnetic field is orthogonal to the electric field, the MEG signal is the product of particularly oriented bands of aligned neurons, whose orientation enable the magnetic field to reach the MEG sensors. MEG has a sub-millisecond temporal resolution and a spatial resolution of few millimeters. An important advantage of MEG compared to EEG is the fact the magnetic signal is not distorted by the different lays of head tissues or by the air between the scalp and the sensors. This implies not only a better signal to noise ratio, but also a better localization of brain sources as the signal is less smeared; for this reason, the MEG approach is particularly suitable for source localization. The frequency band measured with MEG is between 0,5 and 1.000 Hz, whereby the 1-80 Hz range is the most investigated. Since the magnetic signal that can be measures by MEG is on the scale of femtotesla (fT, 10^{-15} T), very sensitive sensors such as the superconducting quantum interference devices (SQUIDs) are needed. The MEG instrumentation used in my studies is the 306-Channels Neuromag system (Elekta, Finnland), which has two different kinds of sensors: while the magnetometer sensor type can be sensitive to sources that are far from the

subjects as well as deeper in the subject's head, gradiometers are sensitive to magnetic fields originating in the head surface. The sensors are located in a helm where the head of the study participant is positioned. The superconducting temperatures, that allow a high signal quality, are enabled by the presence of helium inside a thermally insulated tank in the helm. Differently from EEG, the signal is not referenced to one or more channels and is thus an absolute physical quantity. Due to the high sensitivity of MEG sensors, also moving metal objects or electrical instruments that are not next to the MEG system can interfere with the brain signal because of their magnetic field. To improve the signal, measurements are conducted in a magnetically shielded room. The non-neural noise like heartbeat and muscle activity, which can also be detected by MEG, is semi-automatically identified and corrected during the data pre-processing. Another advantage of MEG compared to EEG is the easier and faster preparation of the participant, as time for mounting electrodes is spared.

1.3.2.2. Event-related potentials/fields (ERPs/ERFs)

The time course and the magnitude of sensory and cognitive processes can be determined by means of event-related potentials or fields. These reflect the processing of the stimulus in the brain and are calculated by averaging trials, which are epochs containing the stimulus repeated across time. ERPs are denoted by both the polarity (positive, negative) and the latency (in ms). Since the amplitude of these components may be modulated by a task, interference or priming effects may become visible through an amplitude decrease or increase. There are a number of components that have been related to different processes such as the sensory (e.g., N100, N170) and the semantic ones (e.g., P300, N400). An early component typically related to the processing of an auditory stimulus is the N100, the amplitude of which may be modulated by the source of the sound: hearing a sound produced by pressing a button elicits a smaller N400 than when the sound is externally produced (Bendixen et al., 2012).

Within the embodied language framework, electrophysiological activation of sensorimotor areas was mainly addressed using stimuli such as single verbs or verbs within sentences (e.g., Dalla Volta et al., 2014; Hauk & Pulvermüller, 2004). Results showed components that emerged already at about 80 till 350 ms (Boulenger et al., 2012; Pulvermüller et al., 2005; Shtyrov et al., 2004; Shtyrov et al., 2014) and partly automatic (independent from attention) semantic effects (Grisoni et al., 2016; Shtyrov et al., 2014). Using interference/priming paradigms, action-related words were shown to induce larger ERPs when presented in body-part-incongruent sound contexts (e.g., "kiss" in footstep sound context) than in body-part-congruent contexts (e.g., "kick" in footstep sound context; Grisoni et al., 2016). In another study, finger button press prior to the presentation of an arm-related word (e.g., "stir") resulted in reduced brain activity in the hand-related motor cortex compared to the incongruent condition (e.g., "jump"); the observed effect latency of 150 ms hinted again at early

semantic information retrieval (Mollo et al., 2016). Overall, results from electrophysiological investigations point to relatively early effects of verb processing in sensorimotor areas and to modulatory effects of motor priming or interference on sensorimotor cortical activation accompanying word processing.

1.3.2.3. Brain oscillations

Brain oscillations are denoted by a rhythmic pattern of activity that can range between low and high frequencies. The acknowledged frequency ranges are the following: delta (0,5-3,5 Hz), theta (4-7 Hz), alpha (8-12 Hz), beta (13-30 Hz) and gamma (>30 Hz). This oscillatory brain activity emerges from the synchronised or desynchronised activation of a neural population. While synchronisation corresponds to an increase in signal amplitude (power), desynchronization corresponds to a power decrease (Pfurtscheller & Lopes da Silva, 1999). Lower frequencies typically show larger amplitude than higher frequencies. The brain oscillatory activation reflects the amount of changes in the membrane potential of a group of cells; although independent from spike activity, the modulation of the membrane potential may still influence spike probability. The oscillatory activity is not necessarily phase-locked to a stimulus or a response and can be spontaneous or induced (Hansen et al., 2010): an example of the spontaneous activity can be observed in the resting state, which is accompanied by increased amplitude of posterior alpha oscillations. The different frequency bands and the related amount of activation within a recorded time-interval can be related to particular brain states. Induced activity typically follows the presentation of a stimulus or the preparation/execution of a movement; the latter is typically accompanied by alpha and beta desynchronization (Babiloni et al., 2002; Koelewijn et al., 2008). Different frequency bands can occur in the same neural network and it is possible that the same rhythms co-occur in different structures and interact (Buzsáki, 2004). While higher frequencies engage small brain regions, low frequencies involve larger networks (Buzsáki, 2004; Pfurtscheller & Lopes da Silva, 1999). Brain oscillations have been proposed to temporally coordinate the information transfer across brain regions and support plasticity (Engel & Fries, 2010).

Only few EEG (Alemanno et al., 2012; Moreno et al., 2015; van Elk et al., 2010) and electrocorticography (ECoG) investigations in the field of embodied semantics have addressed brain oscillations (Canolty et al., 2007). Studies mostly used visually or auditorily presented single action verbs as well as verbs in sentences during lexical-semantic tasks. The observed concomitant modulation of the alpha and beta frequency band was of particular interest given its emergence also during movement preparation, execution, and imagination. In the following sections, I focus on these frequency bands, which were object of my studies, and I introduce the related literature evidence in the field of embodiment.

The oscillatory activity in the alpha range (8-12 Hz) during rest was originally described by Hans Berger (1929): its amplitude was enhanced occipitally when participants closed their eyes. However, the alpha frequency has been related also to other brain states such as illusory perception (Lange et al., 2014), visual discrimination ability (van Dijk et al., 2008), and movement preparation/execution as so-called mu-rhythm. The functional distinction between the mu (8-13 Hz) and the overlapping alpha rhythm is still matter of discussion (Hobson & Bishop, 2016): it has been proposed that sensorimotor alpha oscillations differ from the alpha frequency observed in occipital areas because of the motor cortical localization of its sources (Vukovic & Shtyrov, 2014). The mu rhythm has been associated to movement observation/execution (Caetano et al., 2007; Pfurtscheller et al., 2000; Pfurtscheller & Lopes da Silva, 1999) and motor imagery (Höller et al., 2013; Mellinger et al., 2007; Neuper et al., 2009). This points to the sensitivity of the mu rhythm to cognitive processes that do not require explicit sensory input or motor execution. In the context of language processing, the mu rhythm showed power suppression during presentation of single verbs (Fargier et al., 2012) and action-related sentences (van Elk et al., 2010); interestingly, it was observed also in second language comprehension (Vukovic & Shtyrov, 2014). Stronger mu power suppression was found in left and centro-frontal leads for action versus abstract words (Alemanno et al., 2012; Moreno et al., 2013). Listening to verbal stimuli (pseudowords) that had been previously associated with movements resulted in suppression of the mu rhythm over the centro-parietal region (Fargier et al., 2012). Overall, electrophysiological studies point to an involvement of the 8-13 Hz frequency range over sensorimotor cortical areas in the formation of action representations.

The beta band has been typically related to motor functions (for a review see Cheyne, 2013). Similarly to the alpha band, the beta band shows a desynchronized pattern of activation over the premotor and primary motor cortex accompanying the preparation, initiation, and execution of a movement (Babiloni et al., 2002; Doyle et al., 2005; Koelewijn et al., 2008; Pfurtscheller & Lopes da Silva, 1999); beta power suppression was also described during imagination of a movement (Schnitzler et al., 1997). Beta desynchronization emerges during sustained (isometric) muscular contraction of different body muscles (Crone et al., 1998; Tecchio et al., 2008). Typical of movement execution is also a beta rebound (power increase) in the precentral gyrus after the end of the movement, stronger in the hemisphere contralateral to the movement (Cheyne, 2013). This was interpreted as an off-response to the termination of input to the primary motor cortex (Cassim et al., 2001) and was stronger than the alpha rebound (Hari et al., 1997). Although the hand area appears to be somewhat activated also by actions with other body-parts, mu and beta frequencies showed a somatotopic organization depending on the engaged body-part (Cheyne, 2013). Also, patterns of desynchronized beta activity in the cortical motor area were shown to correspond to neural

activation as measured with fMRI during finger movement (Formaggio et al., 2008). On the base of these findings, the beta frequency appeared especially interesting as a potential neurophysiological marker of motor-related embodiment processes.

1.4 Neural evidence for *sensory* embodied semantics

Although the sensorimotor cortical involvement has so far been mostly addressed in the field of embodied semantics, there is some evidence for embodiment processes also in sensory areas. An fMRI study investigated the simultaneous contribution of five different modalities to semantic word processing (Fernandino et al., 2016): the authors found that both early unimodal and high uni- and multimodal areas were differentially involved in the processing. This is in line with recent investigations of modality-specific recruitment, showing that neural activation for sound and action features of concepts emerged not only in the related sensory and motor regions, but also in higher-level, multimodal regions (Kuhnke et al., 2020). Metaphorical expressions concerning different human senses and including body-related actions were shown to activate related sensory and motor regions of the brain (Müller et al., 2022), thus supporting conceptual grounding. In their meta-analysis Binder and Desai (2011) showed that activations during language processing including sound, color, olfactory, gustatory or emotional content tend to show activation in or near the correspondent sensory areas. For example, odor-related terms (e.g., "cinnamon") were found to activate the primary olfactory cortex including the piriform cortex and the amygdala (González et al., 2006). Taste-related words activated the primary and secondary gustatory cortex stronger than control words (Barrós-Loscertales et al., 2012). As for the auditory sensory modality, areas belonging to the auditory cortex such as the posterior superior temporal gyrus (pSTG) and the middle temporal gyrus (MTG) were activated not only by sounds, but also by words with acoustic features (e.g., "telephone"; Kiefer et al., 2008). Altogether, findings suggest that also sensory brain areas may be recruited by semantic processing of sensory-related linguistic features.

1.5 Causality in motor embodiment

Some questions on the nature of embodied semantics have arisen, that deal with the automaticity of such processes and how far the recruitment of sensory and motor cortical areas is essential for language understanding. Critical perspectives on the embodiment framework propose that this concerns more an after-effect of conceptual understanding (Mahon & Caramazza, 2008). In particular, the motor system could be activated due to "leakage" or collateral activation taking place

at an abstract conceptual level. Sensory and motor cortical engagement would thus be a sort of spreading or parallel activation and would not play a causal role in representation of meanings. One methodological approach used to shed light on this is the investigation of patients with motor cortical related disorders or lesions: the rationale behind this is that lesion or dysfunction of the motor and premotor cortex should result in impaired processing of action-related language. In patients with Parkinson disease (PD), a degenerative disorder of the central nervous system mainly affecting the motor system, an impairment in verb naming or processing (Bak et al., 2001; Piatt et al., 1999; Rodríguez-Ferreiro et al., 2009) and a slowing of reaction times to verb stimuli with motor content were observed (Boulenger et al., 2008a; Fernandino et al., 2013). Further, investigation of a component of motor simulation such as speed implied by action verbs, showed that PD patients had longer reaction times in a semantic similarity judgement task of fast but not slow hand-related actions (Speed et al., 2017). In patients with amyotrophic lateral sclerosis, another neurodegenerative condition affecting the motor system, stronger impairment related to knowledge of actions versus objects was observed (Grossman et al., 2008), which also correlated with cortical atrophy in the motor cortex. In a recent study, patients with mild to moderate paresis after a motor stroke in the left-hemisphere showed impaired comprehension of action metaphors compared to controls (Borelli et al., 2022).

As for sensory cortical areas, an association between lesions of the left pSTG/MTG and behavioral impairment in a semantic task was observed: in particular, slower reaction time and lower accuracy emerged for visual recognition of sound-related versus -unrelated words (Trumpp et al., 2013). Further, a logopenic variant of primary progressive aphasia was found to be associated to selective difficulty in recognizing sound words compared to other modalities (Bonner & Grossman, 2012); these patients also showed gray matter atrophy in the auditory association cortex compared to healthy controls.

Altogether, findings suggest an impairment of semantic processing in patients with motor or sensory cortical related disorders or lesions. However, there are also findings from lesion studies (Arévalo et al., 2012; Weiss et al., 2016), that are contrary to the prediction of the embodied cognition theory. While patient and lesion idiosyncrasy may explain inconsistent results to some extent, it is likely that other left-hemispheric cortical areas beyond the pre-/motor and sensorimotor cortex also play a role in language understanding. The cortical recruitment for meaning representations may thus not be restricted to motor and sensory areas, these being instead part of a larger network.

Another approach aimed at determining the causal impact of motor cortical engagement in language processing and sometimes used to induce a virtual lesion is non-invasive brain stimulation. In the following section, I introduce two stimulation methods: transcranial magnetic stimulation (TMS) and

transcranial direct current stimulation (tDCS). Thereafter, I report the related findings from the research landscape concerning embodiment.

1.5.1   Non-invasive brain stimulation

TMS is applied through a magnetic stimulator consisting in a circular or eight-shaped coil of wire connected to an electrical capacitance. When the electric current flows through the coil, it produces a magnetic field perpendicularly oriented to the coil. This magnetic field induces electrical currents in any conductive structure nearby; in the case of the brain, the skull offers only low impedance to magnetic fields. The neural tissue of a cortical area can be therefore stimulated by modulating the excitability of neurons. The application of TMS can temporally disrupt perceptual, motor, and cognitive processes, an effect questionably called "virtual lesion" (Siebner et al., 2009).

Another non-invasive brain stimulation method is tDCS, which allows bidirectional stimulation of different cortical areas. When applied to the hand-related motor cortex, anodal and cathodal tDCS resulted in motor cortical excitation (depolarization of the neural cellular membrane) and inhibition (hyperpolarization), respectively (Nitsche & Paulus, 2000, 2001). The type of stimulation (anodal versus cathodal) depends on the different orientation of the electric field resulting from the electrodes position and polarity (Nitsche et al., 2008). The current flows from the cathode (the negatively charged electrode) to the anode (positively charged electrode). The current is delivered through two sponge electrodes with a variable size between 3,5 and 35 cm^2 previously immersed in a salty water solution. The use of nonmetallic, rubber electrodes inside the sponges avoids electrochemical polarization. The electrical field strength of tDCS depends on current density, which is the quotient of current strength and electrode size (Nitsche et al., 2008). The focality of tDCS depends on the size as well as the position of the electrodes on the scalp; these may however engage a larger neural population than that one targeted (Nitsche et al., 2008). Differently from TMS, tDCS does not induce neuronal action potentials and is therefore more a neuromodulatory intervention (Nitsche et al., 2008). As a consequence, anodal tDCS may exclusively induce firing of neurons that are near threshold and thus modulate their activity when they are engaged by a task (Miniussi et al., 2013). The application of tDCS is generally well tolerated because it induces an initial light itching sensation that slowly disappears. This is of advantage compared to TMS, which induces stronger cutaneous sensations, thus making easier to distinguish the *sham* (no stimulation, control condition) from the *verum* stimulation and possibly impairing study blinding.

Studies on embodiment mainly applied TMS to the hand-related motor cortex in order to detect consequences in the linguistic processing of effector-related action verbs. Results showed a

stimulation-depend modulation of reaction times and/or cortical excitability as measured with motor evoked potentials (MEPs). Inconsistent findings, however, emerged across studies in particular concerning the direction of the modulation. While some studies showed decreased MEPs and/or longer reaction times (Buccino et al., 2005; Lo Gerfo et al., 2008; Repetto et al., 2013; Scorolli et al., 2012), thus pointing to inhibited cortical motor activation, others showed increased MEPs and/or shorter reaction times (Oliveri et al., 2004; Papeo et al., 2009; Pulvermüller et al., 2005; Willems et al., 2011), which indicated cortical motor facilitation. This inconsistence possibly depended on the different stimulation settings (e.g., supra- versus sub-threshold, single-pulse versus repetitive) as well as the different linguistic tasks. While altogether results speak for cortical stimulation of the motor area affecting the understanding of action words, the issue about the causal involvement of the motor cortex remains elusive. Interestingly, the use of a semantic versus a lexical judgment task enabled the detection of an effect of TMS (Vukovic et al., 2017). This points to the likely impact of linguistic processing depth on simulation and speaks against a whole automaticity of simulation processes, an issue that I address in the following section.

1.6. Automaticity in motor embodiment

There is a broad spectrum of inconsistent findings related to the putative automaticity of simulation processes. In some studies, the language-motor interaction emerged even during subliminal processing (Boulenger et al., 2008b) and modulatory effects of motor priming or interference on cortical motor activation were found also when participants' attention was not required for the linguistic task (Grisoni et al., 2016; Shtyrov et al., 2014). In other studies, the language-motor interaction emerged only when semantic processing was necessary (Mirabella et al., 2012; Sato et al., 2008); when semantic access was irrelevant for task completion, hand-related expressions did not induce significant motor resonance (Garcia & Ibanez, 2016). In a recent study, congruency effects between body-related action verbs and body effectors showed to be larger when the task implied lexical decision versus a task in which verbs were irrelevant (Miller & Kaup, 2020); intermediate performance was achieved when the task consisted in making physical judgments. Although somewhat inconsistent, studies using metaphorical action-language suggest that this does not evoke necessarily or automatically motor cortex activation (for a review see Willems & Hagoort, 2007). Overall, findings point to the depth of processing of linguistic stimuli as a key aspect of embodied-related simulation and argue against automaticity intended as an on/off process of understanding.

2. Summary of selected research articles

2.1 Neural correlates and motor sources of action-word processing

In study 1 (Niccolai et al., 2014) the neural mechanisms of embodiment were investigated with MEG in German monolingual healthy participants while performing a lexical-semantic task. German infinitive single verbs describing hand-related actions (H; e.g., *'greifen' – 'to grasp'*) and foot-related actions (F; e.g. *'rennen' – 'to run'*) were visually presented. Verbs referring to abstract actions that did not involve any body movement were used for the control condition (N; e.g., *'planen' – 'to plan'*). Pseudo-words and filler words appeared pseudo-randomly as a prompt to which participants had to respond by moving their gaze to a target either on the left or on the right side of the screen and thus indicating whether it was an existent word. This task aimed at inducing the processing of the linguistic material and avoiding potentially confounding activation of the motor area like during button press. Study 1 attempted to determine motor-related oscillatory patterns of activation (alpha and beta frequencies) during the processing of body-related (H, F) versus non-body-related (N) verbs in motor areas. In order to localize the motor and premotor areas, a study requiring isometric contraction of the hands and of the feet was conducted separately with the same participants. On the base of the EMG signal, corticomuscolar coherence in the beta range (15-25 Hz) was determined and used to select regions of interest (Figure 3): this is a measure of functional connectivity between a contralateral effector muscle and the sensorimotor/premotor cortex (Mima & Hallett, 1999). The H-N and F-N contrasts were then examined in the hand- and foot-related regions of interest.
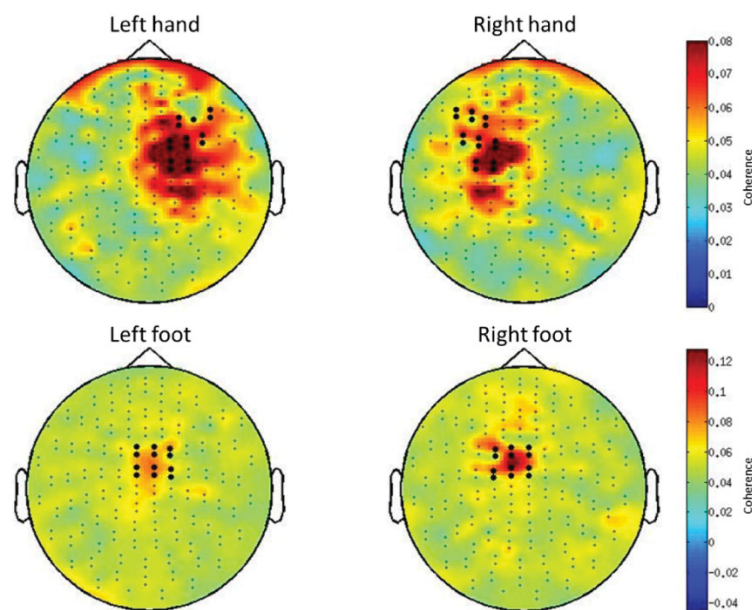

Figure 3. Localizer task: grand-average of corticomuscular coherence in the beta (15–25 Hz) range related to hands (top) and to feet (bottom) isometric contraction. Bold points represent gradiometer pairs selected for frequency analysis in the word paradigm. Figure adapted from Niccolai et al. (2014), distributed under Creative Commons Attribution License.

In the word paradigm, both the H and the F condition showed stronger beta power suppression than the N condition. While the H-N contrast showed stronger beta desynchronization in the left hemispheric selected channels, the F-N contrast showed stronger beta desynchronization in the right centrolateral selected channels (Figure 4).
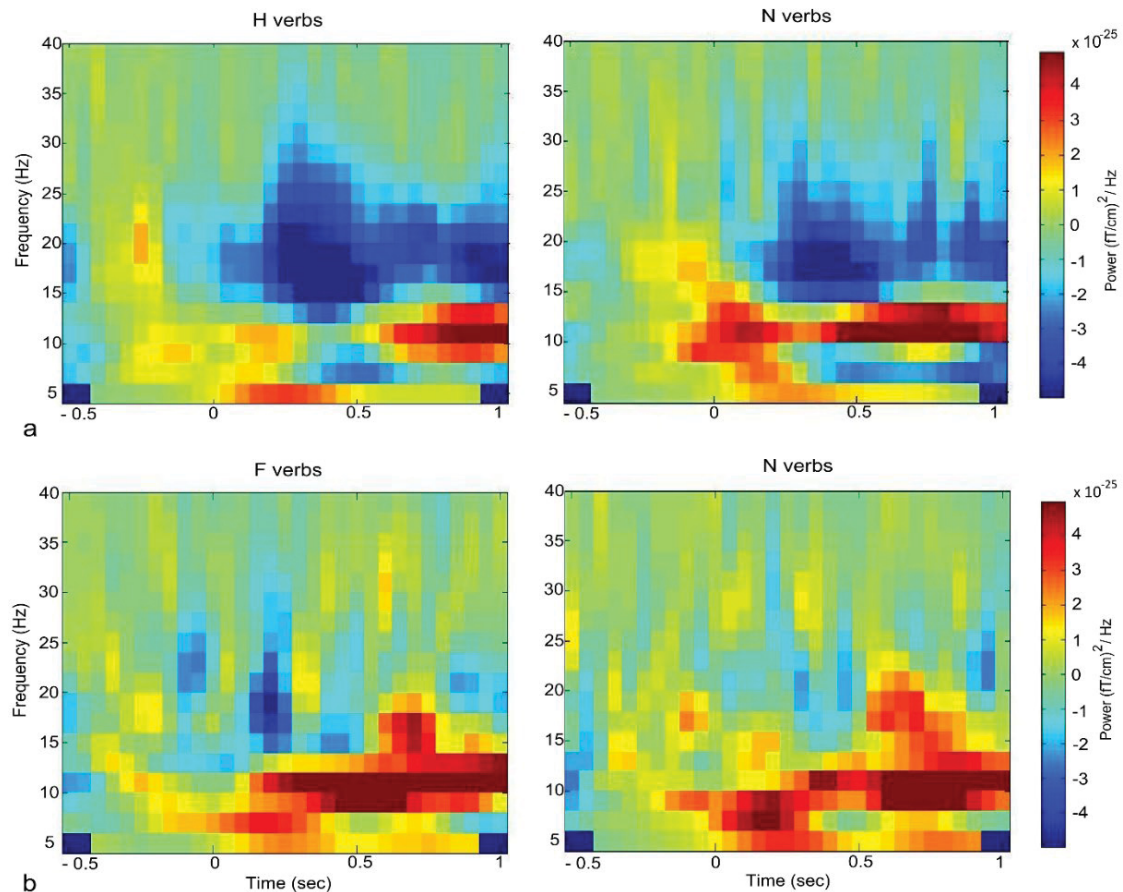

Figure 4. Grand-average of frequency spectra. a) Grand-average of the H (left) and the N (right) condition on the average of the left-hemispheric hand-related sensors selected with the localizer task. b) Grand-average of the F (left) and the N (right) condition on the average of three foot-related sensors showing a significant effect. Figure adapted from Niccolai et al. (2014), distributed under the Creative Commons Attribution License.

Although in both cases the activation emerged in the beta range, slight differences in the frequency subrange were also observed: the effect related to the H-N contrast involved the 20-24 Hz frequency range whereas the effect related to the F-N contrast involved the 15-20 Hz range. This activation emerged at about 200 ms after word onset, therefore in a plausible time-window of semantic processing. Beyond beta, also the alpha rhythm showed stronger desynchronization in the H versus N condition in the left-hemispheric hand-related motor area, although with a later onset (~ 400 ms after word onset). When testing possible activation induced by each contrast on the not-corresponding somatotopical area (i.e., H-N in the foot-related motor area and F-N in the hand-

related motor area), no significant effect emerged; this points to a somatotopical specificity of the cortical motor engagement in language processing. According to the results of a previous survey conducted to select verbs, H and F verbs were more imaginable than N verbs. Since imageability was described as a possible way for semantic processing and learning (see Dual Coding Theory, Paivio 1971), the contrast between high- versus low-imageability words was examined. Results showed no different patterns of activation for either the beta or the alpha frequency in any of the selected motor areas. This indicates that difference in imageability between condition did not result in modulation of the motor cortex and suggests motor simulation as the mechanism responsible for the observed effects.

In addition to oscillatory correlates, study 2 (Klepp et al., 2014) applied a source modeling technique to localize motor-related activity in the brain. Individual neuromagnetic motor sources during the processing of H and F verbs were inspected by looking at the equivalent current dipoles (ECD). In the context of motor preparation/execution two distinct event-related fields have been previously identified: the motor field (MF) and the movement-evoked field (MEF; Kristeva et al., 1991). Specifically, the MF peaks around movement onset and the MEF peaks shortly after movement onset. The MF is located in the motor cortex and is assumed to reflect processes related to motor commands. The MEF instead is located in the postcentral sensory cortex and is related to sensory feedback evoked by a movement (Biermann-Ruben et al., 2012; Cheyne & Weinberg, 1989). To localize neuromagnetic motor sources, a localizer task consisting of alternating hand and, separately, foot movements was used. Neuromagnetic ECD sources for H and F movements in the localizer task were then fitted to the signal of the H, F, and N condition of the word paradigm. The transfer of the ipsi- and contralateral MF sources related to hands and feet movements to the word paradigm resulted in larger hand-related MF source amplitude for H than for F verbs (Figure 5, left plot). Overrepresentation of hand regions in the motor cortex and poorer signal quality for the intra-hemispherically located foot motor area may explain the fact that verb conditions only descriptively differed on foot sources. Motor dipole sources for hands and feet movements also showed to be recruited by the corresponding H versus F verb condition within a semantic time-window (at about 200 ms after word onset; Figure 5, right plot). Results indicate that motor dipole sources, which were individually determined using a localizer task, were involved in the semantic processing of body-related verbs according to the effector required to perform the action described by the verb. Differently, MEF sources did not show activation in the word paradigm, suggesting that the sources related to the sensory aspect of a movement were not sensitive to body-related verb processing.
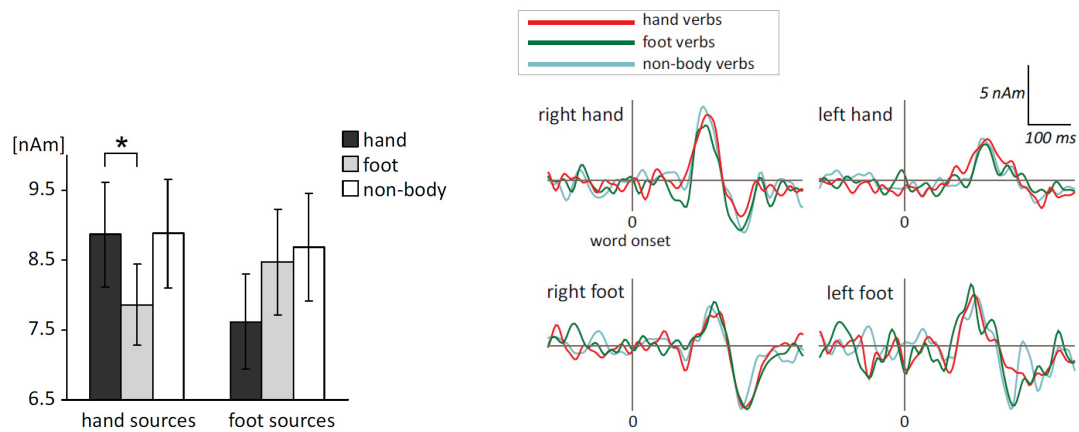
Figure 5. Left: Mean peak amplitudes for MF hand- and foot-related sources in the three verb conditions, averaged across hemispheres. Error bars show SEM, * = p<.05. Right: Grandaverage time course of MF dipole activation during verb processing for the three verb conditions. Figure from Klepp et al. (2014), adapted and reproduced with permission from Elsevier.

In summary, results of study 1 and 2 showed that verb reading activated somatotopically the hand and foot motor areas according to the body-part described by the action verb. This modulation emerged in the beta and alpha range, thus suggesting desynchronization in these frequency ranges as a potential neurophysiological marker of embodiment. In both studies, also neural activation related to the processing of abstract verbs was observed in cortical motor areas. This is likely to reflect the non-dichotomous nature of concrete - abstract words, the latter being not completely disentangled from sensory and motor systems. This aspect has been addressed within the embodiment framework as a possible a continuum between abstract and concrete words mediated by a differential recruitment of cortical areas (Borghi et al., 2017).

2.2 Neural correlates of conceptual processing of acoustic features

In study 3 (Niccolai et al., 2020) a further step was done in order to determine the neurophysiological correlates of embodiment by moving the focus from motor to sensory cortical areas: this study addressed the role of the auditory cortex in semantic processing of acoustic characteristics as implied by action verbs. Specifically, I concentrated on the loudness aspect of actions and investigated the cortical activation related to verbs implying loud (e.g., *'to shout'*) versus quiet (e.g., *'to whisper'*) actions; verbs belonging to the two conditions differed in the loudness parameter according to a previous online rating study involving 30 monolingual German speakers. Verbs of the two conditions were further matched for word length, frequency, bi-/trigram frequency and number of mouth/facial versus limb/whole body actions. Louder actions were expected to be accompanied by stronger activation of the auditory cortical area. While theoretically a no-sound condition would have been

also informative, the scarcity of body-related actions that do not produce sounds made it not possible to create such a control condition. To induce semantic processing of words without explicitly addressing loudness, participants were required to respond either whether the verb was in 1st versus 3rd- person perspective or which body-part was involved in the action (Figure 6).
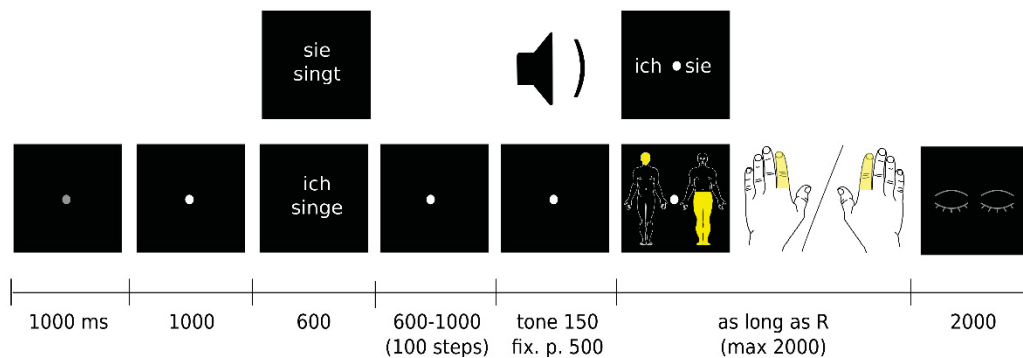

Figure 6. Description of the word paradigm: verbs implicating loud or quiet human actions were shown and participants were asked to indicate either whether the verb was in the 1st/3rd- person (i.e., "ich singe"= "I sing"; "sie singt"="she sings") or which body-part was implicated in the action (fix.p. = fixation point; R = response). Each word was followed by the presentation of the same tone. Figure from Niccolai et al. (2020), reproduced with permission from Elsevier.

To identify the specific cortical temporal areas required for loudness processing, a localizer study was used, that consisted in the presentation of loud versus quiet tones. Previous findings concerning oscillatory activation of the auditory area point to alpha and beta power suppression as a correlate of tone and of phoneme processing (Crone et al., 2001; Weisz et al., 2011). These frequency ranges were thus addressed both in the localizer and in the word paradigm study. Results from the localizer study showed that loud tones were followed by larger N100m amplitude (the magnetic equivalent of the N100) as well as by stronger 10 Hz power suppression than quiet tones (Figure 7a,b,c). To determine the cortical sources of activation I used Dynamical Imaging of Coherent Sources (DICS; Gross et al., 2001), which estimates cortical power on the source level by means of a spatial filter. Results showed that the alpha frequency was more desynchronized for loud then quiet tones in the Broadman areas A22, A41/42, and in the caudoposterior superior temporal sulcus (cpSTS) of the right hemisphere (Figure 7d).
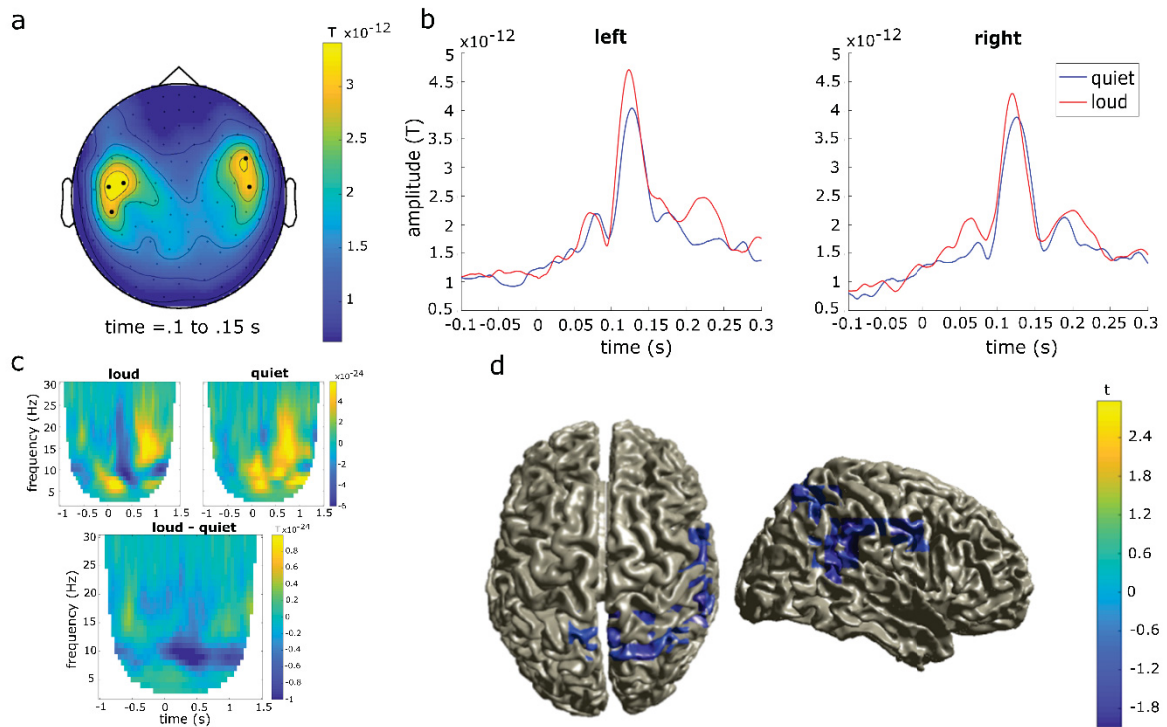
Figure 7. Localizer study. a) Grandaverage of the N100m peak amplitude between 100 and 150 ms after tone onset with channels exhibiting maximum activity depicted by bold points; b) grandaverage N100m time-course for loud (red) and quiet (blue) tones in the left- and right-hemispheric channels showing maximum activity; c) Grandaverage of frequency spectra of the loud and quiet tones condition and grandaverage difference across channels showing a significant N100m amplitude modulation by loudness; d) source estimation of the alpha band in the contrast loud versus quiet tones displayed on a brain template (only significant values shown). Figure from Niccolai et al. (2020), reproduced with permission from Elsevier.

These areas were used as regions of interest in the word paradigm within a virtual channel approach that enables the localization of specific brain areas in the individual brain models based on MEG-MRT co-registrations and according to a brain atlas (Brainnetome; Fan et al., 2016). Results of the word paradigm showed that verbs describing loud actions induced stronger beta (20-26 Hz) desynchronization in the left hemisphere in a time-window where semantic processes take place (Figure 8); in the right hemisphere a similar activation was observable, which however did not reach significance. This is in line with the left-hemispheric linguistic dominance as well as with the finding that the STS show stronger responses to words than to tones particularly in the left hemisphere (Binder & Price, 2001). The alpha frequency was descriptively modulated by loudness, with stronger desynchronization following verbs describing loud actions, but its effect did not reach statistical significance. These findings point again to a main role of the beta frequency in the embodiment of semantic concepts.
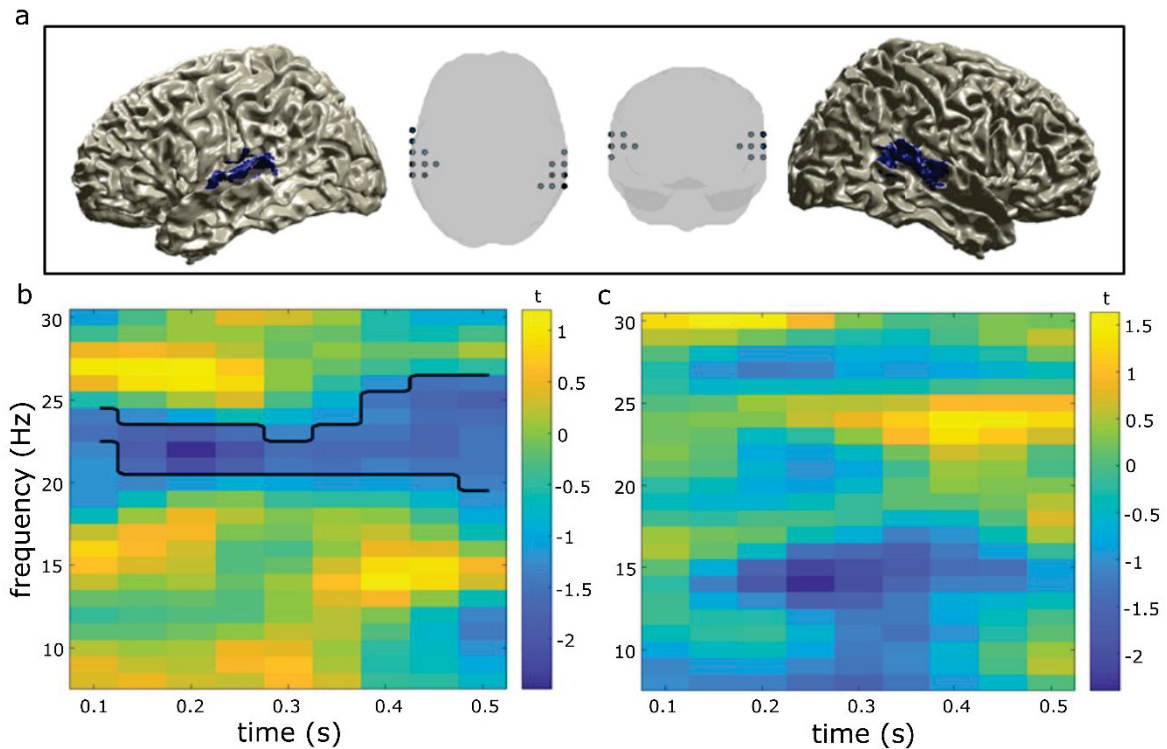
Figure 8. a) Grid points representing virtual channels of area A22, A41/42, and cpSTS displayed on a brain template. b) and c) Results of statistical comparisons on virtual channels between loud and quiet action words (colours represent *t*-values). Data of temporal areas A22, A41/42 and cpSTS were averaged for the left (b) and right (c) hemisphere (significant cluster outlined). Figure from Niccolai et al., 2020, reproduced with permission from Elsevier.

In addition, a sensory suppression paradigm was implemented in the word paradigm in order to investigate whether the sensitivity of the auditory cortex to a tone following the word stimulus (see Figure 6) was differentially affected by the verb semantic loudness. Specifically, increased auditory cortex activation as induced by loud verbs was expected to affect the amplitude of the following magnetic field related to tone presentation. The N100 amplitude is typically suppressed in case of stimulus repetition (Bendixen et al., 2012; Timm et al., 2013). Enhanced engagement of the auditory cortex by action verbs of the loud condition was thus expected to result in a smaller amplitude of the N100m due to inhibition of the auditory neural population. Results showed that the N100m was smaller for tones following verbs of the loud than for tones following verbs of the quiet condition in the left hemisphere. This confirms that the auditory cortex was affected by the semantic loudness of actions described by visually presented words and that it responded differently to a following simple acoustic stimulus.

In addition to the loudness parameter, also movement energy intended as increased body-related movement was inspected in the word paradigm. Indeed, louder actions may be accompanied by stronger or larger movements; this parameter was measured through a rating study. The analysis of

high- versus low-movement action verbs aimed thus at disentangling between the contribution of action-related loudness and that of movement energy required to perform that action. The lateral occipital cortex V5/MT+, which is typically related to the processing of biological movement and is anatomically well defined (Zeki et al., 1991), did show increased beta desynchronization for high versus low-movement action verbs. Crucially, no effect related to movement energy emerged in the selected auditory area, thus suggesting that beta modulation observed in the auditory cortex depended on the loudness parameter.

In summary, study 3 showed that a sensory brain area, namely the auditory cortex, is involved in the semantic processing of verbs implying action-related acoustic features. The modulation of the auditory cortex could be also confirmed by the N100m suppression and could be disentangled from the possible contribute of action-related amount of movement.

To further determine the role of the auditory cortex in processing linguistic stimuli with acoustic relevant features, a peculiar word category was investigated in study 4 (Röders et al., 2022) potentially offering an additional and more sensitive way to tackle the role of the auditory cortex in words processing. Onomatopoetic verbs reproduce the sound of the action that is meant (e.g., *'murmeln' - 'to mutter'*) and are therefore characterized by a close relationship between word phonetic and meaning: the acoustic feature is hence an intrinsic property of the semantic representation of the word. In previous studies, brain activation related to onomatopoeia was frequently investigated with interjections, which are sounds that animals make (e.g., '*kikeriki'* for a rooster call). Results showed stronger activation of the auditory cortex and in particular of the STS and the posterior superior temporal sulcus (pSTS) accompanying interjections compared to control words with similar reading frequency, auditory familiarity, and auditory imageability (Hashimoto et al., 2006; Kanero et al., 2014). While also onomatopoietic adverbs have been addressed in one study (Lockwood & Tuomainen, 2015), there was a lack of studies focusing on the effect of onomatopoetic syntactical components such as nouns or verbs on brain activation; this gap was even more remarkable when considering the investigation of neural oscillatory activity in the field. Study 4 aimed at filling this gap by targeting both event-related fields and brain oscillations accompanying the processing of onomatopoetic verbs. To this aim, onomatopoetic (O) and non-onomatopoetic (NO) verbs were matched for frequency and length, as well as implied loudness to avoid a possibly related cofounding effect concerning acoustic relevance. The onomatopoetic quality of a preselected group of words was determined by means of a previous online rating study. Semantic processing of O verbs was expected to engage the auditory cortex more strongly than that of NO verbs; the left temporal channels resulting from the localizer paradigm in study 3 were chosen as region of interest.

On the base of results of study 3 and of previous studies addressing sensory processing of tones and sounds (Crone et al., 2001; Weisz et al., 2011), desynchronization of the alpha and beta frequencies was targeted as potential neurophysiological correlate of the auditory cortical engagement. Results from study 4 showed a descriptive effect both in the alpha and in the beta frequency range with stronger desynchronization in the O compared to the NO condition, which however did not reach statistical significance. As for ERFs, a larger component was observed at about 240 ms after word onset for O words, starting in centro-parietal channels and moving towards slightly right lateralized channels (Figure 9).
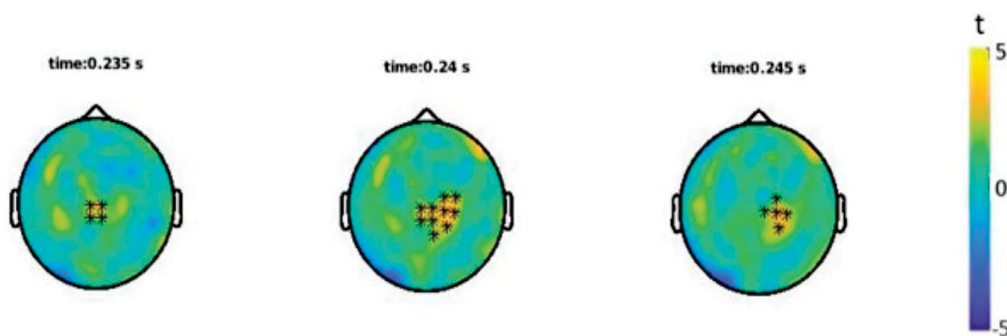

Figure 9. Statistical results of ERFs analysis of the contrast O-NO: channels showing a significant effect (indicated by a star) in the shown time interval. Figure reproduced from Röders et al. (2022), distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

One possible interpretation of this effect is an enhanced effort accompanying the semantic processing of O compared to NO verbs. This is likely to reflect the double information processing that characterizes O words, where both relevant phonetic and semantic features are simultaneously processed. Although it might be argued that the relatedness between the phonetic and the semantic aspect of O words is of advantage for linguistic comprehension, there is so far no sound evidence for a facilitated lexical/semantic processing accompanying O words. Behavioral results of study 4 could not shed light on this issue as the task required participants to respond after a prompt: this, which was needed to control for semantic processing of words, interferes with spontaneous reaction times. From previous electrophysiological studies, inconsistent results emerge. In an EEG study comparing iconic verbal material (ideophonetic adverbs) and arbitrary adverbs, amplitude differences were observed in an early (P200) and in a late positive component at about 600 ms (Lockwood & Tuomainen, 2015). The authors associated the larger P200 following iconic words to the integration of sensory information and the late positive complex with a more effortful retrieval of ideophonetic compared to control words. In another study, a less negative-going N400 and a late positive deflection for onomatopoetic compared to control words were instead observed (Peeters, 2016).

Altogether, the analysis of ERP/ERFs indicates peculiar neurophysiological correlates accompanying the processing of onomatopoetic words. Whether the related double (phonetic and semantic) feature induces a facilitated or a more effortful linguistic processing remains to be determined.

2.3 Neural correlates of perspective-taking

The studies 1 to 4 addressed the modulation of cortical activation induced by motor and sensory processes accompanying action verb understanding. In fact, actions can be experienced from more than one perspective depending on the agent of the action (e.g., *'I grasp'* versus *'s/he grasps'*). There is behavioral evidence for actor perspective affecting the immersion in a story when reading (Hartung et al., 2016). It was suggested that the focus on the personal experience, of 'what something is like', characterizes the 1st- person approach, which is centered on the body (Hornecker et al., 2017); differently, a 3rd- person perspective would imply a more external, objective approach, with a focus on the context. Behavioral evidence for an effect of perspective-taking in the linguistic field comes from studies applying the above introduced ACE effect: this was found using the 1st- person perspective and was abolished when using the 3rd- person perspective (Gianelli et al., 2011; van Dam & Desai, 2017). A study investigating motor-evoked potentials induced by TMS found that motor facilitation was greater for verbs in the 1st- than in the 3rd- person perspective (Papeo et al., 2011); also, without stimulation, reaction times to verbs in 1st- person were shorter, suggesting faster processing. Overall results point to the agent of an action as an important modulatory aspect of embodiment and raise the question whether this effect is accompanied by particular brain correlates. Study 5 (Niccolai et al., 2021) was developed to determine neurophysiological mechanisms at the base of the modulatory role of perspective-taking. To answer the question whether change of agency reflects on the degree of embodiment in cortical areas, study 5 addressed patterns of activation related to semantic processing of verbs presented in the 1st- versus the 3rd- person perspective. To this aim, the dataset of study 3 was used, where each verb was pseudo-randomly presented either in the 1st- or in the 3rd- person perspective ('I' versus *'she'* or 'he'; see Figure 6). Using a virtual channel approach, neuro-oscillatory activation was targeted in the cortical areas shown to be modulated by perspective-taking in previous fMRI studies. Overall, functional neuroanatomical effects were observed in the posterior cingulate gyrus, the right STS, the sensorimotor area and the V5/MT+ area (Ruby & Decety, 2003; Tomasino et al., 2007).

All but the V5/MT+ areas were expected to show increased activation following verbs in the 1st- person perspective, depending on enhanced simulation due to the identification with an 'internal' versus 'external' agent. As for the V5/MT+ area, this was assumed to be inversely modulated due to its sensitivity to biological motion and to the related observer perspective. MEG results showed

increased beta desynchronization in the right posterior ventral cingulate gyrus and the right pSTS, thus supporting a functional role of these areas in the implementation of action perspective. The unexpected finding of increased beta desynchronization also in the right V5/MT+ area may depend on the partial overlap of this brain region with fractions of the extrastriate body area; interestingly, this overlap was shown to be larger in the right hemisphere (EBA; Ferri et al., 2013). Possibly, this contributed to the observed increased right-hemispheric V5/MT+ activation following verbs in the 1st- person perspective.

Beyond oscillations, ERFs induced by the pronoun-verb pairs in the two conditions were also inspected in study 5. Results showed a larger component between 110 and 170 ms following 1st- person perspective, that broadened from occipital toward central and then left-hemispheric temporal areas. This result adds to previous EEG findings of larger potentials induced by 1st- person perspective (Brilmayer et al., 2019; Shi et al., 2011) and indicates an increasing recruitment of brain regions involved in semantic processing.

Another aim of study 5 was to detect a possible influence of linguistically based perspective-taking on following sensory processes. The auditory component N100 was previously shown to be sensitive to the agent: this effect, called sensory attenuation, consists in smaller N100 amplitude when language or tones are self- versus externally-produced (Bendixen et al., 2012; Ross et al., 2017). Analogously to study 3, a modified sensory attenuation paradigm implemented in the linguistic task was expected to reveal whether perspective-taking affects the amplitude of an auditory sensory component. In particular, the N100m related to tones following stimuli in 1st- person perspective was expected to be smaller due to the related simulation of a self-produced action. No difference in N100m amplitude however emerged between the conditions, possibly depending on the overall weak link between the stimuli and auditory activation.

In summary, the study confirmed the sensitivity of the right ventral cingulate cortex and pSTS to the agent of an action. This suggests that simulation of actions in the 1st- and in the 3rd- person perspective modulates the engagement of these brain areas. Also, ERFs results pointed to modulation of early cortical recruitment by perspective-taking as induced by pronoun-verb pairs.

2.4 Motor-semantic interaction and semantic processing depth

While studies 1 - 5 used MEG to target linguistic embodiment, study 6 (Klepp et al., 2017) and 7 (Niccolai et al., 2017) applied a behavioral and stimulation approach to detect modulation of the motor cortical activation as well as automaticity of simulation processes. In particular, study 6 addressed this issue by tackling the interaction between processing of body-related verbs and motor

response during a semantic versus non-semantic task. A double dissociation priming paradigm was used that consisted in the visual presentation of hand-related (H), foot-related (F), and non-body (N) verbs followed by right hand or foot responses; each response effector was hereby prompted by a specific geometrical shape (e.g., a shape with rounded corners for hand responses and a shape with pointed corners for foot responses; Figure 10). The idea behind this was that priming effects consisting in faster hand responses to H versus F verbs and faster foot responses to F versus H verbs should enable to disentangle the contribution of the respective body-specific motor brain area to the processing of H and F verbs. This paradigm was applied in two different experiments using different tasks: in the first experiment, no requirement was made concerning verb reading or understanding and the task consisted in responding with the correct effector as required by the prompt (non-semantic task). In the second experiment, the additional use of a Go-NoGo task required to respond exclusively to concrete and not to abstract verbs (semantic task).
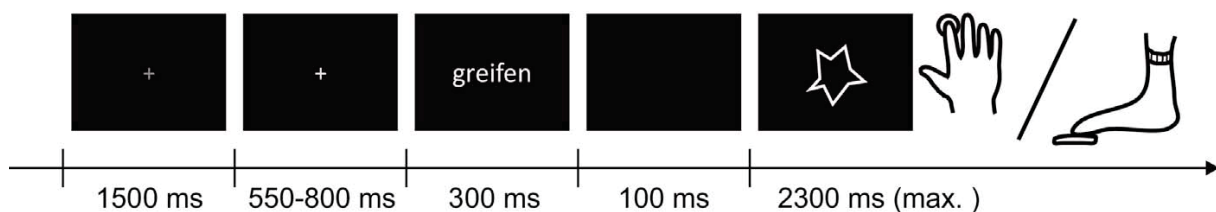

Figure 10. Experimental procedure: the verb prime was followed by a prompt consisting in a geometric shape with either pointed or rounded corners. The type of corners determined the response effector (i.e., the right hand or the right foot). In Experiment 1, responses were executed in all trials. In Experiment 2, responses were exclusively required for concrete verb primes. Figure from Klepp et al. (2017), reproduced with permission from Elsevier.

The analysis of accuracy and reaction times was conducted using linear mixed models in order to capitalize on the sensitivity of this method to differences among individuals as well as on its robustness to unequal sample sizes; beyond that, this approach enables to account for variance related to verb understanding. Results showed that an interaction between body-related verbs and effector type emerged only when semantic decision was required: hand responses were faster following H than F words and the opposite pattern was observed for foot reactions (Figure 11). The lack of priming in the non-semantic task suggests that either simulation processes did not take place or that they were too weak to be caught using this paradigm.
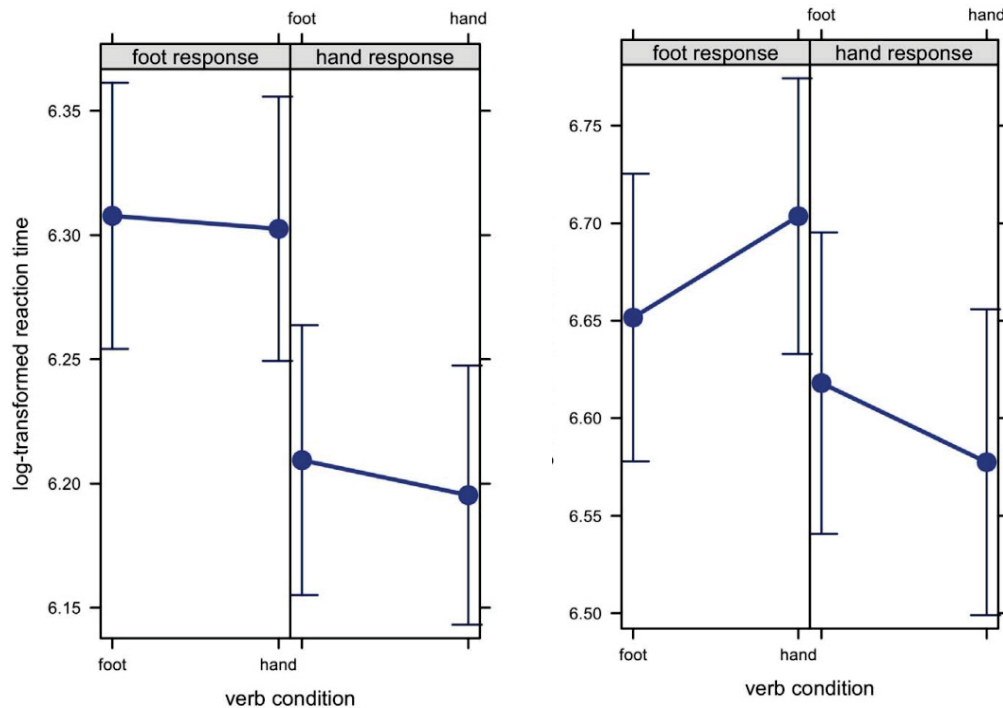
Figure 11. Predictor estimates and confidence intervals for the mixed model on logarithmically transformed reaction times for experiment 1 (non-semantic task, left) and experiment 2 (semantic task, right). Figure from Klepp et al. (2017), adapted and reproduced with permission from Elsevier.

Moreover, further semantic parameters of verbs were considered: the prototypicality of the action described by the verb, that is, how clearly a verb invokes an associated action, and the effector-specific movement, describing the amount of movement in the major executing limb that subjects associate with a given verb. The result of shorter reaction times following verbs that where more prototypical and verbs implying more effector-specific movement emerged in the experiment with the semantic task. This suggested less effort in processing and facilitated access to verb concepts. Interestingly, also in the first experiment, where no semantic processing was required, a priming effect for verbs with high effector-specific movement emerged for hand responses, thus pointing to subtle semantic processing of words.

The role played by the depth of semantic processing in embodiment was further investigated in study 7 (Niccolai et al., 2017) using electrical stimulation of the hand-related motor cortex by means of tDCS. Moreover, study 7 attempted at shedding light on the functional relevance of the motor cortex in verb understanding. Study 1 to 6 addressed the question whether and how motor and sensory cortices are engaged in linguistic processing and showed overall that brain oscillations in the

alpha and beta range as well as magnetic sources are indicators thereof. The correlational nature of these findings however leaves the causality issue unanswered. The application of tDCS on the motor area allows tackling this aspect and telling how far linguistic representations of body-related actions depend on the recruitment of the motor cortex. To this aim, the hand-related motor cortex was first localized through TMS and then continuously stimulated using tDCS to detect possible effects on the simultaneous semantic processing of H- and F-related words. In particular, tDCS was expected to inform on the neural sign of the modulation (facilitatory versus inhibitory) of semantic-motor interaction: using a controlled double-blind cross-over design, opposite effects of anodal and cathodal versus sham tDCS on task performance were expected. The semantic double-dissociation task used in the second experiment of study 6 was applied: participants were required to respond to concrete body-related H and F verbs either with the hand or with the foot according to the prompt. Stimulation of the left hand-knob, contralateral to the hand effector, was expected to affect processing of H but not F verbs. Thereby, the synergy between cortical stimulation and semantic processing depth, as measured from the individual accuracy in the verb categorization task was assessed: to this aim, d-prime related to the performance at the Go-NoGo task was used to distinguish between high and low semantic discrimination.

Results showed a priming effect across stimulation conditions in form of interaction between verb and effector both in reaction times and accuracy (Figure 12); this was in line with experiment 2 of study 6. One main outcome was that the cathodal versus sham contrast showed a priming effect for the high but not for the low semantic discrimination subset: thereby, responses were faster to prompts following H verbs in the cathodal compared to the sham condition independently from response effector (Figure 13). No tDCS effect was observed for reaction times to F verbs. Results suggest that the cortical inhibitory effect of cathodal stimulation selectively decreased cortical motor activation induced by hand verb processing and by hand response preparation thus reducing the related interference. Overall, study 7 confirmed the recruitment of cortical motor areas by body-related verb semantic processing and pointed to the modulating role of semantic processing depth.
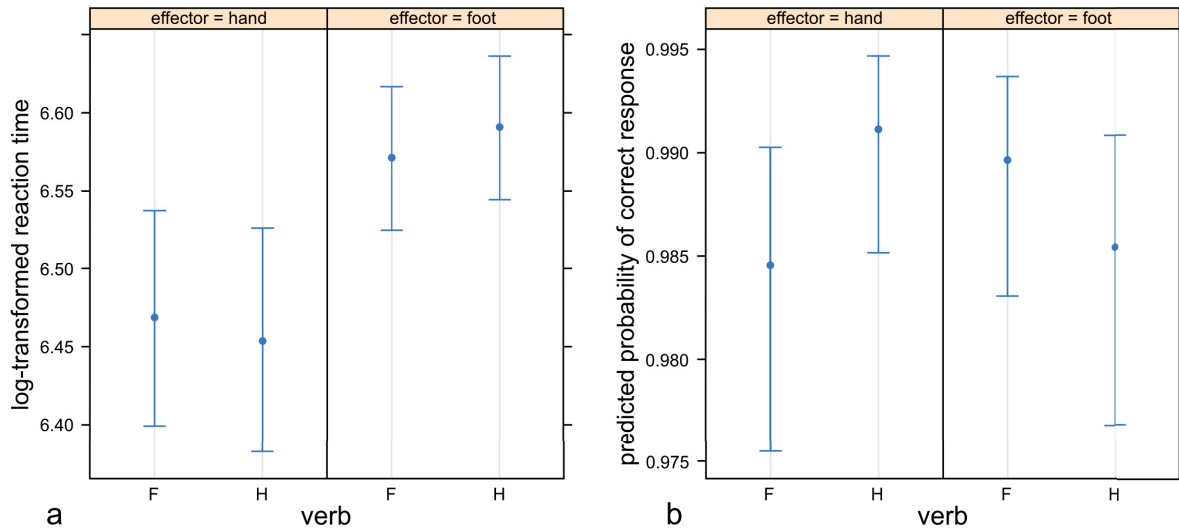
Figure 12. Estimates and confidence intervals for verb type (H=hand, F=foot) and response effector: the priming effect across tDCS conditions emerged both on reaction times (a) and on shape-response accuracy measures (b). Figure from Niccolai et al. (2017), distributed under the terms and conditions of Creative Commons Attribution 4.0 International License (https://creativecommons.org/licenses/by/4.0/).
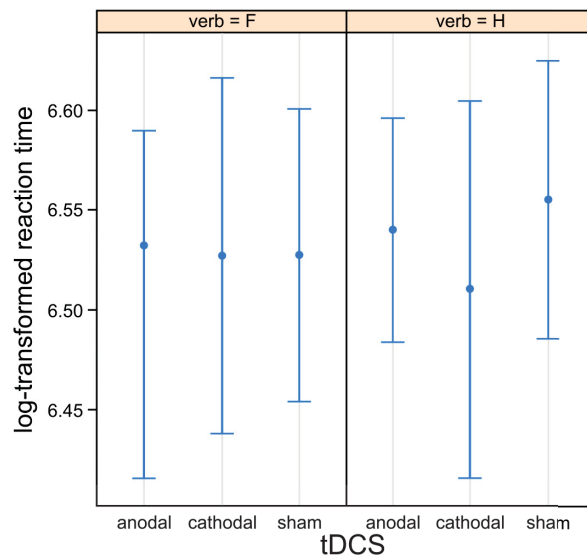

Figure 13. Estimates and confidence intervals for tDCS and verb type (H=hand, F=foot) on logarithmically transformed reaction times for the subgroup with high semantic discrimination. Figure from Niccolai et al. (2017), distributed under the terms and conditions of Creative Commons Attribution 4.0 International License (https://creativecommons.org/licenses/by/4.0/).

3. Discussion and Outlook

The selected studies aimed at tackling the engagement of the motor and sensory cortex in language processing by means of electrophysiological, neuromodulatory, and behavioral approaches. Results suggest alpha and beta power suppression as a plausible neurophysiological marker of motor and sensory cortical recruitment accompanying representation of word meaning. Specifically, the sensorimotor area was recruited by body-related action verbs and the engagement of the auditory cortex was modulated by the relevance of the acoustic features of actions depicted by body-related verbs. The observed cortical activation started early, accompanied word processing, and was somatotopically distributed. The left lateralization of the oscillatory correlates in study 1, 3, and 4 together with the left lateralization of the sensory suppression of the N100m are consistent with the left hemispheric language dominance in right-handed persons (Knecht et al., 2000).

Different subranges of the beta frequency appear to be engaged by embodied semantics related to hand- versus foot-related verbs thus pointing to oscillatory rhythms intrinsic to the particular sensorimotor region. Analogously, oscillatory patterns of activation accompanying cortical engagement in localizer tasks do not completely overlap with those related to linguistic processing, thus suggesting qualitatively different functional correlates of motor and sensory perception on one side and word representation on the other side. This might indeed be an interesting aspect of the translation from the motor/sensory to the semantic neural domain. The precise neural mechanisms subtending embodiment remain indeed to be determined: which specific neural systems make the sensorimotor-linguistic translation possible? In other words, how can sensorimotor areas be engaged by as well as disentangle between motor/perceptual and linguistic information processing? Zones of convergence where the semantic information from different networks become integrated have been put forward (Barsalou et al., 2003; Damasio et al., 2004). A neurocomputational model suggests particular hub areas to link the motor and the sensory semantic information (Tomasello et al., 2017). As such semantic hubs have been proposed to be responsible for a coherent semantic representation (Patterson et al., 2007), shedding light on the localization and the functional mechanisms of these hubs is the next step for research on language comprehension.

Further, the role of imagery processes remains to be determined. Study 1 showed that the contrast of high- versus low-imageable actions did not result in any activation in the selected hand- and foot-related sensorimotor areas. Although these results do not speak against a partial entanglement of simulation and imagery processes, these may be characterized by distinct qualities of oscillatory activation as well as by different latencies.

In a further attempt to target sensory embodiment, I investigated the effect of processing onomatopoetic words, characterized by an intrinsic relationship between phonetical and semantic

acoustic features. While centro-parietal activation at about 240 ms possibly indicated an increased recruitment of attentive resources, stronger alpha and beta power suppression for onomatopoetic words in the left auditory cortex was limited to a descriptive effect. This weak activation may depend on some factors: first, the lower familiarity of onomatopoetic versus control verbs may have interfered with the related cortical recruitment. Second, the use of onomatopoetic verbs describing both body-related human actions and environmental events (e.g., "plaetschern" – "to platter") might have moved the attentional focus to an extra-personal space thus weakening the related simulation processes.

This issue was indeed target of study 5, which investigated possible different cortical recruitment depending from an internal versus a more external perspective on the action described by the verb. A larger component emerged at about 150 ms in occipito and left temporal sites during the processing of actions in the 1st- person perspective. Also, the right pSTS, PCC and V5/MT+ were more engaged by 1st- versus 3rd- person perspective, as indicated by stronger beta power suppression. This is in line with previous fMRI findings showing a role of pSTS and PCC in body-related action-perspective (Allison et al., 2000) and in external versus internal perspective change, also found using a virtual environment (Buckner et al., 2008; Vogeley et al., 2004). The right lateralization might depend on the recruitment of this hemisphere by the experiential mode, in contrast with the more meaning-based processing mode of the left hemisphere (Tops et al., 2014). Hereby, the fact that verbs were body-related actions might also have played a role, as observation-execution of such actions was shown to predominantly activate the right hemisphere (Biermann-Ruben et al., 2008).

Results of study 5 point thus to a *context*-dependent processing of single words (i.e., the agent of the action). Analogously, the contextual task (semantic versus non-semantic) and the depth of the linguistic processing affected cortical recruitment as shown in study 6 and 7. Here, behavioral as well as neuromodulatory effects emerged only when the semantic processing was deep enough. In fact, a wide spectrum of contextual constrains exists, that encompasses acoustic-phonetic, semantic and environmental features to make few examples (Spivey & Huette, 2016). The motor features of verb meanings are likely not always accessed to the same extent on every occasion (Kemmerer, 2015). Study 6 showed that although semantic processing of verbs was required for priming effects to become visible, subtle priming effects emerged also during a non-semantic task when effector-specific movement was high. Results of study 5 - 7 thus point to a shift from an embodied to a more *situated* language processing, where situational and linguistic contextual factors play a modulatory role. Overall, results suggest that linguistic comprehension is not an all-or-none phenomenon and that it may be affected by interacting contextual parameters. Causality and automaticity of cortical

activation in language understanding should thus not be considered as an on/off quality of embodiment: the role played by the context instead indicates that embodied semantics is more a continuum of complexity, flexibility, and idiosyncraticity. Determining their effects on behavior and brain activity poses indeed the next research challenge, to which the growing field of virtual reality may substantially contribute.

Finally, an interesting possible scenario for the embodiment framework is that one of the clinical application. Whether a clinical approach based on embodiment may offer a supportive or preventive therapy option to patients with aphasia or with motor lesions is still hypothetical. Here, one focus of research could be the intersection between motor training and linguistic recovery through neuroplastic changes. Besides, another clinical field that might profit from research in embodied semantics is psychotherapy: the interface between the linguistic content and the perceptual experience as proposed by the embodiment framework offers an experiential basis of language comprehension. Considering that psychotherapy is a talking cure, such interface might be an interesting target to determine changes in the therapeutic process as well as therapeutic effectiveness.

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5. Danksagung

6. Appendix

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Grasping Hand Verbs: Oscillatory Beta and Alpha Correlates of Action-Word Processing

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Abstract

The grounded cognition framework proposes that sensorimotor brain areas, which are typically involved in perception and action, also play a role in linguistic processing. We assessed oscillatory modulation during visual presentation of single verbs and localized cortical motor regions by means of isometric contraction of hand and foot muscles. Analogously to oscillatory activation patterns accompanying voluntary movements, we expected a somatotopically distributed suppression of beta and alpha frequencies in the motor cortex during processing of body-related action verbs. Magnetoencephalographic data were collected during presentation of verbs that express actions performed using the hands (H) or feet (F). Verbs denoting no bodily movement (N) were used as a control. Between 150 and 500 msec after visual word onset, beta rhythms were suppressed in H and F in comparison with N in the left hemisphere. Similarly, alpha oscillations showed left-lateralized power suppression in the H-N contrast, although at a later stage. The cortical oscillatory activity that typically occurs during voluntary movements is therefore found to somatotopically accompany the processing of body-related verbs. The combination of a localizer task with the oscillatory investigation applied to verb reading as in the present study provides further methodological possibilities of tracking language processing in the brain.

Data Availability: The authors confirm that all data underlying the findings are fully available without restriction. All relevant data are within the paper and its Supporting Information files.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

Two main theories make assumptions on how the brain processes language and concepts. The amodal approach proposes that all concepts are processed in an amodal unit, independently from their modality [1,2]. Differently, grounded (or embodied) cognition theories postulate that perceptual-motor processes are crucial in concept representation [3–5]. In this context, it is assumed that body-related action words are handled by the same brain areas involved in the execution of the respective movements. Language processing would thus include cortico-cortical connections between the classical temporal (Wernicke's area) and inferior frontal (Broca's area) language regions and the motor system [5]. It has been proposed that mirror neurons [6] and Hebbian association mechanisms [5,7,8] implement the functional overlap between action comprehension and execution. A middle ground between the embodied and disembodied cognition hypotheses has also been suggested [9].

A number of functional magnetic resonance imaging (fMRI) studies have tested the grounded cognition hypothesis and, with a few exceptions [10], have demonstrated the recruitment of cortical premotor and primary motor regions for the processing of action words or sentences [11,12,13,14,15,16]. Moreover, transcranial magnetic stimulation (TMS) of the hand and foot motor areas during the processing of effector-specific action verbs and

sentences modulates reaction times and cortical excitability [17–19]. Recently, our research group showed by means of magnetoencephalography (MEG) somatotopic activation of motor areas accompanying the processing of visually presented single verbs [20]. These findings consistently point to a somatotopically organized engagement of cortical motor areas in the understanding of written and spoken action.

Although specific patterns of cortical oscillatory activation are known to accompany limb movement execution, observation [21,22,23], and motor imagery [24,25,26,27,28], the oscillatory correlates of action word processing have hardly been addressed [29,30,31]. Power suppression of beta frequency is typically elicited by the preparation and execution of movements [21,23,32,33] and by the isometric contraction of different body muscles [34,35]. Similarly, a decrease of the alpha rhythm is known to accompany movement execution as well as motor imagery [36,37]. In line with the postulation of grounded cognition theory, it is conceivable that the processing of body-related verbs induces beta and alpha power suppression in motor cortical areas that are engaged in the respective action execution. A few studies have focused on oscillatory cortical motor correlates of action words. Testing whether motor activation in verb processing reflects motor imagery or semantic processing, van Elk et al. [31] found stronger mu (10–14 Hz) and beta power suppression starting about 200 msec after verb onset in motor

areas while processing animal compared to human action sentences. Due to early onset and inverse correlation to N400 peak amplitudes, the authors concluded that this may be a sign of lexical-semantic integration. Generation of an unspecific verb associated to a series of acoustically presented single nouns was shown to be accompanied by power suppression in the 15–25 Hz beta range on the left premotor cortex [38]. In addition to this, when reading hand-action versus abstract sentences, a decrease of mu rhythm was observed on left and central frontal leads [39]. Listening to verbal stimuli (pseudowords) that had been previously associated with movements resulted in suppression of the mu rhythm over the centro-parietal region [40]. What remains to be assessed is the somatotopic distribution of oscillatory modulations in motor brain areas. This is the first study that combined a localizer task with the oscillatory investigation of single verb processing, in order to explicitly test the embodiment theory. Using MEG, we compared hand- and foot-related verbs to verbs that involve no body movement, to which we refer as abstract verbs. We expected body-related words to induce a stronger beta (15–25 Hz) and alpha (7–11 Hz) power suppression in the respective sensorimotor cortices compared to non-body-related actions. As hands/arms occasionally move during foot-related actions, we chose to contrast each body-related verb condition against abstract verbs instead of against each other to maximize the sensitivity of the contrast. To localize hand and foot representations of the motor cortex, subjects performed isometric contractions of hand and foot muscles in two separate measurements which were further analysed offline. The resulting corticomuscular coherence represents the functional connectivity between a contralateral effector muscle and the sensorimotor and, possibly, the premotor cortex [41].

Capitalizing on the high time resolution of electroencephalography (EEG), it was shown that lexico-semantic processing related to bodily action words activated the cortical motor area around 200 msec after the presentation of the visual stimulus [13,42]. Similarly, spoken body-related verbs elicited preponderantly left-hemispheric event-related potential or field in the sensorimotor cortex between 140 and 200 msec after stimulus onset [43,44]. Since grounded cognition theories propose that the sensorimotor activation contributing to language understanding should occur within the time frame of lexico-semantic processes [45], we expected oscillatory modulations to emerge at about 200 msec post-stimulus onset. To select stimulus material and to control for psycholinguistic parameters that may affect word processing, rating studies were performed in advance. Individuals who did not take part in the MEG study were asked to evaluate the verbs' body-relatedness, familiarity, and imageability. Although the task applied in the present MEG study did not demand movement imagery, we additionally tested whether implicit imagery processes affected the oscillatory modulations related to lexico-semantic processes.

Materials and Methods

Participants

Fifteen university students (8 women, aged 22 years, SD = 1.8), all monolingual German native speakers, took part in the MEG study. All participants were right-handed, with an average laterality quotient of 84.1% (SD = 16.2%; Edinburgh Handedness Inventory, [46]), and right-footed (Lateral Preference Inventory, [40]). The subjects had normal or corrected-to-normal vision and none reported neurological or psychiatric disorders or made use of neuro-modulatory medications. Participants provided written informed consent prior to the MEG and received financial

compensation for their participation. The study was in accordance with the Declaration of Helsinki and was approved by the local Ethics Committee of the Medical Faculty of the Heinrich Heine University, Düsseldorf (study number 3400).

Materials

Stimuli consisted of German disyllabic infinitive verbs describing actions done with the upper extremities (hand, H), actions done with the lower extremities (foot, F), and actions in which no body part was involved (N). To find suitable stimuli, 339 verbs were used in a computerized rating study. In the first rating study, 30 monolingual German speakers (17 women, aged 29.7 years, SD = 6.8) specified which body part they usually use to perform the action described by each verb. Possible answers were "hands/arms", "feet/legs", "the whole body uniformly", "mouth/face", "no body part" and "I don't know". Categories that were not part of the main experimental focus ("mouth/face", "whole body") were applied to prevent forced choices of inaccurate answers. To be included in the sets of H, F and N, verbs had to be rated as describing actions of the respective body part by at least 80% of the subjects. For F, ratings were often split between "feet/legs" and "whole body", possibly due to locomotion verbs (e.g., *to run*) being rated as "whole body" by some participants, who focused on the body's change of location rather than the movements of the lower extremity. Therefore, for the F category, verbs were also included if the sum of "feet/legs" and "whole body" answers reached the 80% threshold, as long as at least 40% of the ratings were "feet/legs". The resulting 219 H, F and N verbs were subjected to a second computerized rating study (n = 30, 16 women, aged 28.8 years, SD = 6.4) in which subjects had to assess familiarity and imageability on 4-point rating scales. Mean familiarity, imageability, word length and word frequency class [47] (http://wortschatz.uni-leipzig.de) were used to define suitably matched groups of stimuli, resulting in 48 verbs per condition. While familiarity did not differ between groups (ANOVA, $p = .54$), residual differences were found for the other parameters (ANOVA, all $p < .01$). More precisely, according to paired 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 ($t_{94} = 2.79$, $p = .006$). The conditions H and F showed no significant differences (all $p > .13$). Fifty percent of the H verbs were unilateral actions. To control for the influence of imageability, stimulus sets were further divided into high and low imageability by a median split. For the lexical decision task introduced below, 18 pronounceable non-existent words (pseudoverbs) were created by reassembling the first and second syllables of the stimulus verbs. To this end, all first and second syllable occurrences in the data set were counted. Frequencies of pseudoverb endings (for German, typically '-en', '-ern' or '-eln') as well as the initial letters of the first and second syllables were chosen to broadly resemble the main data set in order to avoid introducing a processing bias. Another 18 verbs (6 for each condition) that were discarded during the matching procedure were used as fillers. A list of the stimuli and relative parameters values is presented in Table S1.

Procedure

Subjects removed all metallic objects and put on non-magnetic clothes prior to the MEG measurement to prevent recording artifacts. During the experimental session, participants were comfortably seated in a magnetically shielded room and viewed a screen at a distance of 83 cm. Black words were centrally presented against a light grey background and subtended a visual

angle of 3.4° by .7° on average. Presentation software (version 14.9, Neurobehavioral Systems, Albany, California, USA) was used to display the stimuli. Each trial began with a central fixation cross displayed for 500 msec, followed by a word or a pseudoword that remained on the screen for 500 msec. The fixation cross then appeared again for 2 s and was followed by an eye symbol shown for 2 s, which indicated the time for blinking. A fixation cross with a jittered duration of between 400 and 600 msec ended the trial without perceivable intersection to the following trial (Fig. 1). Participants were instructed to identify whether the stimulus was an existing word. Responses had to be given in only 20% of all trials, namely with filler verbs and pseudoverbs. In these trials, responses were prompted by a central arrow pointing to one of two lateral fixation crosses at a distance of 6.8° to the centre of the arrow. This screen lasted for 1500 msec and was inserted after the fixation cross following verb presentation. Subjects had to switch their gaze from the centre to one of the lateral fixation crosses. In cases where a real verb (the filler) was presented, they had to look at the cross pointed to by the arrow. If it was a pseudoverb they had to look into the opposite direction. The arrow pseudo-randomly pointed to the right and left side. The response cue was followed by the eye symbol which was displayed for one second. To avoid alteration of brain oscillations due to eye movements, only stimuli that were not followed by a response cue were analysed. Importantly, the fillers were indistinguishable from the analysed stimuli. Stimuli were randomly presented and they were repeated in a second block. A break was inserted every 5 minutes. Overall, the measurement lasted about 40 minutes. A total of 16 stimuli (10 pseudowords/fillers and 6 action verbs) different from those of the main study were used in a practice session preceding the experiment. Horizontal eye movements were calibrated to improve the analysis of behavioural accuracy.

Localizer task

To localize cortical sensorimotor areas corresponding to upper and lower extremities, subjects performed two isometric muscle contraction tasks. With their elbows resting on a table, they were required to bend their arms to about 30° and to simultaneously spread their fingers. Controlled by means of electromyographic (EMG) recordings, the contraction was limited to about 50% of the maximal strength. In the foot contraction condition, subjects raised their feet and toes upwards towards the body. Rest and contraction phases lasting one minute each were alternated twice. Participants were asked to fix their gaze straight ahead and to avoid eye movements during the contraction phase. Practice trials were performed before starting the measurement.

Data Acquisition and Analysis

Neuromagnetic brain activity was continuously recorded with a 306-channel MEG system (Elekta Neuromag, Helsinki, Finland), including 204 orthogonal planar gradiometers and 102 magne-tometers. A bipolar horizontal and vertical electrooculogram (EOG) was recorded for the offline detection of eye movements. Additionally, a bipolar EMG was recorded from the extensor digitorum communis (EDC) muscle of each forearm and from the tibialis anterior (TA) muscle of each leg. Four coils were attached to the subject's head bilaterally on the forehead and behind the ears. The position of these coils, prominent anatomical landmarks (right and left preauricular points and nasion) and some additional points along the subject's head were digitized (Polhemus Isotrak) to map functional MEG data to individual anatomy. MEG data were digitized at 1000 Hz, band-pass filtered from 0.03 to 330 Hz online, and stored on a computer hard disk. As for the analysis of behavioural data, the response accuracy of each subject was visually inspected on EOG traces using the Neuromag software package (Elekta Neuromag, Helsinki, Finland). MEG data were analysed with Matlab 2012a (Mathworks, Natick, MA, USA) and FieldTrip (http://fieldtrip.fcdonders.nl), a Matlab software tool-box for MEG and EEG analyses [48]. Data from 204 gradiom-eters were analysed.

Pre-processing of MEG data. Epochs from −500 to 1000 msec relative to verb onset were gathered from the continuous data. An additional 440 msec of data at the beginning and at the end of the epoch was included to avoid edge effects at low frequencies. Segments were created for the three conditions H, F, and N. For analyses of imageability effects, epochs from each
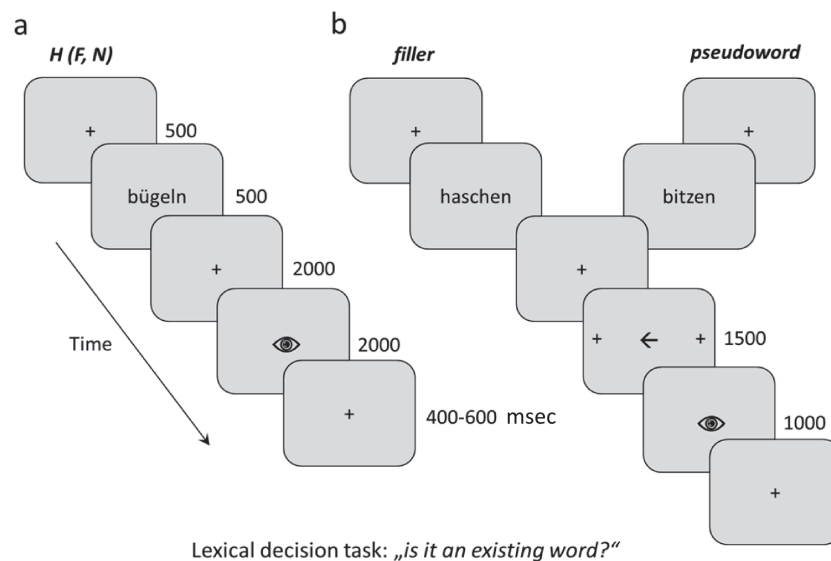
Figure 1. Experimental design. Trials which were not followed by a cue (a) were included in the analysis. The prompt to respond followed fillers and pseudowords (b).
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condition were further segmented into high and low imageable sub-conditions. Data were filtered with a high-pass filter of 2 Hz and with band-stop filters at 49–51, 99–101, 149–151 Hz; a Butterworth IIR zero-phase forward and reverse filter was used. Segments containing artifacts related to blinks and to movements of the eyes, hands, and feet were removed by means of a semi-automatic algorithm. An average of 81 trials (± 7 SD) in the H, 79 (± 8 SD) in the F, and 79 (± 9 SD) in the N condition passed artifacts rejection per subject. There was no significant difference among number of trials per condition (ANOVA, $F_{(2,44)} = .24$, $p = .78$). Channels with bad signal were replaced with the average of their intact neighbours (nearest-neighbour approach; [20]). Independent component analysis (ICA; [49]) applied to the output of a principal component analysis was run to identify cardiac artifacts. Fifty components per subject were estimated and visually inspected. One to two components representing cardiac artifacts were eliminated from the data of each subject.

Channel selection. The localizer tasks described above analysed in terms of corticomuscular coherence provided channel selections for the analysis of the verbal paradigm. To this end, two data epochs of about 1 minute each during muscle contraction were used for coherence analysis. EOG artifacts were rejected. Both MEG and EMG data were notch-filtered at 50 Hz power-supply noise frequency. EMG data were additionally filtered using a high-pass Butterworth IIR zero-phase forward and reverse filter at 10 Hz and rectified. The data were then segmented in 1 s trials. Time-frequency representations (TFR) were calculated using a multitaper method based on discrete prolate spheroidal sequences (DPSS) tapers which created a spectral smoothing of ± 5 Hz. Cross-spectra frequency and coherence were computed between MEG channels and each EMG channel. Grand-average maps were visually inspected and MEG sensors showing coherence to right and left hand and foot were selected for further analyses of the word paradigm.

Time-frequency analysis. TFR were calculated by means of a fast Fourier transform (FFT). An adaptive window including 5 cycles was shifted in steps of 50 msec from -500 to 1000 msec. Data were padded up to 3 s. A Hanning taper was applied to the epochs. Power was estimated between 5 and 39 Hz in steps of 2 Hz. A time-frequency analysis was separately applied to horizontal and vertical planar gradiometers. The pairs of planar gradiometers were then combined and trials were normalised with respect to the baseline, which included pre-stimulus data between -500 and -100 msec. Importantly, power representations in the baselines did not significantly differ between the H and N or between the F and N condition (all $p > .2$), according to the cluster-based randomization test described in the 'Statistical analysis of MEG data' section. To avoid an overlap in the frequency resolution between beta and alpha oscillations, the alpha rhythm was defined as being between 7 and 11 Hz while beta rhythm was specified as 15 to 25 Hz. Time-frequency analysis resulted in a resolution of 3–5 Hz for beta and 1.4–2.2 Hz for alpha.

Statistical analysis of MEG data. Statistical analysis of the MEG data consisted of a two-step procedure that effectively corrects for multiple comparisons and that has been applied previously [50–52]. First, the power difference between condition H and control condition N was calculated by means of t-values. T-values were calculated for each sensor, frequency bin and time point of each subject. In a second step, a cluster-based non-parametric randomization approach was used to test significance at group level [53]. The group analysis was run based on the average of the selected sensors (see *Channel selection*) and on a time-window of interest between 150 and 500 msec after word onset. According to the null hypothesis, the difference between H

and N should not significantly differ from zero, that is, t-values should be replaceable by zero. Thus, resulting t-values of each subject and values from a pseudo-dataset consisting of zeros went through a random partition which involved a shuffling of data between the two datasets. Time-frequency maps exceeding an a priori threshold (uncorrected $p < .05$) were combined into clusters. A cluster containing the summed t-values was used to calculate a cluster-level test statistic. The random partition was repeated 1000 times, every time resulting in a cluster-level test statistic calculated for the re-shuffled data. The subsequent histogram of the summed t-values constituted the cluster-based randomization test. The proportion of test statistics which were larger or smaller, respectively than the calculated statistic based on the observed original H-N contrast constituted the p-value. In cases where the p-value was smaller than an alpha-level of 0.05, we concluded that data in the two conditions H and N were significantly different. Given the well-known left-hemispheric specialization for language, this two-step statistical procedure was applied separately to the averages of the selected sensors of the left and right hemisphere for the H-N contrast. Due to the central location and overlap, the sensor selection for the F-N contrast included those related to the right and to the left foot taken together (Fig. 2), thus resulting in a total of 8 channels pairs, not averaged.

Using a similar statistical procedure, we tested whether the lexico-semantic oscillatory modulations were confounded by imageability effects. To test the main effects of imageability, we calculated the mean power across the H, F, and N condition (high vs. low imageability), thus resulting in two datasets each including all conditions, and we compared high versus low imagery subconditions on the selected hand and foot motor areas by means of the cluster randomization approach described above. To test a possible interaction between imageability and lexico-semantic effects, we calculated the differences between the H and N as well as between the F and N condition (high vs. low imageability), and we compared high versus low imageable datasets on the selected concordant hand and foot motor areas.

Results

Behavioural results

Participants successfully performed the task with an average accuracy of 89% (SD = 6.2%). This indicates that they were paying attention to the presented words. All subjects responded to each prompt with the exception of one subject, who failed to respond to 12% of the cued trials.

MEG results

Localizer task. Corticomuscular coherence in the 15–25 Hz beta-range during isometric contraction of hands showed a fronto-parietal distribution on the hemisphere contralateral to the contracted hand (Fig. 2). Contraction of feet activated a centrally located motor area and showed only slight lateralization. Eight hand channel pairs per hemisphere (bold points in Fig. 2) were selected for analysis of the H-N contrast in the word paradigm. As the two groups of foot-related channels largely overlapped, the sum of them (8 channel pairs) was selected for the analysis of the F-N contrast.

Word paradigm. We compared beta and alpha power between each experimental condition (H, F) and the control condition N on those channels selected with the localizer task. Both the H and the F condition showed significantly stronger beta suppression than N after stimulus onset. Specifically, the H condition showed stronger beta modulation than N in the left hemisphere ($p = .04$; Fig. 3a), whereas no cluster was found in the
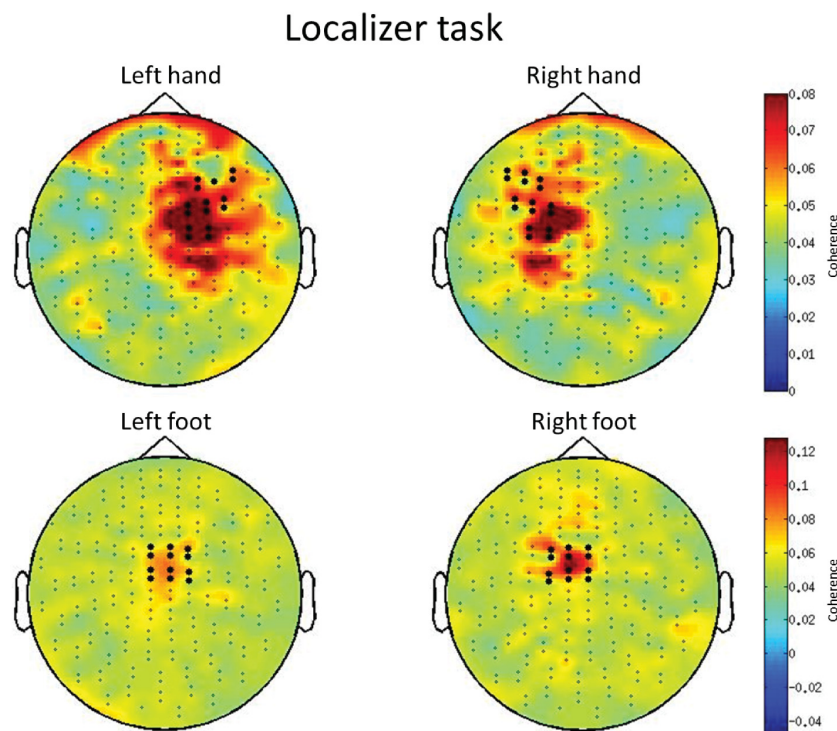
Localizer task

Figure 2. Grand-average of corticomuscular coherence in the beta (15–25 Hz) range related to hands (top) and to feet (bottom) isometric contraction across 15 subjects. Bold points represent gradiometer pairs selected for frequency analysis in the word paradigm.
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right hemisphere. As shown in Fig. 4a, the oscillatory effect related to H verb processing became significant at around 200 msec post-stimulus onset. Similarly, the F-N contrast revealed significant beta modulation starting at around 200 msec post-stimulus onset on three right centrolateral channel pairs ($p = .04$; Fig. 3b and 4b), while no significant effect was observed on the left centrolateral sensors. While the H-N contrast showed an oscillatory modulation in the 20−24 Hz beta range, lower beta band modulation was observed in the F-N contrast (15–20 Hz). To confirm somatotopic distribution of beta modulation, we contrasted H and F conditions with N condition in the sensors selected for the non-corresponding extremity. No significant cluster emerged in either case (all $p>.1$). The alpha rhythm also showed significant suppression in the H-N contrast on left hemisphere hand-related channels ($p = .03$; Fig. 5). The oscillatory modulation occurred later compared to beta, namely at around 400 msec post word onset. No significant cluster emerged for the F-N contrast on foot-related channels ($p = .46$). Also in the alpha frequency range, the contrasts H-N and F-N on the sensors selected for the non-corresponding extremity provided no significant result ($p = .34$).

To determine the influence of imageability on oscillatory patterns of activation, we contrasted all high versus low imageability words independently from condition on the selected motor areas. No main effect of imageability on the selected motor regions was found during early lexico-semantic verb processing, as no significant cluster ($p = .17$) was found on the hand- and foot-related channels in the beta range. Besides, the analysis of possible interaction between imagery and condition resulted in no significant cluster for the H-N contrast ($p = .18$) and in no cluster for the F-N contrast. Similarly, no main effect of imagery and no interaction between condition and imagery were found for the alpha oscillations (all $p>.1$). To check whether the lack of

significance was due to the halved number of trials in the high and low imagery condition, we tested the lexico-semantic effect on those same trials for the following contrasts: (a) the high imageable H-N and F-N contrasts and (b) the low imageable H-N and F-N contrasts. Indeed, the H-N contrast remained statistically significant both for the high ($p = .007$) and the low ($p = .04$) imageability subcondition, thus suggesting that the number of the trials was adequate. This was however not the case for the F-N contrast, which did not reach significance neither in the high nor in the low imageability condition (all $p>.5$).

Discussion

The aim of the present study was to test the somatotopically distributed recruitment of cortical motor areas during action verb understanding in terms of modulations in the beta and alpha frequency ranges. The somatotopic information derived by a localizer task and the application of a cluster-based non-parametric statistical approach allowed us to find significant oscillatory effects accompanying the processing of single verbs. Specifically, we hypothesized that the processing of body-related verbs produces beta and alpha power suppression at around 200 msec post word onset in sensorimotor cortical areas that are engaged in the respective action execution. While we did observe power suppression in both frequency bands, different pattern emerged as for timing. As predicted, lexico-semantic processing of hand- and foot-related actions was accompanied by a stronger beta power suppression than the processing of non-body-related verbs on the cortical motor portion of hands and feet, respectively, around 200 msec. The H-N contrast revealed beta and alpha modulation in the left, but not in the right hemisphere. This asymmetric pattern of activation is in line with previous results
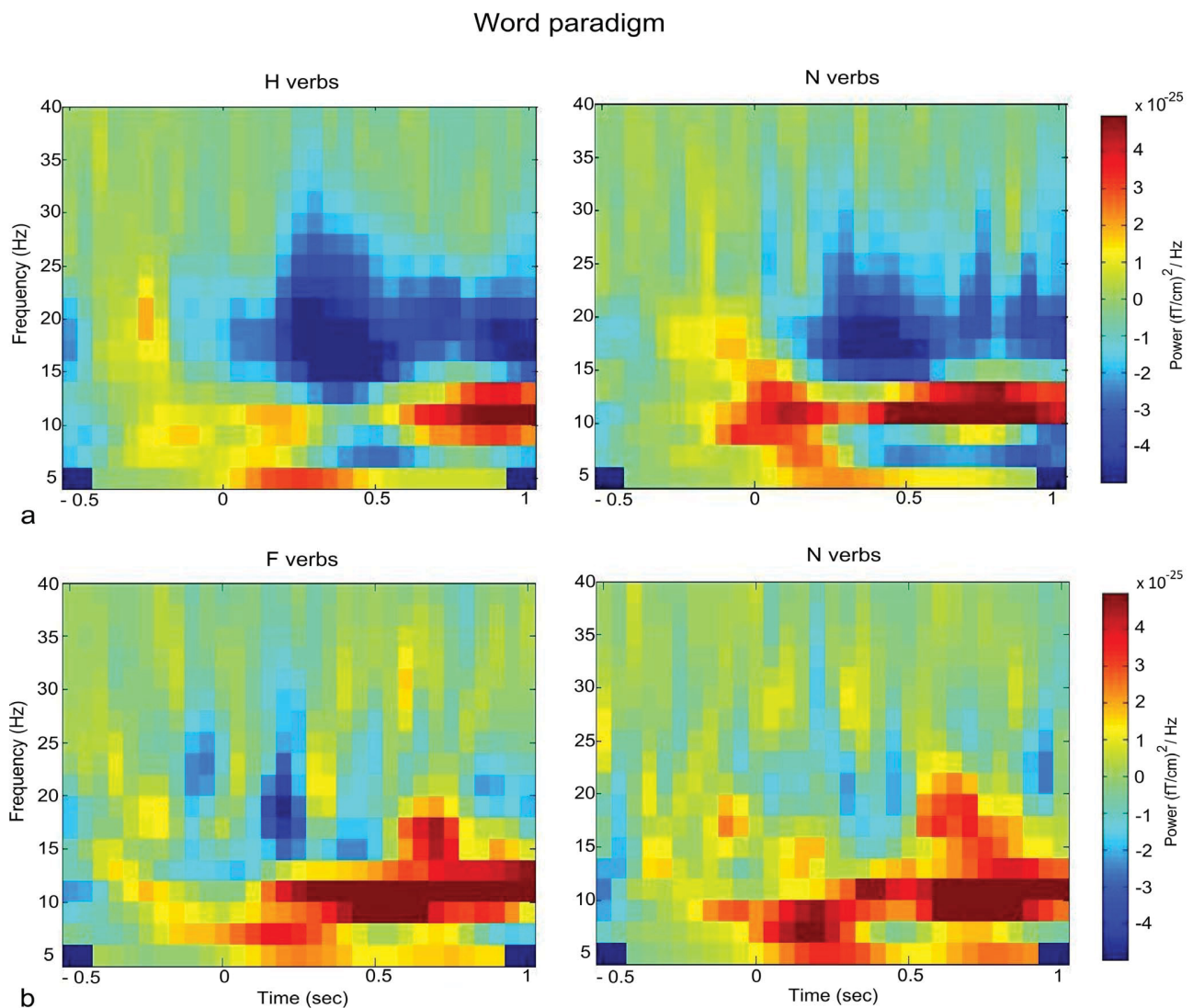
Word paradigm

Figure 3. Grand-average of frequency spectra. a) Grand-average of the H (left) and the N (right) condition on the average of the left-hemispheric hand-related sensors selected with the localizer task. b) Grand-average of the F (left) and the N (right) condition on the average of three foot-related sensors showing a significant effect.
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showing left-lateralized power decrease during the reading of hand verbs [39] and covert verb generation [38]. Under the assumption that beta suppression represents neural activation [54,55,56], our findings also agree with those from fMRI studies showing left-lateralized neural activity during action-related language processing [11,12,14,15,16]. Consistently, inhibition of reaction times during the processing of hand action verbs was induced with TMS on the left, but not on the right hemispheric hand portion of the motor cortex [57]. Investigating the relation of lesion sites and behavioural performance on lexical and conceptual action processing, Kemmerer et al. [58] behaviourally tested 226 patients with cerebral lesions, from 147 of whom anatomical data were also obtained. Significant impairment of lexical and conceptual knowledge of actions was exclusively found in patients with left hemispheric lesions including hand-related motor areas. Although less prominently, the right hemisphere is also likely to play a role in verb processing, as shown in a study on patients with right frontal lobe lesions [59]. Beta suppression on bilateral mouth and hand

regions was previously found during silent noun reading followed by delayed reading aloud, where suppression was further reinforced [60]. However, beta suppression in left-hemispheric cortical mouth areas started earlier and was stronger compared with the right hemisphere in fluent speakers. It is worth noting that while Salmelin et al. [60] addressed mental preparation for speech production as a possible explanation for the 20 Hz attenuation, the beta suppression found in the present study emerged in effector-related (hand and foot) motor areas and was stronger for H/F than N verbs. Furthermore, we did not apply a word generation task, thus minimizing the articulatory preparatory mechanisms related to overt speech in motor areas. Our results therefore point to a genuine difference between body-related and non-body-related verb processing and provide additional evidence for a prevalent role of the left cortical motor areas in processing action words.

In the studies mentioned above, all participants (and the large majority in Kemmerer et al.'s study [58]) were right-handed.
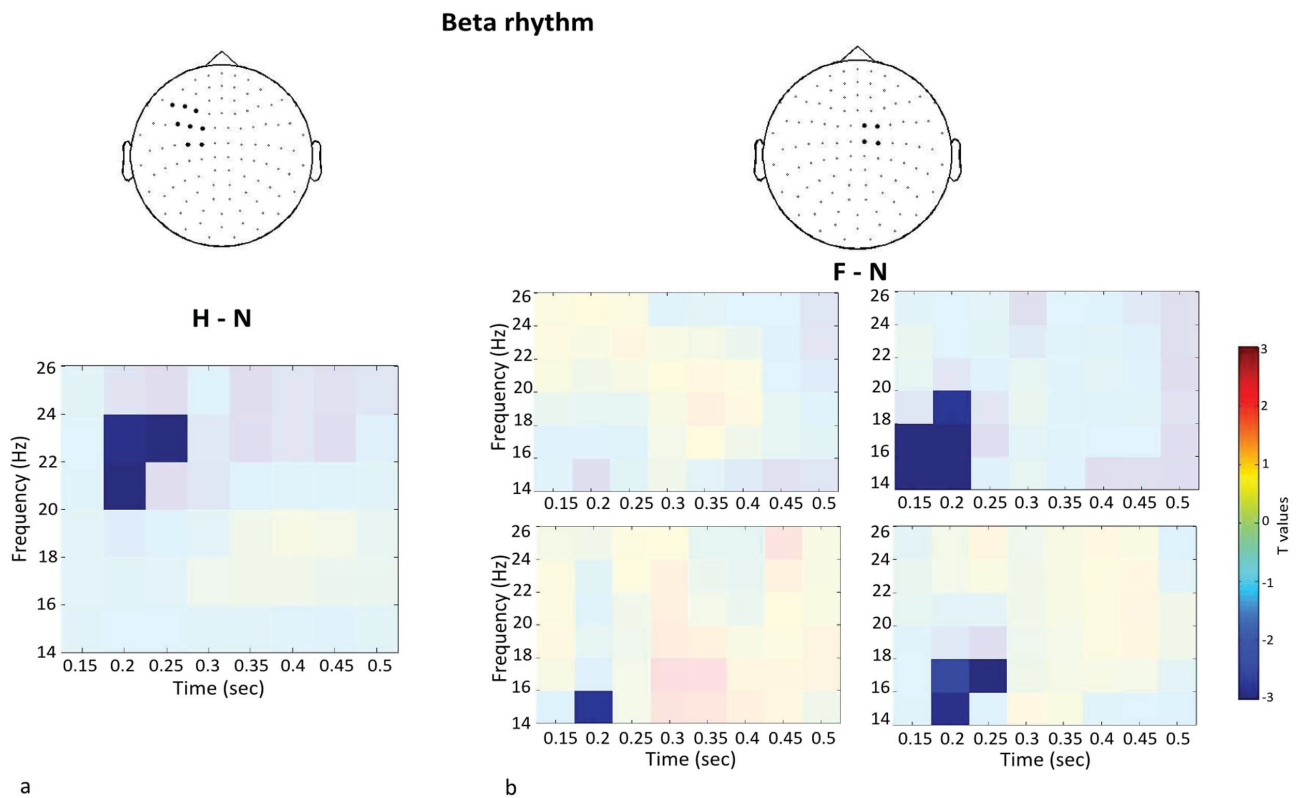
Beta rhythm

Figure 4. Statistical outcomes for the beta rhythm. a) T-values on a time-frequency map related to the H-N contrast, showing a significant cluster (saturated colours) on the average of the selected left-hemispheric hand-related sensors. b) Time-frequency maps of the F-N contrast showing a significant cluster on three foot-related sensors.
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Given that the processing of uni-manual action words is biased towards the dominant hand [61], left-lateralized brain activation in right-handed subjects, as found in the present study, is no great surprise. Indeed, the well-known left-biased asymmetry related to language processing seems to depend on handedness, as shown by an almost linear relationship between the degree of handedness and the direction of language dominance in terms of word generation in 326 healthy individuals [62]. Moreover, co-lateralization of praxis and language networks was demonstrated in individuals with right and with left language dominance [63]. In this context, it is of interest that lateralized beta power suppression may serve as an indicator of the side of language lateralization as well [64,38].

The use of non-body-related verbs in our paradigm permitted us to gain a view of neural activations subtending abstract words. As shown in Fig. 3a, the processing of abstract (N) verbs was also accompanied by beta suppression on the hand-related motor area, although this was significantly less when compared to the H condition. This finding agrees with the claim that abstract words are also embodied in perception and action. Specifically, Barsalou [65] proposed that abstract concepts are grounded in complex simulations of combined physical and introspective events that convey sensorimotor details. Vigliocco et al. [66] interpreted the apparent dichotomy between concrete and abstract word meanings as a preponderance of sensorimotor information, which is more abundant in concrete than abstract words. The hypothesized embodiment of abstract concepts is supported by neuroscientific studies. Using a similar paradigm to ours, Rüschemeyer et al. [15] found sensorimotor blood-oxygenation-level-dependent (BOLD)

activation both for concrete and abstract verbs, although less prominently for the latter. Similar results were observed for the comprehension of concrete and abstract sentences [67]. Both metaphoric/idiomatic and literal action sentences were shown to activate regions associated with sensorimotor processing [12,68,69]. Glenberg et al. [70] showed that task-related modulation of the motor system by means of manually transferring items towards or away from the body affected the comprehension of abstract as well as concrete sentences referring to transfer. Altogether, these findings point to a recruitment of motor cortical areas also for the processing of abstract words. Interestingly, implicit processing of ortho-phonological statistical regularities also activated the motor area, as shown in the fMRI study of Zubicaray et al. [71]. The authors found that non-words containing endings with probabilistic cues predictive of verb status, evoked enhanced activity compared with non-words with endings predictive of noun status, in a similar motor area as the one activated for action verbs. It might be reasoned that beta suppression shown by abstract verbs in motor areas in the present study partly depends on the typical verb ending. However, this is not the case because the hand and the non-body conditions showed a statistical difference that can not be explained by the typical verb ending.

Some differences between the H and the F condition emerged in the beta range, as shown by the respective contrasts with the control condition (Fig. 4). First, hand and foot verbs modulated beta oscillations in slightly different frequency bands. As suggested by Pfurtscheller et al. [72], each primary sensorimotor area may have its own intrinsic rhythm. Also, the corticomuscular analysis conducted for localization purposes showed on average highest
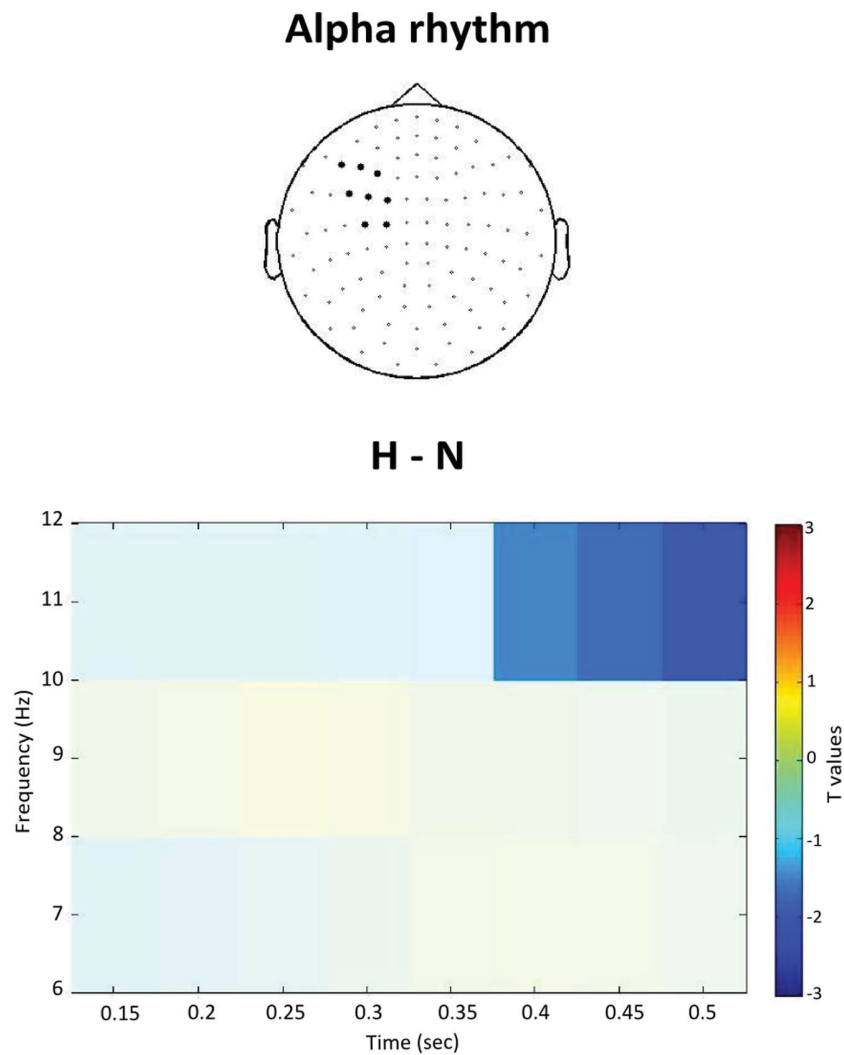
Alpha rhythm

H - N

Figure 5. Statistical outcome for the alpha rhythm. T-values on a time-frequency map related to the H-N contrast, showing a significant cluster (saturated colours) on the average of the selected left-hemispheric hand-related sensors.
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coherence in the 20–24 Hz beta range both for hands and feet contraction (data not shown), which is in agreement with previous reports [73]. This beta band is identical to the one showing an effect during linguistic processing of hand verbs. In our data, foot contraction and foot word processing apparently do not share the same beta frequency band. This difference possibly arises due to the fact that coherence measures (corticomuscular coupling) and power measures are not identical. Alternatively, it is possible that beta oscillations exhibit task-specificity and do not completely overlap between an isometric contraction and a linguistic task. However, since the time window of effect is comparable for the H-N and F-N contrast, both processes are likely to share the same function. Second, while beta suppression emerged on the left hemisphere in the H-N contrast, it was slightly right-lateralized in the F-N contrast. In our opinion, the foot-related lateralization results should be interpreted with caution. As the foot motor representation is to some extent buried in the interhemispheric fissure, it is difficult to accurately localize its activation by means of MEG. This is confirmed by the large overlap between sensors showing activation during right and left foot contraction (Fig. 2)

and might also explain why the F-N contrast did not reach significance neither in the high nor in the low imageability condition.

The pattern of beta decrease found in the present study is in line with previous investigations on verb generation [38] and silent sentence reading [31] as regards timing and hemispheric lateralization, respectively. Although in the study of van Elk et al. [31] the beta suppression during action verb processing reached significance at 400–600 ms after word onset, it was visibly present as early as 200 ms. It should also be noted that the task applied in our study required neither semantic processing nor awareness of the stimuli's body-relatedness. Our results therefore imply that even lower linguistic processing levels than the semantic one may engage motor brain regions, thus corroborating previous findings [42]. An interesting issue which remains to be addressed is whether the depth of cognitive action processing modulates the power of beta oscillations on motor regions.

Like beta, the alpha rhythm was also modulated by the body-relatedness of verbs, as hand-related verbs showed significantly stronger alpha suppression than non-body verbs. This finding

replicates that of van Elk et al. [31] at single verb level, although at a longer latency, namely at 400 instead of 200 msec post-stimulus onset. In contrast to beta oscillations, which are thought to largely reflect activity of the motor cortex, the 10 Hz signal was suggested to have a somatosensory origin [74]. It is therefore possible that reading body-related verbs also elicited a somatosensory component beyond the motor one associated to beta oscillations. In a similar manner to an executed movement, the processing of an action verb may be also sequenced into earlier processing steps, i.e. motor command associated with beta modulation and a later processing paralleling sensory feedback associated with alpha rhythm. This assumption would further expand the embodiment framework into the temporal domain, which should be focussed on in later studies. However, the processing of foot-related verbs did not result in alpha modulation. Possibly, the hand area is in closer contact with language as language has been suggested to evolve from manual gesture [9]. An alternative hypothesis on the functional role of alpha is that alpha reflects later semantic processes that dissociate from somatotopic language-related aspects. This might explain the absence of alpha modulation in the foot region.

As abstract verbs were less imageable than concrete verbs, we tested whether the level of imageability corresponded to significant oscillatory modulation and whether imagery processes played a role in the oscillatory effect found in the H-N and F-N contrast. The results showed similar oscillatory correlates for high and low imageable verbs and no interaction between imageability and condition on the selected hand and foot motor areas. Imageability appeared to play no role in the time-window between 150 and 500 msec post-stimulus onset. One noteworthy aspect is that a later onset of oscillatory modulations related to motor imagery processing has been reported previously [25,26,27]. Altogether, these findings rule out the hypothesis that imagery processes might have caused or modulated the oscillatory activation during lexico-semantic processing.

One limitation of the present study is that the match of the stimuli across conditions resulted in higher database frequency of non-body compared to body-related words. However, high-frequency words were shown to elicit a larger beta power suppression than low-frequency words [75]. If frequency had affected our results, we should have found larger beta suppression for the N than for the H/F condition. Alternatively, the higher

frequency of abstract words might have hidden a power difference between the experimental and control conditions. In fact, our results show that both experimental conditions induced larger beta suppression than the control condition. It is therefore unlikely that this oscillatory modulation depends on differences in lexical frequency between conditions.

To summarise, we tested the grounded cognition framework on brain oscillatory activity and showed for the first time that silent reading of action words in a lexical decision task elicited significant beta power suppression in a similar fashion to limb movements and according to a somatotopic distribution. The differential engagement of motor areas in body-related versus abstract verb processing was time-specific, as it was observed between 200 and 250 msec after word onset. Moreover, a possible somatosensory processing accompanying hand-related verb reading was suggested by significant power suppression in the alpha frequency range at later latencies. The present study lays the groundwork for an investigation of interaction and coherence between different brain areas that are involved, possibly essentially, in the neurobiology of language.

Supporting Information

Table S1 Stimuli used in the three conditions and relative indexes of familiarity (Fam.), imageability (Imag.), frequency (Freq.), and length (Lgth.). Means and standard deviations of various parameters are shown for each condition.
(DOC)

Acknowledgments

Author Contributions

Conceived and designed the experiments: AS KBR. Performed the experiments: VN AK HW KBR. Analyzed the data: VN AK. Contributed reagents/materials/analysis tools: NH. Wrote the paper: VN. Interpretation of the data: VN AK NH KBR. Revision of the article: AK HW NH AS KBR.

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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.

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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 (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

"I dont 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° horizontally by 0.7° 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) × 2 sides (right, left) × 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 centrolateral 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 (±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, it 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
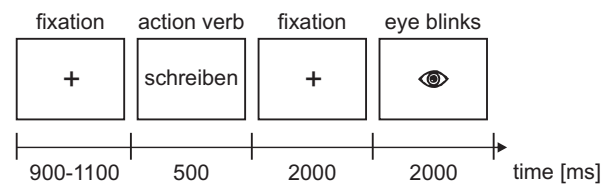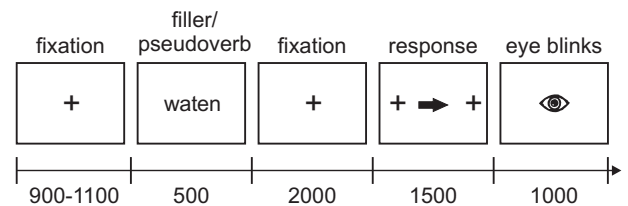

20% lexical decision

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 (Rüschemeyer 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, Rüschemeyer, & Bekkering, 2010), but also distinctly in the primary motor cortex (compare also Hauk & Pulvermüller, 2004; Rüschemeyer 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
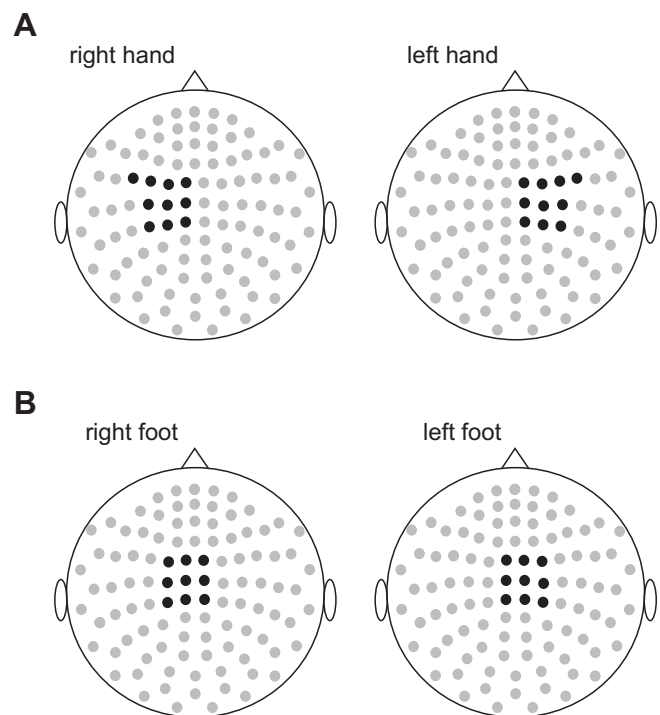

Fig. 2. MEG channel selection for dipole fitting of MF and MEF. Selected channels are indicated by a black dot, other channels are shown in grey. Each dot represents one pair of orthogonal gradiometer sensors, i.e., 102 channel locations are depicted for the 204 gradiometers. (A) Hand movements (B) foot 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
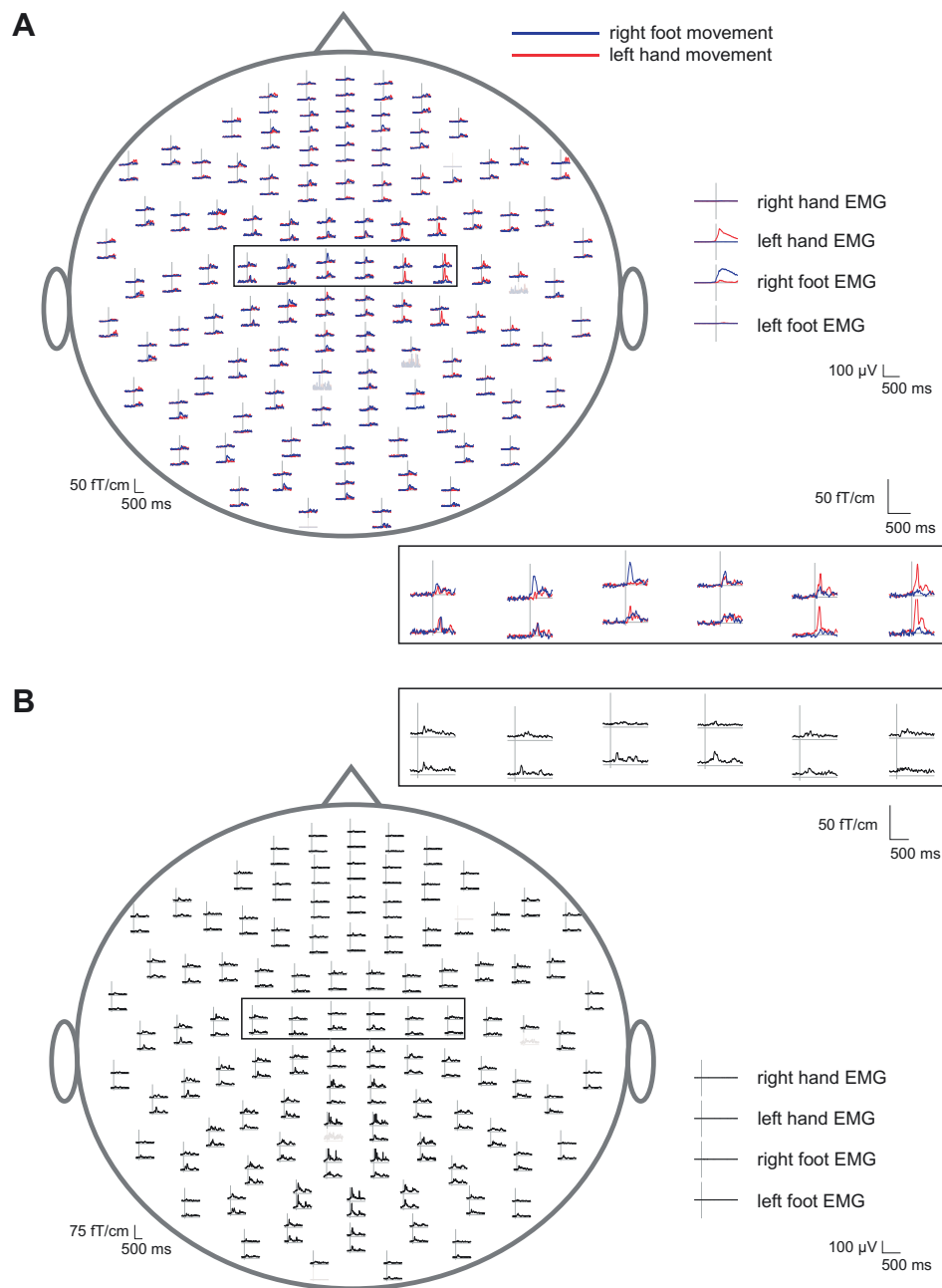
Fig. 3. Grandaverage root mean square evoked responses during the movement task and the verb paradigm in the 204 planar gradiometers. Top view, left is left, anterior is up. Bad channels are semi-transparently masked. (A) Movement task. An enlarged selection of sensorimotor channels is shown separately 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
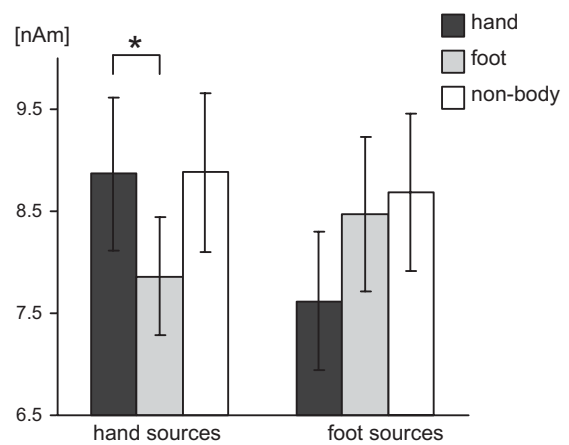

Fig. 5. Mean peak amplitudes for MF hand and foot sources in the three verb conditions, averaged across hemispheres. Error bars show SEM. * = $p < .05$
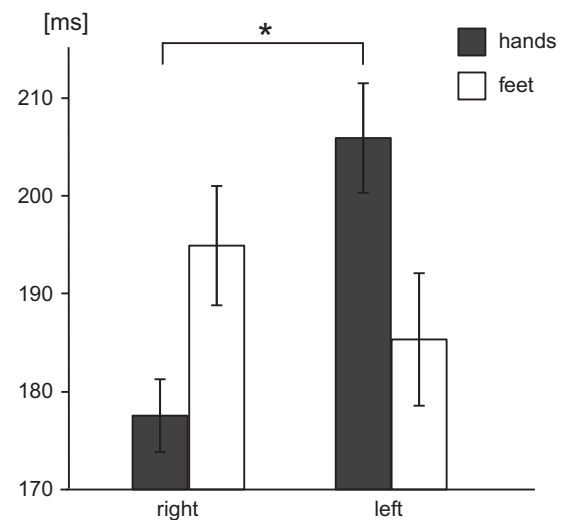

Fig. 6. Peak latencies for hand and foot MF sources, averaged across the three verb conditions. Note that right limb sources correspond to left hemispheric ECDs and vice versa. * = $p < .008$ (according to Bonferroni correction).
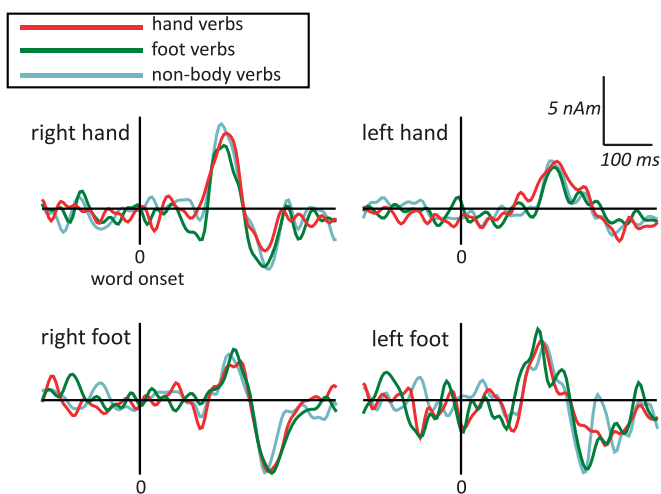
is building up across time but nevertheless smeared in averaged evoked responses as it is no longer phase-locked to the stimulus. Thus there would not only be simulation activation differing from baseline around 200 ms, but even a peak as seen in the current results and previous studies, implying fluctuations 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.

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.

Acknowledgments

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	pellen	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
H	**Mean**		**3.27**	**3.45**	**14.94**	**7.15**
H	**±SD**		**±0.29**	**±0.25**	**±2.45**	**±1.25**
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

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
F	**Mean**		**3.21**	**3.36**	**14.21**	**7.08**
F	**±SD**		**±0.47**	**±0.35**	**±3.05**	**±1.35**
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	bangen	to tfear	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	**Mean**		**3.31**	**2.17**	**12.63**	**6.42**
N	**±SD**		**±0.50**	**±0.29**	**±2.48**	**±1.05**

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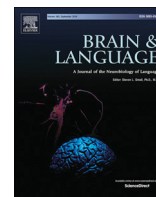
Auditory cortex sensitivity to the loudness attribute of verbs

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A B S T R A C T

The auditory cortex was shown to be activated during the processing of words describing actions with acoustic features. The present study further examines whether processing visually presented action words characterized by different levels of loudness, i.e. "loud" (to shout) and "quiet" actions (to whisper), differentially engage the auditory cortex. Twenty healthy participants were measured with magnetoencephalography (MEG) while reading inflected verbs followed by a short tone and semantic tasks. Based on the results of a localizer task, loudness sensitive temporal Brodmann areas A22, A41/42, and pSTS were inspected in the word paradigm. "Loud" actions induced significantly stronger beta power suppression compared to "quiet" actions in the left hemisphere. Smaller N100m amplitude related to tones following "loud" compared to "quiet" actions confirmed that auditory cortex sensitivity was modulated by action words. Results point to possible selective auditory simulation mechanisms involved in verb processing and support embodiment theories.

1. Introduction

Two main theoretical approaches have addressed cortical processes related to language and concepts understanding. According to amodal theories all concepts are processed in an amodal unit independently from their modality, thus excluding a contribution of perceptual-motor systems to language comprehension (Fodor, 2001; Pylyshyn, 1984). Differently, grounded (or embodied) cognition theories postulate that perceptual-motor processes are crucial in concept representation (Barsalou, 2008; Lakoff & Johnson, 1999; Pulvermüller, 2005). This latter framework predicts that sensory and motor systems are engaged not only in perception and motor execution, respectively, but also in language processing. Simulation has been suggested as a possible mechanism thereof (Barsalou, 2008; Gallese & Lakoff, 2005). While the role of the motor system in language processing has been the focus of extensive research, sensory systems have been addressed to a lesser extent (see Binder & Desai, 2011 for a review).

As for the auditory system, behavioural evidence for its involvement during visual word processing was found using a sound detection task embedded in a lexical decision task (Cao, Klepp, Schnitzler, Gross, & Biermann-Ruben, 2016). Here, participants with high lexical decision performance showed improved auditory perception when sound verbs instead of sound-plus-action verbs or abstract verbs were presented.

The cortical activations induced by animal and objects sounds as well as by words with acoustic features (e.g., "telephone") were shown to overlap in the posterior superior temporal gyrus (pSTG) and middle temporal gyrus (MTG; Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008). This suggests common neural sources underpinning auditory perception and processing of words with auditory features. In a study in which participants were trained to associate new objects with conceptual features, the STG was preferentially activated by objects associated with auditory compared to action features (James & Gauthier, 2003). In another study on retrieval of perceptual knowledge from long-term memory, sound judgments selectively activated the left pSTG and the adjacent parietal cortex (Kellenbach, Brett, & Patterson, 2001). Lesions of the left pSTG/pMTG were shown to be accompanied by slower reaction time and lower accuracy in visual recognition of sound related words, while no difference was found for sound-unrelated words (Trumpp et al., 2013a). Moreover, source estimates of scalp potentials related to word priming pointed to neural generators of sound words in temporal (BA21 and BA22) and in frontal areas (Trumpp et al., 2013b; Trumpp, Traub, Pulvermüller, & Kiefer, 2014). Together, these findings point to a crucial role of the auditory cortex, and specifically the STG, in coding sound-related conceptual information. The present study aims at further examining whether reading action verbs characterized by different levels of loudness, i.e. "loud" (to shout) and "quiet" actions (to

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whisper), differentially engage the auditory cortex.

Amplitude variation of cortical neural oscillations (e.g., alpha or beta) has been related to different cognitive and sensory-motor processes (Engel & Fries, 2010). In the auditory context in particular, tone and phoneme stimulation was accompanied by cortical recruitment in form of alpha power suppression (Crone, Boatman, Gordon, & Hao, 2001; Krause, Lang, Laine, Kuusisto, & Pörn, 1995) and sometimes additional beta suppression (Leske et al., 2014; Ross, Barat, & Fujioka, 2017; Weisz, Hartmann, Müller, Lorenz, & Obleser, 2011). Within the auditory system alpha power was specifically suppressed in locations most robustly responding to particular sound stimuli such as speech, music or animal stimuli (Pesters et al., 2016). The illusory perception of increased loudness as induced by large notch width was also reflected in decreased alpha power in auditory areas such as Heschl's gyrus and the MTG (Leske et al., 2014). To determine the oscillatory signal correlates of loudness modulation and to localize the specific cortical temporal areas engaged by loudness processing, we used a localizer task involving loud and quiet tone stimuli. The resulting specific temporal areas were then selected for word paradigm analyses to test the hypothesis of stronger auditory cortical activation following loud than quiet action words.

In the present study we further examined auditory cortex sensitivity after it had been modulated by reading action verbs. A short tone of stable intensity was presented after each verb to test whether word-dependent loudness affected tone-related N100m amplitude. Typically, the N100 amplitude is suppressed in case of stimulus repetition (Timm, SanMiguel, Saupe, & Schröger, 2013; see Bendixen, SanMiguel, & Schröger, 2012 for a review). This suppression was suggested to depend on refractory properties of the neuronal populations (Näätänen & Picton, 1987). We hypothesized that enhanced engagement of the auditory cortex induced by reading actions verbs with implied louder sounds would diminish the N100m amplitude of following tones due to inhibition of the auditory neural population.

Finally, we explored the role of movement amount, a parameter that is naturally related to action loudness as louder actions tend to involve more body movement. This relationship emerged in a study addressing the role of multiple sensory-motor modalities in semantic processing: subthreshold activation of the left STS and pMTG for sound-related words was shown to reach significance once rating norms for motion-related semantic word attributes were left out of the model (Fernandino et al., 2016). Notably, the area V5/MT+, which is associated with biological motion perception, was activated by the processing of motion concepts in a number of studies (see Binder & Desai, 2011 for a review) as well as of fictive motion sentences (e.g., "The hiking trail crossed the barren field"; Saygin, McCullough, Alac, & Emmorey, 2010). There is only little evidence on the oscillatory correlates of visual motion processing; it shows that an increased 15–20 Hz power suppression in the V5/MT+ area sustainedly accompanied video motion stimuli compared to static stimuli (Fawcett, Hillebrand, & Singh, 2007). To disentangle the effect of movement amount from that of loudness we split the original stimulus set into verbs with high and low movement amount according to subject ratings and investigated the 15–25 Hz frequency range in the V5/MT+ area.

We predict loudness variation as implied by loud and quiet action verbs to reflect in modulation of oscillatory patterns in temporal areas that are responsible for loudness processing; these areas are previously targeted via a localizer study applying loud and quiet tones. In the word paradigm we further expect loudness-dependent auditory cortex recruitment to affect the N100m amplitude related to a tone immediately following word presentation: lower N100m amplitude should follow increased cortical recruitment as for loud compared to quiet action sound words. Finally, we aim at disentangling cortical activation related to the amount of action loudness from that related to the amount of movement implied by the action.

2. Materials and methods

2.1. Participants

Twenty healthy volunteers (12 females) on average 24 years old (SD = 4.2), all monolingual German native speakers, were included in the study. Participants were right-handed (laterality quotient = 84.8; SD = 3.2; Edinburgh Handedness Inventory, Oldfield, 1971). The subjects had normal or corrected-to-normal vision and none reported neurological or psychiatric disorders. Participants provided written informed consent prior to magnetoencephalography (MEG) and received financial compensation for their participation. The study was in accordance with the Declaration of Helsinki and was approved by the local Ethics Committee of the Medical Faculty of the Heinrich Heine University, Düsseldorf (study number 4814R).

2.2. Stimuli and procedure

2.2.1. Localizer

For the tone paradigm sinusoidal 150 ms long tones with frequencies of 220, 440, or 880 Hz were created. Tones were presented binaurally. For 440 Hz tones, used as standard tones in an oddball task, a louder and a quieter version was used. Tones of 220 and 880 Hz were used as deviating tones and had an intermediate intensity. The relationship of quiet-intermediate-loud regarding tone intensity was 1:2:4, with the loudest tone being 85 dB. To determine loudness-sensitive cortical regions and loudness-related frequency activation patterns the difference between loud and quiet 440 Hz-tones was analysed. To help subjects paying attention to tones an oddball task was applied: participants had to respond to those tones deviating in frequency; these target tones did not deviate in loudness), i.e. 220 Hz and 880 Hz by lifting the right index finger. They were instructed to ignore loudness. A total of 50 loud and 50 quiet tones interspersed with 10 deviating tones was presented. As the study focussed on loudness, deviating target tones were excluded from the analyses. A fixation point was shown for the whole trial length. One second after the beginning of the trial a tone was presented (Fig. 1a). Inter-stimulus time was 2–3 s jittered in steps of 100 ms. In the case of a target stimulus, the trial ended 2 s after tone offset. The experiment lasted about 5 min and always followed the word paradigm. Practice trials were performed before starting the measurement.

2.2.2. Word paradigm

Word stimuli were German verbs describing human actions. A total of 268 suitable stimuli in the infinitive form were first sorted and then selected based on the results of an online rating study involving 30 monolingual German speakers. They were asked to report the loudness of each action via a Likert scale (0 = low, 5 = high) as well as the amount of the involved person's and object's movement separately. The resulting suitable 52 loud and 63 quiet action verbs showing an inter-subjects variance in loudness ratings ≤ 0.9 were then matched semi-automatically according to word length, frequency, bi-/trigram frequency and number of mouth/facial versus limb/whole body actions (Match program; van Casteren & Davis, 2007). The resulting 40 loud and 40 quiet action verbs (Table S1) were similar in word length ($t_{(77.8)} = 0.084$, p = .932), word frequency ($t_{(77.8)} = 0.395$, p = .693), bigram- ($t_{(77.8)} = -0.343$, p = .731) and trigram-frequency ($t_{(77.8)} = 0.499$, p = .618) as well as in amount of mouth/facial versus limb/whole body actions ($\chi_{(1)} = 0.450$, p = .502), while they differed in the implied loudness ($U = 820$, p < .001) and in the average amount of person and object movement ($U = 631$, p < .001) For additional follow-up analysis, a high and a low movement amount condition was determined by means of median split. The resulting conditions were similar in word frequency ($t_{(77.8)} = -0.131$, p = .895), bigram- ($t_{(77.8)} = 0.170$, p = .865), and trigram-frequency ($t_{(77.8)} = 1.044$, p = .299). Kendall's rank correlation between loudness
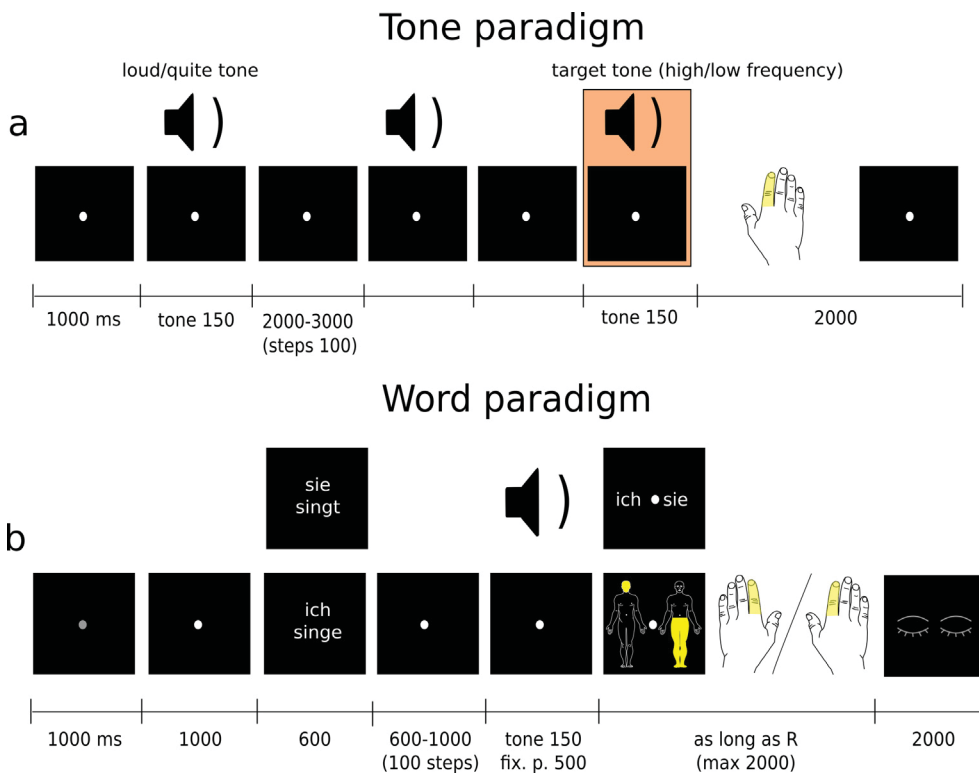
Tone paradigm

and movement amount was positive and significant (tau = 0.155; p = .042).

Trials started with a grey fixation point lasting 1 s and turning white 1 s before word onset. Each verb was projected on the screen and was conjugated in the first or third singular person; the related pronoun was centred above the verb (Fig. 1b). Each pronoun-verb pair remained on the screen for 600 ms and was repeated once across the course of the experiment with the subsequent tasks balanced (see below). Thereafter a fixation point was presented for an interval of 600–1000 ms jittered in steps of 100 ms. A 440 Hz-tone lasting 150 ms with stable intermediate intensity as that used in the localizer task followed. To ensure semantic processing participants were required to indicate after each verb either which body part was involved in the action or which pronoun had been presented. The pronoun-related task was designed to additionally induce different mental simulation of the action depending on the agent, a topic that is not covered in the present study and which will be addressed in a different investigation. Participants responded by lifting the right or the left index finger according to the position of the correct answer displayed on the screen. To this end, one of two response prompts pseudo-randomly appeared 350 ms after tone offset: for the pronoun task, the response prompt showed the two pronouns in first and third person, one on the left and one on the right half of the screen. For the body part task, two body silhouettes were shown on the left and right half of the screen, with different body parts highlighted in yellow (arms, head, legs, or entire body). The two types of prompts were counterbalanced regarding lateralisation of correct responses. The prompt remained on the screen until a response occurred but for a maximum of 2 s. Subjects were subsequently encouraged to blink and after 2 s the following trial started. Practice trials were given before starting the measurement.

2.3. Data acquisition and analysis

Neuromagnetic brain activity was continuously recorded with a 306-channel MEG system (Elekta Neuromag, Helsinki, Finland) including 204 orthogonal planar gradiometers and 102 magnetometers. A

bipolar horizontal and vertical electrooculogram (EOG) was recorded for the offline detection of eye movements. Four coils were attached to the subject's head bilaterally on the forehead and behind the ears. The position of these coils, prominent anatomical landmarks (right and left preauricular points and nasion) and additional points along the subject's head were digitized (Polhemus Isotrak) to map functional MEG data to individual anatomy. MEG data were digitized at 1000 Hz, bandpass filtered from 0.03 to 330 Hz online, and stored on a computer hard disk. MEG data from gradiometers were analysed with Matlab (Mathworks, Natick, MA, USA) and FieldTrip (http://fieldtrip. fcdonders.nl), a Matlab software toolbox for MEG and EEG analyses (Oostenveld, Fries, Maris, & Schoffelen, 2011).

2.3.1. Localizer

Epochs from −1 s to 1.5 s relative to the standard 440 Hz tone onsets were collected from the continuous data. Sensor jumps were eliminated with semiautomatic and visual artefact rejection. Continuous data were filtered with a high-pass filter of 2 Hz to remove DC drifts and with band-stop filters at 49–51, 99–101, 149–151 Hz; a Butterworth IIR zero-phase forward and reverse filter and a padding of 5 s were used. Independent component analysis (Jung et al., 2000) was applied to remove eye- and heart-related artefacts. Channels with no or defective signal were replaced with the average of their intact neighbours. To determine loudness-related oscillatory patterns and the specific brain regions of the temporal area involved in loudness processing, the following steps were used: first, the loudness effect on the N100m was localized at channel level. The N100 was addressed as this is a main human auditory evoked component and is also sensitive to loudness variation (Näätänen & Picton, 1987). Second, the frequency range of the induced activity in that area was identified. Third, source analysis was performed on the resulting frequency range and finally, virtual channels belonging to the significantly activated brain areas were selected for analyses of the word paradigm.

For the analysis of event-related fields data were filtered with a low-pass filter of 30 Hz and trials were averaged. Time-frequency representations (TFRs) were calculated by means of a fast Fourier

transform (FFT). An adaptive time-window including 5 cycles was shifted in steps of 50 ms from −1 s to 1.5 s. Data were padded up to 5 s. A single Hanning taper was applied to the epochs and power was estimated between 5 and 40 Hz in steps of 1 Hz. The time-frequency analysis was performed separately for horizontal and vertical planar gradiometers and the pairs of planar gradiometers were combined afterwards.

Dynamical Imaging of Coherent Sources (DICS; Gross et al., 2001) was applied to identify the cortical source of interest. DICS estimates cortical power on the source level by means of a spatial filter. The brain volume was discretized to a 3-D grid with 1 cm resolution. For each grid point the cross-spectral density matrix between all artefact-free MEG gradiometer sensor pairs was computed for the alpha band (8–12 Hz) by applying a Fourier transformation estimated with a multitaper method on a time window between 0 and 500 ms post-stimulus onset. Alpha frequency selection was based on the peak activity observed in the grandaverage TFRs, which was in line with that observed in earlier studies (Lehtelä, Salmelin, & Hari, 1997; Weisz et al., 2011). The leadfields were calculated for each grid point from a subject-specific realistic single-shell model of the brain derived from individual T1-weighted structural magnetic resonance images (MRIs; Nolte, 2003). Head models were created by co-registering individual MRIs with MEG data. For one subject the Montreal Neurological Institute (MNI) template was used instead due to a technical problem during MRI recording.

2.3.2. Word paradigm

Epochs from 1 s before verb-pronoun pair onset to 1 s after tone onset were collected from the continuous data. Only stimuli followed by correct responses entered the analysis. Sensor jumps, eye-, and muscle-related artefacts were eliminated with semiautomatic and visual artefact rejection. Data were filtered and channels with no or defective signal were replaced as described in the localizer study. Individual co-registered MRI-MEG data were used for analysis of regions of interest (ROIs); one subject (female, 28 years old) with deviant MRI settings was not included in the ROI analyses. Data from the remaining 19 subjects (11 females, average age = 24 ± 4.38) entered the analyses. The brain volume was discretized to a 3-D grid with 1 cm resolution, grid points were warped to the normalized brain and those belonging to the defined ROIs were determined by means of Brainnetome atlas (Fan, Li, Zhuo, Zhang, Wang, Chen, Yang, Chu, Xie, Laird, Fox, Eickhoff, Yu, & Jiang, 2016). Preprocessed MEG data were projected through an MNI normalized subject-specific linearly constrained minimum variance (LCMV) filter for the selected virtual channels. Display of whole-head source grandaverage of the loud-quiet contrast was done with the same approach as for the source analysis in the localizer study.

2.4. Statistical analysis

2.4.1. Localizer

Event-related field (ERF) amplitude values as well as oscillatory power values related to loud and quiet tones were measured across all channels and grid points, respectively. Considering the multi-dimensionality of the MEG data, a nonparametric randomization test (Maris & Oostenveld, 2007) was used that effectively corrects for multiple comparisons. First, we addressed the effect of loudness on the N100, as this component is strongly related to auditory perception (Näätänen & Picton, 1987). In the case of ERF, data were averaged across time between 100 and 150 ms after tone onset as this is the typical N100 time-range. For every channel the two conditions were compared across subjects by means of a *t*-test for dependent samples. All samples with a *t*-value larger than the threshold (corresponding to p < .05) were selected and clustered with spatially adjacent bins. A cluster-level statistic was then calculated by taking the sum of the *t*-values of the samples within every cluster. Nonparametric permutation testing, which consisted in computing 5000 random sets of

permutations between the two conditions in the sensor space, was used to obtain a distribution of cluster statistics and the significance level of the observed cluster (p < .05). The same approach was used for the statistical comparison of oscillatory sources. Brain areas corresponding to significant cortical sources were identified using the Brainnetome atlas integrated into FieldTrip.

2.4.2. Word paradigm

Atlas labels of the temporal areas showing a significant effect in the localizer source analysis, i.e. a sensitivity for loudness of auditory stimuli, were used to select the corresponding virtual channels for statistics in the word paradigm. Here, a two-step statistical procedure was used: first, the power difference between the loud and quiet condition was calculated by means of t-values. These were calculated for each virtual channel, frequency bin and time point of each subject. In a second step, the cluster-based non-parametric randomization approach described above was used to test significance at group level (Maris & Oostenveld, 2007). The group analysis was run on the average across the virtual channels, on a time-window between 100 and 500 ms after word onset, and on a frequency range between 8 and 30 Hz. This broad frequency range was chosen to detect possible paradigm-dependent differential activation and was motivated by the lack of leading literature findings concerning loudness modulation as induced by word processing. According to the null hypothesis, the difference between the two conditions should not significantly differ from zero, that is, t-values should be replaceable by zero. Thus, resulting t-values of each subject and values from a pseudo-dataset consisting of zeros went through the nonparametric randomization test. Analyses were run separately on the left and right hemispheres due to the different role of the two hemispheres in sound processing (Lewis, Wightman, Brefczynski, Phinney, Binder, & DeYoe, 2004; Pizzamiglio et al., 2005; see Discussion) and the predominant contribution of the left hemisphere in linguistic processing in right-handers (Knecht et al., 2000; Vingerhoets et al., 2013; Willems, Hagoort, & Casasanto, 2010). Using the same method, analysis of high versus low movement amount verbs was conducted in the right and left V5/MT+ area between 15 and 25 Hz and from 100 to 500 ms after word onset. This more narrow frequency range was chosen on the base of earlier findings related to visual motion processing (Fawcett et al., 2007). Logarithmically transformed power values were used in order to improve analysis sensitivity. To better evaluate the anatomo-functional specificity of the loudness effect in auditory areas, we additionally tested for an effect of word-related loudness in the area V5/MT+ between 8 and 30 Hz and from 100 to 500 ms after word onset.

Tone-related ERF analysis in the word paradigm included 19 subjects (12 females, average age = 24 ± 4.05), as no tone was presented to one participant (male, 32 years old) due to a technical issue. For each hemisphere, ERF data were contrasted between the loud and quiet verb condition in the time-window between 100 and 150 ms after tone onset on the averaged channels showing the strongest peak amplitude across subjects (Fig. 5a).

3. Results

3.1. Localizer

Participants attended to the tones as demonstrated by an average accuracy of 96.5% (SD = 5.7) in the oddball task. The N100m was observable bilaterally with a peak between 100 and 150 ms (Fig. 2a). It was bilaterally modulated by loudness, with loud tones inducing larger N100m amplitudes (Fig. 2b). Grandaverage TFRs in channels showing a significant N100m loudness effect (p = .003) indicated a power suppression centred around 10 Hz (Fig. 2c). Based on this and on previous evidence (Lehtelä et al., 1997; Weisz et al., 2011), source analysis was centred in the alpha frequency (8–12 Hz). Results showed significantly stronger alpha suppression following loud tones in areas including A22, A41/42, and caudoposterior STS (cpSTS) of the right hemisphere
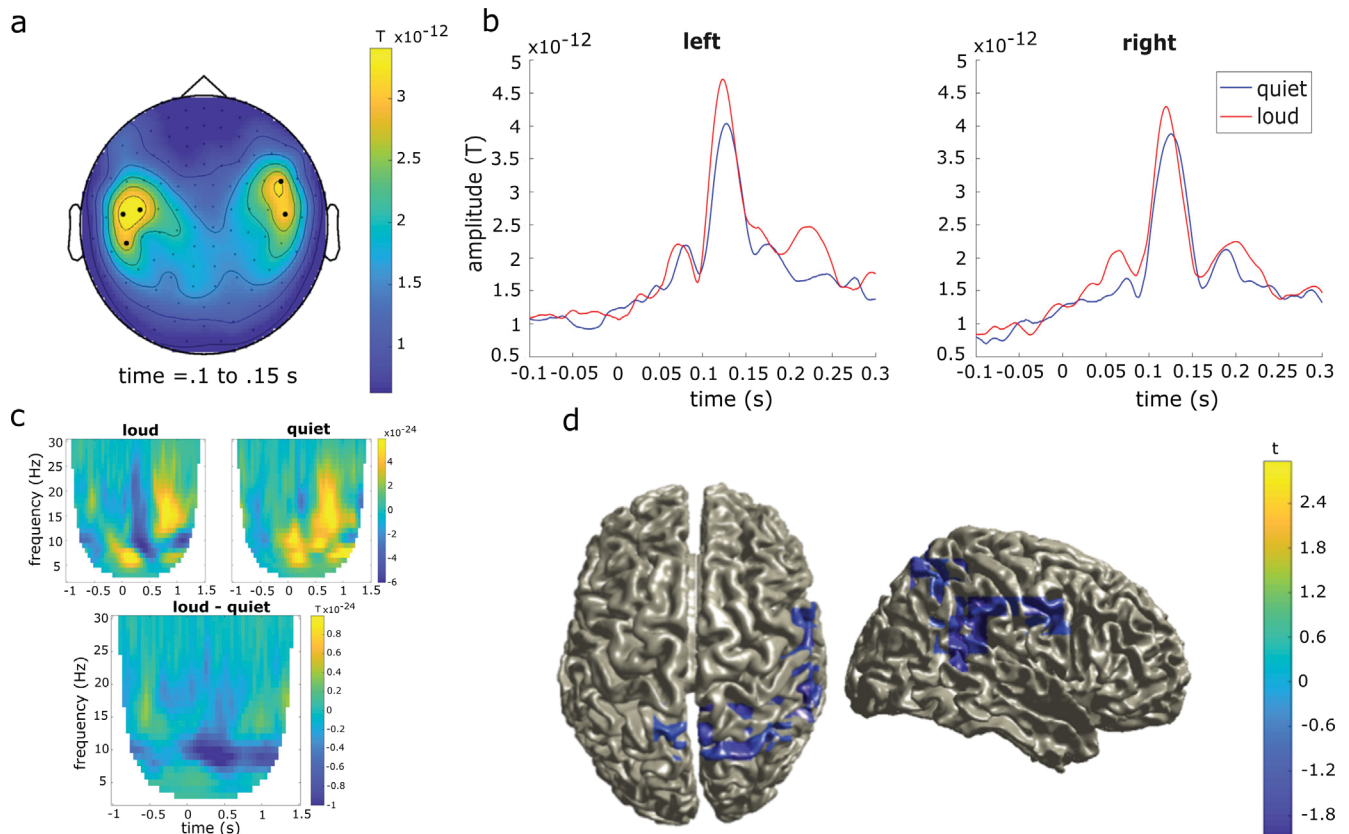
Fig. 2. Localizer study. (a) Grandaverage of the N100m peak amplitude between 100 and 150 ms after tone onset with channels exhibiting maximum activity depicted by bold points; (b) grandaverage N100m time-course for loud (red) and quiet (blue) tones in the left- and right-hemispheric channels showing maximum activity; (c) Baseline corrected grandaverage TFRs of the loud and quiet tones condition (baseline = −600 to −100 ms) and grandaverage difference across channels showing a significant N100m amplitude modulation by loudness; (d) source estimation of the alpha band in the contrast loud vs. quiet tones displayed on the MNI template brain (only significant values shown).

(p = .035; Fig. 2d) together with other areas such as right inferior parietal lobule and precuneus. As we were interested in the activity of the auditory cortex, the specific areas belonging to the STG (i.e., A22 and A41/42) and to the posterior STS (i.e., cpSTS) were further inspected in the word paradigm (Fig. 3a) in homologous areas of both hemispheres.

3.2. Word paradigm

A behavioural average task accuracy of 94.3% (SD = 7.3) indicated that the presented words were attended to by the participants. The "loud" vs. "quiet" contrast on the averaged selected temporal areas including 12 virtual channels per hemisphere showed significantly stronger beta power suppression following "loud" compared to "quiet" verbs in the range between 20 and 26 Hz in the left hemisphere (p = .015; Fig. 3b); the effect survived Bonferroni correction for multiple comparisons related to the two hemispheres. Grandaverages of the single conditions showed that the amount of power suppression was modulated by loudness both in the alpha and in the beta range and that the effect was limited to the time-window related to word processing (Fig. 4). While low beta suppression was also visible in the right hemisphere, the related negative cluster did not reach significance (p = .114; Fig. 3c). All analyses were conducted on virtual channels. For an additional overview of the effects across all cortical (non-virtual) sensors please refer to Figure S1, which shows whole-brain grand-averages for the loud versus quiet contrast in the alpha and the beta frequency range in the 500 ms after word-onset. N100m amplitude related to tones following verbs was significantly smaller after loud than quiet actions and survived Bonferroni correction for multiple

comparisons (p = .012; Fig. 5). Consistent with oscillatory source results for the verbal processing, this effect emerged in the left hemisphere while no cluster was found in the right hemisphere. Grand-average source plots for the tone-related 8–12 Hz modulation following loud versus quiet actions in the word paradigm are shown in Fig. S2; no significant effect emerged at source level (p = .764). A follow-up contrast of actions implying high and low movement amount resulted in stronger beta suppression following high movement verbs in the 24–25 Hz frequency range in the right V5/MT+ (5 virtual channels; p = .049; Fig. 6) starting shortly after 200 ms after visual word onset until almost 500 ms. No significant cluster was found either in the left hemisphere nor, more importantly, in the selected auditory areas. The contrast loud versus quiet actions resulted in no significant effect either in the left (p = .555) nor in the right (p = .665) V5/MT+.

4. Discussion

The current study aimed at identifying modulation of cortical engagement depending on loudness variation in visually presented action verbs. To identify loudness-sensitive temporal areas a tone localizer study was used. This showed a bilateral N100m following tones, with loud tones eliciting significantly larger amplitudes than quiet tones. The loudness effect also consisted in increased power suppression after loud tones centred in the alpha frequency range. Source analysis confirmed a significantly stronger alpha suppression in the right temporal areas A41/42, A22, and cpSTS. These results are consistent with previous EEG/MEG reports of alpha power decrease accompanying tone processing in superior temporal areas including the auditory cortex (Lehtelä et al., 1997; Weisz et al., 2011). The right lateralization of the
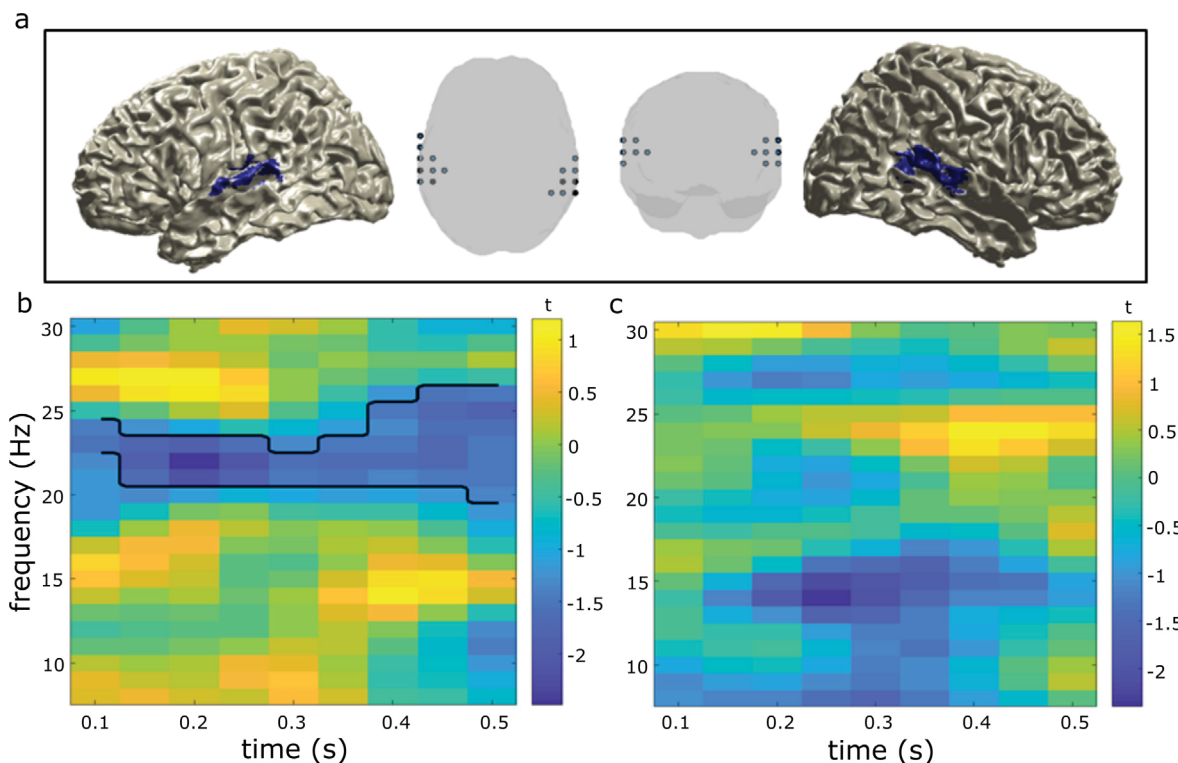
Fig. 3. (a) Grid points representing virtual channels of area A22, A41/42, and cpSTS displayed on an MNI template brain. (b) Result of statistical comparisons on virtual channels between loud and quiet action words (colours represent t-values). Data of temporal areas A22, A41/42 and cpSTS were averaged for the left (b) and right (c) hemisphere (significant cluster outlined).

loudness effect in the context of the applied frequency detection task is in line with results showing that the cortical network of loudness-discrimination and that activated by unexpected pitch changes overlap in the right STG (Rinne et al., 2007).

Stronger power suppression in temporal areas also accompanied increased action-related loudness in the word paradigm, although in the beta range. While the effect was significant in the left hemisphere, the cluster in the right hemisphere did not reach significance. Beta suppression emerged at about 200 ms after word onset (Fig. 4b), in line with semantic processing latency (Hauk & Pulvermüller, 2004; Pulvermüller, Härle, & Hummel, 2001; van Elk, van Schie, Zwaan, & Bekkering, 2010) and in line with our previous results on motor cortex engagement while reading body-related verbs (Niccolai et al., 2014). The increased auditory cortical recruitment in form of power suppression related to loudness both in the localizer and in the word paradigm suggests a role of auditory areas not only in perception of acoustic stimuli, but also in understanding written language with acoustic connotation.

Yet some peculiarities of these two processes, i.e. linguistic and auditory processing, were also observed. Linguistic processing induced suppression of higher frequencies, namely beta, compared to tone processing, which was mainly characterised by alpha suppression and only weakly by beta suppression (Fig. 2c). On the one hand, beta suppression was previously found to accompany tone presentation (Weisz et al., 2011) and tone loudness modulation (Leske et al., 2014) in addition to alpha suppression thus hinting to commonalities between alpha and beta oscillations. On the other hand, the two paradigms of the current study had important differences: first, beyond the fact that stimuli were auditory in one paradigm and visual (plus a tone) in the other, single tones as those used in the localizer task imply a far narrower qualitative acoustic spectrum then the variegated sounds implied by actions. Stimulus complexity indeed has an effect on the
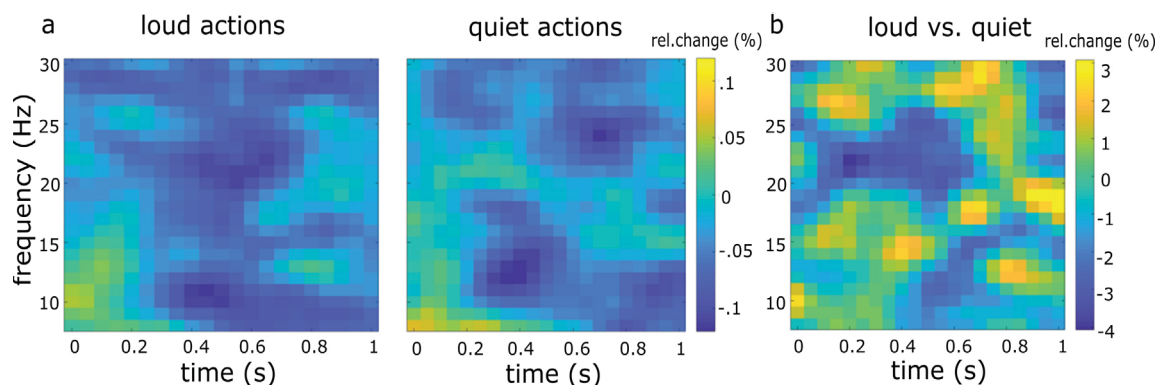

Fig. 4. (a) Baseline-corrected grandaverages of the loud and quiet action verb condition on the left hemisphere virtual channels of the areas A22, A41/42, and cpSTS; baseline time-window is 600 until 100 ms before word onset. (b) Grandverage of the difference between the loud and quiet action verb condition on the selected left-hemispheric virtual channels.
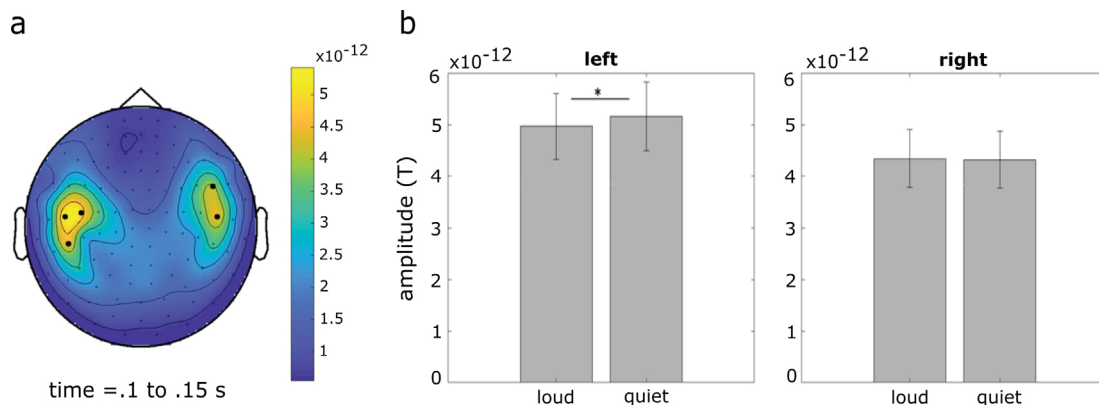
Fig. 5. Tone-related grandaverages in the word paradigm. (a) N100m peak amplitude between 100 and 150 ms after tone onset; (b) mean and standard error of the mean amplitude values of the N100m in the 100–150 ms time-window after tone onset following loud and quiet action verbs in the averaged left- and right-hemispheric channels exhibiting maximum activity across subjects (depicted by bold points).
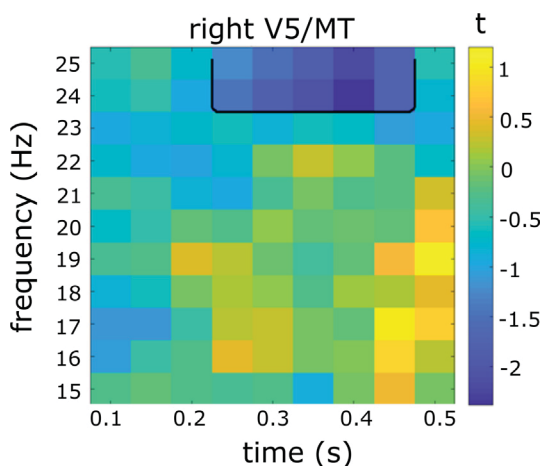

Fig. 6. Statistical comparison on virtual channels in the right V5/MT + area for high versus low movement amount action verbs (significant cluster outlined).

preponderance of a particular frequency range as shown by some investigations: an ECoG study showed that visual spatial contrast patterns (luminance gratings) were accompanied by 50 Hz gamma oscillations in the visual cortex, while higher frequencies around 150 Hz emerged when natural images were presented (Hermes, Miller, Wandell, & Winawer, 2015). In the linguistic context, while words were shown to elicit increased coherence in the alpha (8–13 Hz) and high gamma (60–90 Hz) frequency bands, symbols elicited increased coherence in the high beta (21–29 Hz) and low gamma (30–45 Hz) frequency range (Liljeström, Vartiainen, Kujala, & Salmelin, 2018). Second, tones in the localizer study were non-target stimuli and thus implied more superficial processing, whereas words had to be not only semantically processed but also retained for a while in order to respond to the following prompt. Task differences can affect the preponderance of an oscillatory frequency as shown by varying instructions. Shahin, Picton, and Miller (2009) let participants perform either a semantic or an auditory task on the same auditory word material spoken by a male vs. a female voice: the semantic task resulted in enhanced upper beta and gamma band activity as compared with the auditory task. Therefore, although different frequency ranges observed in the localizer and in the word paradigm point to only partial qualitative overlap between the subtended neural mechanisms, stimulus and task peculiarities may have played a role as well.

The left dominance of the loudness effect in the word paradigm may be explained by the hemispheric specialisation for linguistic material in our right-handed subjects. Lateral parts of the area BA42 in the language dominant hemisphere were shown to include Wernicke's area, a region involved in language comprehension (Démonet et al., 1992). A positron emission tomography (PET) study in which subjects performed auditory tasks including tone frequency discrimination, syllable perception, and lexical decision based on word/non-word stimuli showed that lateralization patterns differed as a function of stimulus type (Poeppel, 2004). While the lexical decision task generated stronger responses in the left hemisphere, frequency discrimination induced a stronger response in the right pSTG and MTG. Predominantly left hemispheric activation by semantic hallmarks of human action sounds, including the posterior superior temporal area, was also shown by previous fMRI studies (Gazzola, Aziz-Zadeh, & Keysers, 2006; Pizzamiglio et al., 2005). Also, while human action sounds elicited larger 8–13 Hz power suppression over the left hemisphere, non-human sounds were accompanied by stronger activation over the right hemisphere (Pineda et al., 2013; Specht & Reul, 2003). The lateralisation patterns observed in the word and tone paradigm of the current study agree with these findings and further suggest that loudness characteristics embedded in verb semantics specifically activate the left auditory areas in a comparable way to human action sounds.

We further examined auditory cortex sensitivity after it had been modulated by the aforementioned action words. In the word paradigm, the tone-related N100m showed smaller amplitude for tones following loud action verbs compared to those following quiet action verbs in the left hemisphere. The N100 suppression likely depends on refractory properties of the neuronal populations (Näätänen & Picton, 1987). Possibly, the N100m suppression observed in the present paradigm reflects reduced neural resource availability following verbs that activate the auditory cortex more strongly as in the case of loud actions. The lateralisation of this effect is consistent with the left lateralisation found for action loudness, thus suggesting that verb processing affects following engagement of auditory cortical areas. Further interpretations of the N100 suppression propose that it depends on self-generation compared to external generation of tones (Bendixen et al., 2012; Ross et al., 2017) with suppressions being stronger in the self-generated mode. Another factor of influence is expectancy of the stimulus, i.e. consistency between the anticipated and perceived stimuli (Hsu, Hämäläinen, & Waszak, 2016). Accordingly, self-generated tones would be highly expected, reveal no new information and thus do not need to be processed deeply (Bendixen et al., 2012). From this perspective, a tentative interpretation of our N100m suppression result might be that a tone occurring while processing loud actions and thus inducing enhanced auditory cortex activation would be less salient and less informative (in the sense of less new information) than a tone occurring while processing quiet actions.

Interestingly, imagined syllable loudness was shown to affect auditory cortical activation thus suggesting that it can directly influence auditory processes (Tian, Ding, Teng, Bai, & Poeppel, 2018). While this

is in line with our findings of N100m modulation by word condition, the question remains whether auditory cortical activation in the current study constitutes a core representation of verbs or whether active cognitive processes are required. Since participants were unaware of the aim of the study and of the loudness conditions, the observed auditory modulation is probably not elicited in a top-down manner. However, semantic processing might play a relevant role independently from the loudness aspect: whether auditory cortical modulation is influenced by the depth of processing (i.e., lexical vs. semantic) and from being or not being aware of the loudness variable remain open questions for further investigations.

As a natural implication loud actions are often characterised by a higher amount of body-related movement than quiet actions. This was the case for our word stimuli according to results of the rating study. Additional analyses were thus conducted on verbs with high versus low movement amount to disentangle its effect from that one of action loudness. Actions implying higher movement amount induced stronger beta suppression in the 24–25 Hz range in the right V5/MT+. On the opposite, no movement amount effect emerged in the right or left auditory areas, thus suggesting that the reported loudness effect did not depend on the movement amount implied by the action. Although the study material was not specifically selected for the aim of testing movement amount, these preliminary results suggest that loudness and movement amount probably reflect two independent processes occurring in the left auditory and the right biological motion area, respectively. However, multisensory areas of the pSTS/pMTG have been shown to be activated by nouns related to both sound and visual motion (Beauchamp, 2005; Fernandino et al., 2016). In principle, louder actions may imply enhanced multimodal activation compared to quiet actions not only with regard to motion but also for example sensory feedback. Further studies targeting the various sensorimotor aspects elicited by linguistic material may shed light on the multimodal engagement of the STS.

Beyond auditory areas, tone loudness also modulated activations in sensorimotor and parietal areas. This is consistent with previous results showing that increased tone loudness was accompanied not only by enhanced activation of predominantly right MTG but also right inferior parietal lobule and middle frontal gyrus (Leske et al., 2014) as well as primary visual and somatosensory cortex (Wyss et al., 2014). Considering that alpha suppression was shown to play a role in the engagement of visual (Clayton, Yeung, & Cohen Kadosh, 2018), sensorimotor (Haegens, Nácher, Luna, Romo, & Jensen, 2011), somatosensory, and auditory regions (Haegens et al., 2015), current and earlier results (Weisz et al., 2011) add evidence to a possible common function of alpha desynchronization across different sensory modalities (Haegens et al., 2015). In this regard, it has been suggested that alpha oscillations may constitute a selection mechanism across large, spatially separated areas and thus play a role in regulating information flow within the brain (Haegens et al., 2015; Pesters et al., 2016).

One limitation of the current study is the lack of a 'no-sound' semantic condition: one requirement for the study was the body-relatedness of actions. Considering that each body action may potentially produce a noise, we considered the loud vs. quiet contrast safer than no-sound vs. sound action. Another critical aspect is that while a localizer was applied for the loudness effect, no localizer was used to select the visual-motion area. The choice of targeting this area by means of a brain atlas was motivated by the fact that this area, differently from loudness-sensitive areas, is both anatomically and functionally well defined.

In conclusion, differential auditory cortex recruitment was observed both for loudness modulation in a tone paradigm as well as for implied loudness in an action verb reading paradigm. Increased auditory cortical recruitment by loud compared to quiet action sound words was associated with a suppression of the N100m to a subsequent tone. Results point to possible selective auditory simulation mechanisms involved in verb processing and provide support to embodiment theories.

Declaration of Competing Interest

None.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandl.2019.104726.

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Induced and Evoked Brain Activation Related to the Processing of Onomatopoetic Verbs

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Abstract: Grounded cognition theory postulates that cognitive processes related to motor or sensory content are processed by brain networks involved in motor execution and perception, respectively. Processing words with auditory features was shown to activate the auditory cortex. Our study aimed at determining whether onomatopoetic verbs (e.g., "tröpfeln"—to dripple), whose articulation reproduces the sound of respective actions, engage the auditory cortex more than non-onomatopoetic verbs. Alpha and beta brain frequencies as well as evoked-related fields (ERFs) were targeted as potential neurophysiological correlates of this linguistic auditory quality. Twenty participants were measured with magnetoencephalography (MEG) while semantically processing visually presented onomatopoetic and non-onomatopoetic German verbs. While a descriptively stronger left temporal alpha desynchronization for onomatopoetic verbs did not reach statistical significance, a larger ERF for onomatopoetic verbs emerged at about 240 ms in the centro-parietal area. Findings suggest increased cortical activation related to onomatopoeias in linguistically relevant areas.

Keywords: onomatopoeia; verbs; beta; alpha; ERF; MEG

1. Introduction

The theory of grounded cognition proposes that cognition is dependent on the brain's modal systems for perception, action and introspection [1]. This theory postulates that the sensory and motor brain areas are activated not only during perception or action, but also by cognitive processes such as understanding words related to these modalities. Some studies show that this is true, for example, for the motor area: reading hand- and foot-related action words activate areas belonging to the motor cortex and responsible for hand and foot movements, respectively [2–8]. Analogously, words implying acoustic features were shown to activate, beyond other areas, part of the same temporal brain area also recruited during sound perception [9]. Behavioural findings showed that reading auditory-related verbs improved the detection of subsequent hardly audible sounds in participants with high lexical decision performance [10]. So far, there is a lack of research about such cognitive simulation processes involving the auditory system during word processing and even less studies focussed on neural oscillations in this context. The power of brain oscillations can be used as an index of neural activation level. While synchronized beta oscillations (12–25 Hz) have been proposed to maintain the current cognitive or sensorimotor state, desynchronized beta oscillations have been interpreted also as local cortical activation, for example, related to movements or to auditory processing [11]. Synchronization of the alpha frequency (8–12 Hz) is viewed as an idle state of the brain [12] while, e.g., alpha (8–12 Hz) desynchronization in the auditory cortex has been shown to accompany auditory stimulation [13]. Within the framework of the grounded cognition theory, it

was found that visually presented words describing loud actions induced stronger beta frequency desynchronization in the left auditory cortex compared to words describing quiet actions [14].

Onomatopoetic words are especially interesting in this context as they tend to acoustically reproduce the sound (and sometimes the shape or even other semantic qualities) of the object or action they refer to [15,16]. In earlier studies, onomatopoetic words were shown to be accompanied by stronger activation in those areas that are usually activated by the related real-sound stimuli: for example, animal sound-related onomatopoetic words (e.g., the Japanese word "wanwan" indicating the dog's barking) activated areas responsible for the perception of non-verbal sounds [17–22]. However, these studies exclusively focussed on interjections, that is, words that only imitate a sound (e.g., "kikeriki" for a rooster call); these, however, are neither verbs, nor nouns, nor adjectives. Profiting from the strong onomatopoetic quality of interjections, most studies so far compared these to other non-onomatopoetic word classes to determine the effect of onomatopoeias on brain and behaviour [15,17–20,22–26]. Auditorily presented onomatopoetic interjections were shown to activate the auditory cortex and, specifically, the bilateral middle and anterior superior temporal sulcus (STS) more strongly than non-onomatopoetic nouns with the same reading frequency, auditory familiarity and auditory imageability [22]. Similarly, activation of the right posterior superior temporal sulcus (pSTS) following onomatopoetic word presentation was also found in another study [24]. Whereas these studies hint at a peculiar effect of onomatopoetic words, the comparison of interjections with non-onomatopoetic words belonging to different grammatical classes is problematic. Since the grammatical class of the word stimuli influences the localization and strength of brain activation as well [23,27], comparing interjections with verbs might result in effects going beyond onomatopoeias.

Few electroencephalography (EEG) studies applied onomatopoetic words instead of interjections; auditorily presented onomatopoetic adverbs (e.g., the Japanese "gatagata" for "rattling") were found to elicit a larger late-positive sustained complex at about 400–800 ms than control adverbs, thus reflecting increased post-lexical processing [23]. In another study, processing visually presented onomatopoetic verbs resulted in a less negative-going N400 component and late-positive deflection compared to non-onomatopoetic control verbs [28]. The authors interpreted their findings as onomatopoeias being easier to process. However, results from an additional behavioural task in Peeters' study showed that participants were not faster in differentiating onomatopoetic verbs from non-words than differentiating non-onomatopoetic verbs from non-words. This behavioural finding thus does not support the notion of the easier processing of onomatopoeias. Altogether, the literature is scarce and inconsistent, to some extent.

In the current MEG study, we aimed at determining the oscillatory as well as evoked neurophysiological activation related to onomatopoeias by comparing German onomatopoetic verbs (e.g., "brummen"—to hum) to non-onomatopoetic verbs matched for frequency, length and implied loudness. The latter was meant at controlling for a dimension of acoustic relevance. We focussed on the temporal cortical areas, because of their role in auditory processing and on the base of the literature on onomatopoeias [22,24]. For the aim of the current analyses, we selected the MEG channels resulting from a previous auditory localizer paradigm from our work group [14]. Here, onomatopoetic verbs were expected to induce larger alpha and beta frequency desynchronization in comparison to non-onomatopoetic verbs as a consequence of the increased engagement of the auditory cortex. Regarding evoked fields, we expected an overall facilitated linguistic processing of onomatopoetic verbs to reflect onto a lower amplitude than non-onomatopoetic verbs [28].

2. Materials and Methods

2.1. Participants

Twenty (10 females, 10 males, average age = 28.9 ± 6.9) right-handed (laterality Quotient = 94.2 ± 9.6 [29]), monolingual, German native speakers with no formal training in linguistics participated in the MEG study. Subjects had normal or corrected to normal vision,

had no neurological or psychiatric disorder and were not using psychotropic medications. Left-handed people were excluded, as right- and left-handed participants show different cortical language dominance [30]. Linguists were excluded to avoid focussing on specific linguistic aspects of the presented words and an implicit advantage compared to non-linguists. Non-native speakers were not included in the study because different brain language areas have been found to be activated by foreign versus native [31]. Even if onomatopoetic foreign words may be intuitively easier to understand for non-native speakers than non-onomatopoetic ones [32], the related cortical activation might still be qualitatively different from that of native speakers. Participants were kept unaware of the purpose of the study to prevent interference with cognitive processes. After the completion of the experiment, participants were asked to guess the study purpose, and they were debriefed.

2.2. Stimuli

An initial list of 136 German verbs describing actions related to sounds was created, and they were initially pre-grouped in onomatopoetic and not onomatopoetic words. These verbs were then evaluated by means of an online questionnaire (https://soscisurvey.de, 15 August 2019) by German native speakers. Only fully completed questionnaires were used (n = 38, 20 females, 18 males, average age = 32.7 ± 14.5). Participants were asked to rate each verb regarding familiarity, onomatopoeias, sound source (human vs. environmental sounds) and loudness on a 1–4 Likert scale. To ensure that the participants had a sufficient understanding of the concept of onomatopoeias, they were told that an onomatopoeia describes how much the pronunciation of the verb imitates the sound associated with the implied action. Participant were then asked to "please rate how much the pronunciation of the following word imitates the sounds associated with them". They were also given example words, such as "to excavate" (baggern) as an example for a non-onomatopoetic word and "to hiss" (fauchen) as an example for a very onomatopoetic word. These participants were not included in the MEG study to prevent a priori knowledge of the stimuli. Items were presented in a random order to avoid systematic confounding effects (e.g., tiredness). Based on the results of the questionnaire, 49 words with the highest (3.1–2.5) and 56 with the lowest (2.2–1.3) onomatopoeia rating values were preliminarily assigned to the respective conditions. The two groups of verbs were further matched for length ($p = 0.407$), word frequency ($p = 0.105$), sound source ($p = 0.736$) and loudness rating values ($p = 0.189$). The resulting onomatopoetic and non-onomatopoetic words differed significantly for onomatopoeias (average 2.8 vs. 1.9; v = 0; $p < 0.001$). The matching procedure resulted in 34 verbs for each condition. Non-onomatopoetic verbs were significantly more familiar than onomatopoetic words ($p = 0.020$). Since this could not be avoided without drastically shrinking the number of words per category, we opted for these verbs. The length and word frequency values were tested for significant differences with a Student's *t*-test. All other values were tested with a Wilcoxon test. All the above-mentioned tests were run with R version 3.5.2 (https://www.r-project.org/, 28 January 2019). The matching process was performed in a semiautomatic way with the program Match [33]. Verbs used in the MEG study (34 per group) are presented in Table S1.

During the MEG measurement, the following task and trial design was applied (Figure 1): a grey fixation point was presented for 1 s, followed by a white fixation point lasting 1 s and indicating the upcoming verb. The word then appeared for 1 s, followed again by a fixation point lasting 500 to 750 ms with a jittered interval in steps of 50 ms; a jitter was used to prevent response automatization. The prompt displayed one out of three possible symbols representing a glass of water, a mouth and an electric outlet with a plug (Figure 1). In order to induce the semantic processing of word stimuli and to keep the participant unaware of the study conditions and purpose, each symbol was associated with one of the following questions, respectively:

1. Has the process implied by the verb anything to do with liquids?
2. Is the process implied by the verb performed with the mouth?
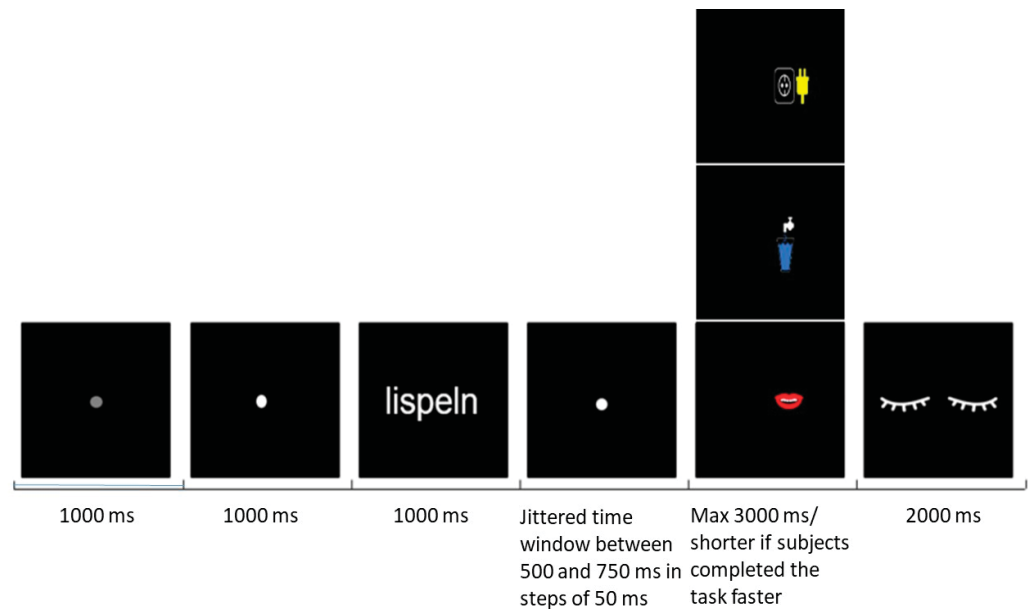3. Is the process implied by the verb performed with an electric tool?

Figure 1. Experimental design.

The prompt was presented either on the right or on the left side of the screen. The participants were required to respond "yes" to the prompt by lifting the index finger of the hand positioned on the same side as the presented symbol and "no" by lifting the index finger of the opposite hand. Left- and right-hand responses were balanced pseudo-randomly in order to trigger 50% right- and 50% left-hand responses. To reduce eye movement-related artefacts, participants were asked to avoid blinking until the end of the trial, when an eye symbol lasting 2 s indicated to blink. All 68 verbs were presented 3 times across 3 blocks. Each word was always followed by one of the questions above (Table S1). Blocks were separated by pauses as long as needed by the participant. Words were presented in a randomized order within each block. The measurement lasted about 35 min, depending on participants' reaction and pause time.

2.3. Procedures

After signing informed consent and data privacy forms, participants filled out the Edinburgh Handedness Inventory [29]. They were asked to remove metal belongings, and if needed, were offered metal-free cotton clothes as well as individually calibrated metal-free glasses with corrective lenses. For electrooculography (EOG), four electrodes were placed around the eyes: one above and one under the left eye for vertical EOG and two at about 1 cm from the left and the right eye for horizontal EOG. These bipolar electrodes were used to detect eye movements and blinks. Four coils were placed on the forehead and behind the ears. The positions of the coils were digitized (Polhemus Isotrak) for later estimation of the head position during MEG measurements. During the MEG measurement, the participants were seated comfortably with their hands resting on two pads and their index fingers on two photoelectric switches. Instructions and word stimuli were projected onto a screen in front of the participant. After three demonstration trials, participants performed three practice trials that could be repeated, if needed, before starting the measurement.

2.4. Data Acquisition and Analysis

Neuromagnetic brain activity was recorded with a 306-channel MEG system (Elekta Neuromag, Helsinki, Finland). The channels consisted of 102 magnetometers and 204 orthogonal planar gradiometers. MEG data were digitized at 1000 Hz, bandpass filtered from 0.03 to 330 Hz online and stored on a computer hard disk.

MEG data were analysed with Matlab R2017b and fieldtrip toolbox [34]. Behavioural data analysis was run with R version 3.5.2 [35].

2.5. Meg Data Pre-Processing

Epochs were cut from the continuous data and included the time window between 1 s before word onset and 1 s after word onset. Only correct trials entered the analysis. Trials with answers at wrong time points or double answers were excluded from analyses. Semiautomatic jump and muscle artifact rejection was applied to the selected epochs. A notch filter was used to filter out the frequencies 49–51, 99–101 and 149–151 Hz. A high-pass filter of 2 Hz and a padding of 5 s were used as well. Heart and eye-related artifacts were removed via independent component analysis [36]: this resulted in the elimination of, on average, 2.6 components per subject. Noisy or faulty channels were repaired by interpolating data from neighbouring channels. An average of 6 surrounding gradiometers of the same type were used for each faulty channel. Trials were visually inspected for residual artifacts and then assigned to the two conditions.

2.6. Time–Frequency Representations and Event-Related Field Analysis

Time–frequency representations were calculated by using a fast Fourier transformation. An adaptive sliding time window including 5 cycles was shifted in steps of 50 ms from −1 s to 1 s after word onset. Data were padded up to 5 s. A single Hanning taper was applied, and power was estimated in steps of 1 Hz between 2 and 40 Hz. The time–frequency analysis was performed separately for horizontal and vertical planar gradiometers, and the pairs of planar gradiometers were combined afterwards. The time from 600 ms before word onset to 100 ms before word onset served as a baseline.

For the computation of ERFs, data were filtered with a low pass filter of 30 Hz. For each subject episodes from −1 s to 1 s after word onset were averaged; the time interval from −200 ms to word onset (=0 ms) served as the baseline. Horizontal and vertical planar gradiometers were combined.

2.7. Statistics

Difference in reaction time between word conditions and question types were tested with an ANOVA.

Considering the multidimensionality of MEG data, for the frequency and ERFs analysis, a procedure that effectively corrects for multiple comparisons, a non-parametric randomisation test, was used [37]. With regard to frequency analysis, the contrast between onomatopoetic and non-onomatopoetic words was run in the alpha and beta range (8–25 Hz), across the time window between 0 and 1 s after word onset (no average over time) and on the average of the activity of 9 left hemispheric temporal channels (Figure S1) that were selected on the base of results of a previous MEG localizer study targeting the auditory cortex [14]. A one-sided *t*-test for dependent samples was used. T-values of the time–frequency samples passing the significance threshold ($p < 0.05$) were selected and clustered with adjacent time and frequency bins. A cluster-level statistic was then calculated by taking the sum of the *t*-values of the samples within every cluster. A non-parametric permutation test, which consisted in computing 1000 random sets of permutations between the two conditions, was used to obtain a distribution of the cluster statistic; the significance level was set to $p < 0.05$.

The same procedure was applied to the statistical analysis of ERFs for the contrast between the onomatopoetic and non-onomatopoetic verb condition. The analysis included all channels. Considering the evidence for early semantic processes [38–41], we targeted

the time window between 100 and 300 ms after word onset to detect semantically related components. Group differences in ERFs amplitude were also tested with a one-sided *t*-test, as onomatopoetic verbs were expected to elicit larger amplitudes.

3. Results

3.1. Behavioural Results

The reaction time for onomatopoetic verbs (on average, 741 ms $\pm$ 266 ms) was significantly shorter than for non-onomatopoetic words (on average 748 ms $\pm$ 326 ms; ($p < 0.001$)). The type of question did not have a significant effect on reaction times ($p = 0.465$). Missing responses were, on average, 0.3% per subject.

Incorrect responses occurred in an average of 6.4% of trials per subject. No participant thus exceeded the 15% error cut-off, at which the participant's data would have been discarded: this suggests that the task was not too difficult for the participants. As no participant was able to correctly guess the purpose of the study, correct trials of all subjects entered the analyses.

3.2. Time–Frequency Representations

A statistical analysis of alpha and beta power on the nine selected channels yielded no significant result; no negative cluster emerged. However, on a descriptive level, differences in alpha and beta power emerged mainly in the left temporal channel selection (Figure 2). Here, a desynchronization in both frequency ranges was visible starting at about 200 ms after word onset, both in the onomatopoetic and the non-onomatopoetic verb condition (Figure 2a,b). The onomatopoetic condition showed a slightly increased alpha desynchronization, between 400 and 600 ms, and beta desynchronization between 0 and 200 ms as well as at about 700 ms after stimulus onset (Figure 2c). A descriptively stronger synchronization in the alpha range between 200–400 ms and in the beta range around 400–500 ms was also visible.
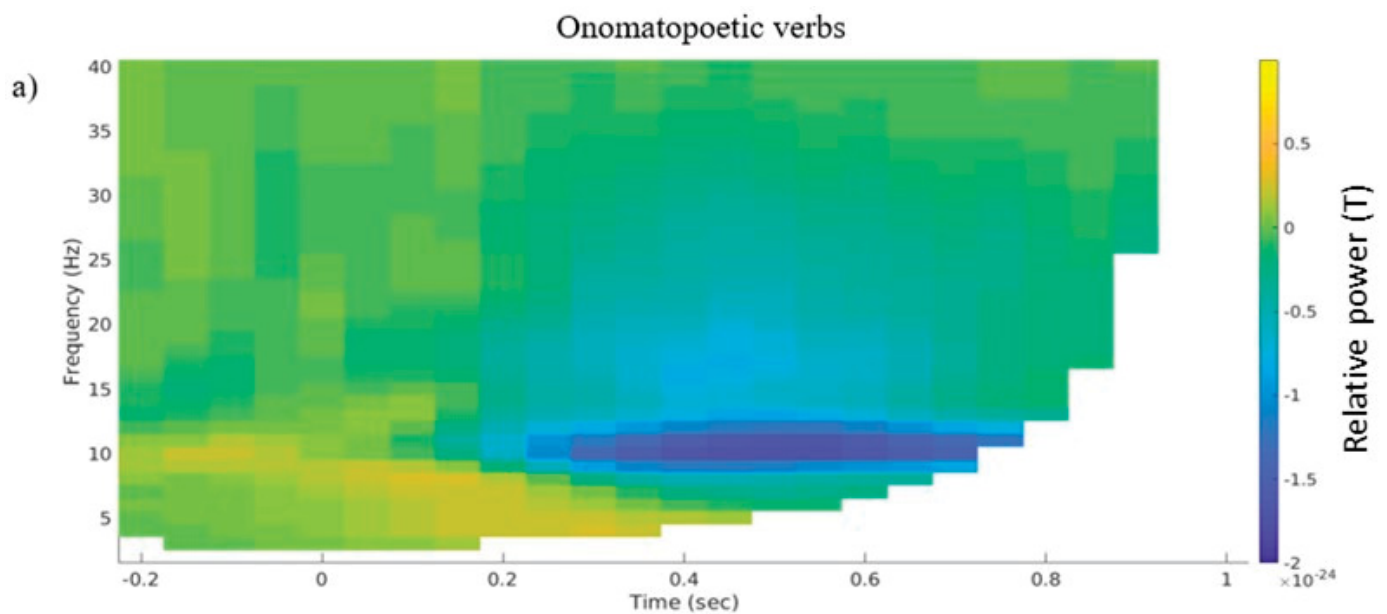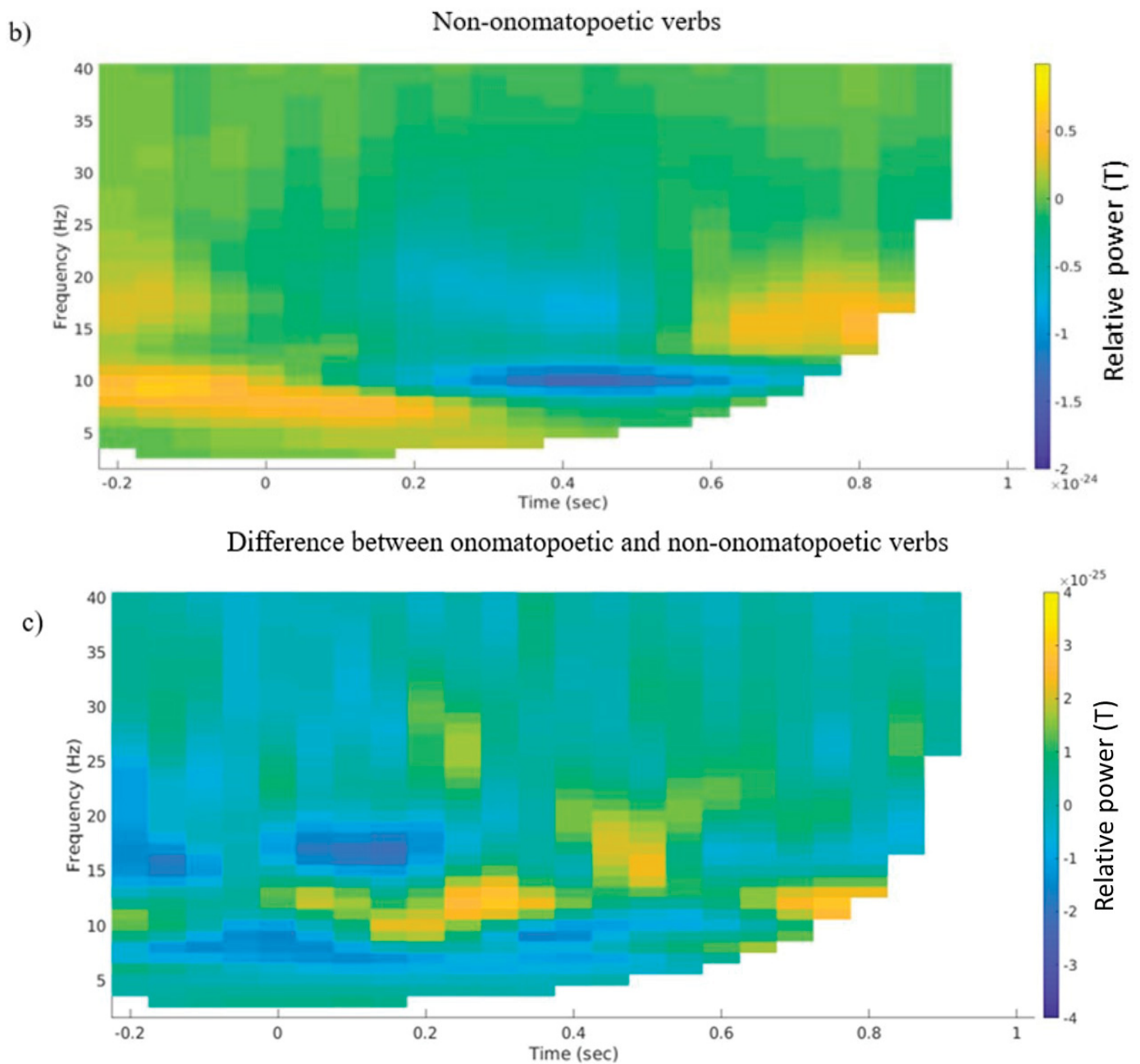

Figure 2. *Cont.*

Figure 2. (**a**) Grand average time–frequency representations of the averaged selected left temporal channels for (**a**) the onomatopoetic verb condition, (**b**) the non-onomatopoetic verb condition and (**c**) the difference between onomatopoetic and non-onomatopoetic verb condition.

3.3. Event-Related Fields

ERFs analyses showed a statistically significant difference ($p = 0.033$) between the onomatopoetic and non-onomatopoetic condition around 240 ms after word onset with larger amplitudes for onomatopoetic words (Figures 3 and 4). The difference emerged on centro-parietal channels and then shifted to slightly right lateralised sites.
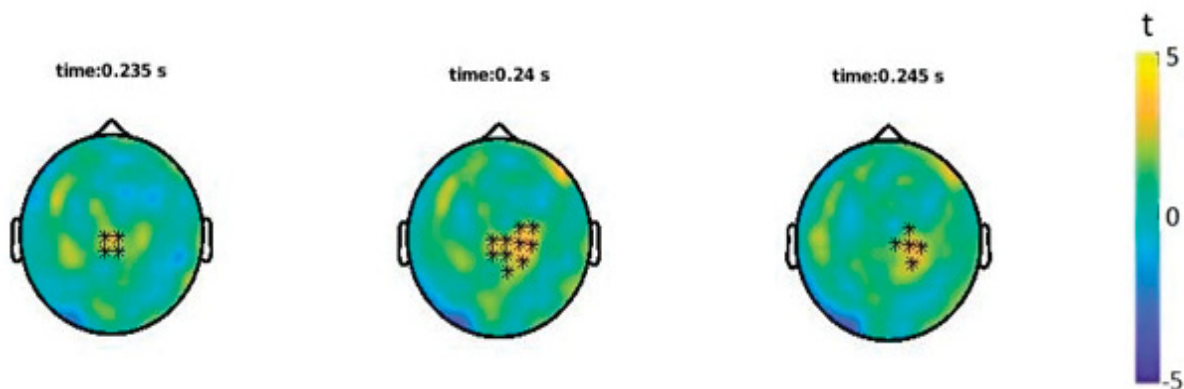
Figure 3. Statistical results of ERFs analysis: channels showing a significant effect (*) in the shown time interval.
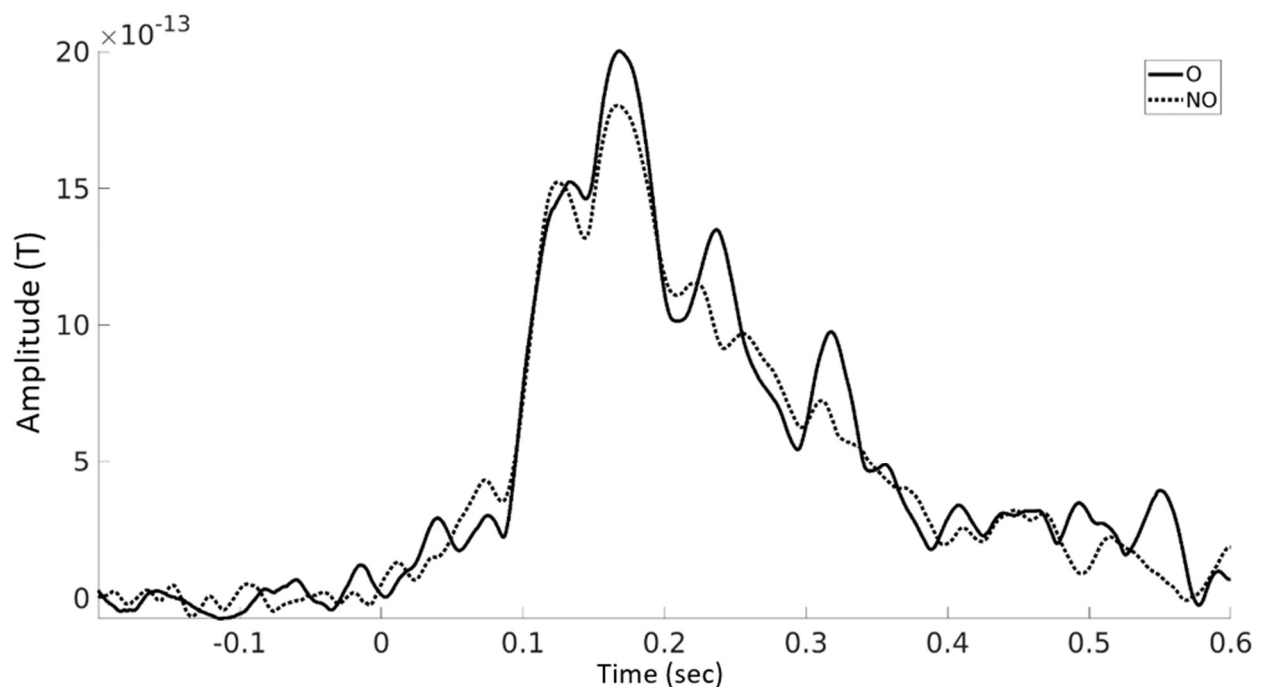

Figure 4. Averaged ERF amplitudes for onomatopoetic verbs and non-onomatopoetic verbs until 600 ms after word onset across all channels showing a significant effect (see Figure 3).

4. Discussion

Accuracy results showed that the participants did semantically process the words in the given time. Reaction time was shorter for onomatopoetic in comparison to non-onomatopoetic verbs, even though familiarity was significantly lower for onomatopoetic verbs and should thus increase reaction time. This suggests that onomatopoetic words are easier to understand, possibly depending on the non-arbitrary link between the word sound and its meaning. In contrast, the oscillatory and the ERFs patterns of activation seem to indicate a more effortful processing of onomatopoetic verbs. In a behavioural study also applying auditory onomatopoetic versus control verbs, no difference in reaction time emerged [29]. Since in that study the task consisted in distinguishing words from pseudo-words, a possible difference in processing ease was suggested to be obscured by task-related decision making and motor processes, which might require more time than the lexical processing. This suggests that semantic versus lexical processing, which reflects the depth of linguistic processing, may be responsible for the emergence of behavioural effects. A role of the depth of semantic processes in the emergence of embodiment effects was

indeed shown in a previous study of our group, where semantic discrimination impacted the modulation of verb processing as induced by electrical stimulation [42]. However, differences in reaction time in the current study should be interpreted with caution, since our task was not a simple reaction time task as in Peeters' study.

Both onomatopoetic and non-onomatopoetic words showed alpha and beta desynchronization starting at about 200 ms after word onset in the left temporal lobe: this result adds evidence to the role of alpha and beta desynchronization as a marker of semantic processing. Although not reaching statistical significance, the slightly decreased alpha and beta power accompanying onomatopoetic verbs in the selected left temporal channels suggests that this linguistically predominant hemisphere might be sensitive to onomatopoeias. Similarly, increased left temporal beta desynchronization accompanies words implying loud vs. quiet actions [14]. On the base of these results, onomatopoetic verbs were expected to cause a stronger recruitment of the auditory cortex due to their linking function between semantics and phonetics. The synchronization visible in the alpha band around 200–400 ms and in the low beta band around 400–500 ms is more difficult to explain. It was not expected to be a marker of increased cortical engagement in the context of embodied semantics, but considering its latency, we cannot exclude a relation to particular semantic diverging aspects between the two conditions. Beta oscillations in particular are also related to complex linguistic sub-processes, to expectancy violation and attention as well as to working memory [43]. Whether familiarity, which was rated higher for non-onomatopoetic words, might be responsible for this effect, remains unclear. One limitation of the current study is that additional word-related parameters such as imageability, age of acquisition and emotional valence were not rated and controlled for. Possibly, even more linguistic parameters might affect ERF amplitude or brain oscillations; this needs to be further determined with studies specifically designed for this purpose. To our knowledge, this is the first study addressing oscillatory correlates of onomatopoetic versus non-onomatopoetic verb processing, and we cannot report a significant difference in brain oscillations. Previous studies using interjections compared to verbs point to stronger onomatopoetic qualities of these words and to a stronger activation of the auditory cortex. This might be an explanation as to why our word stimuli with weaker onomatopoetic qualities did not engage the auditory cortex as much as previously used stimuli. Although previous studies have matched interjections and control words for imageability, familiarity and age of acquisition [24], the two conditions included different grammatical categories. The use of verbs in the present study allowed a better control of grammatical aspects as well as of other related parameters such as length, word frequency and loudness. By controlling for linguistically confounding effects, we improved the comparability between conditions. Increasing semantic task difficulty might help determining a neurophysiological effect of this subtle semantic quality that is the onomatopoeia. It is worth noting that half of the words used in our study described events that were not primarily associated with human actions, but more with environmental events (e.g., "surren"—to whir, "zischen"—to hiss and "plaetschern"—to platter). Since environmental events and human actions were balanced between conditions, and the sound source should not have affected results. Still, it might have impaired simulation processes by moving the attentional focus to an extra-personal space. Verbs related to actions in which participants can envision themselves as actors are likely to induce stronger simulation.

ERF analysis showed a significant effect emerging at about 240 ms after word onset in the centro-parietal sensors, suggesting increased cortical activation related to onomatopoetic verbs. This hints at a more effortful processing of onomatopoetic verbs: as proposed in a previous study [28], onomatopoetic verbs have a duality of lexical and sound components, which creates a processing conflict. Peeters [28] argued that this is compensated by an easier understanding due to the link between the word content and the way the word is pronounced. While this was not confirmed by the behavioral results, the current findings point in that direction and show faster reaction times following onomatopoetic verbs despite the jittered time interval between the word and prompt onset.

The current results are in line with those of EEG studies showing differences in the ERPs when comparing acoustically presented onomatopoetic verbs to control verbs [28] as well as comparing visually presented ideophones (which are regarded as either very similar to or as the same as interjections) to control adverbs [23]. Peeters [28] found a significant amplitude decrease of the N2 component, a less negative-going N400 and a late-positive deflection compared to the control words distributed over all cortical areas. Lockwood and Tuomainen [23] found ERP effects at roughly the same time points as Peeters [28], but with a more negative going N400 for ideophones than for control words. We found significant differences in ERFs at about 240 ms after stimulus onset. This result might depend on similar mechanisms as those related to P2 modulation in Lockwood and Tuomainen's [23] study, that is, the load of sensory (auditory) information embedded in onomatopoetic word. There was no significant late-positivity effect as in the two mentioned studies in our data [23,28]; however, the interpretation of more effortful retrieval might as well be dependent on the use of ideophones, and the enhanced difficulty of making meta lexical decisions [28] is fairly task-specific.

Clinical Applications

Possible clinical applications of the grounded cognition framework have been previously proposed [44]. It was proposed that patients with aphasia and lesions in motor areas could benefit from cognitive training with words that imply movement. This might add to conventional movement therapies and is supposed to induce neuroplasticity and regeneration in the affected areas. The effects of linguistic cognitive training on neural plasticity have been shown in healthy volunteers, thus delivering encouraging results [45]. First clinical tests have also been performed, but only as proofs of concepts and not in large cohorts of patients [46]. A similar cognitive improvement might be aimed at in patients with aphasia and lesions in auditory areas by applying linguistic training with sound-related words. The current ERFs results suggest that onomatopoetic verbs might suit such cognitive therapy programs.

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Neurophysiological mechanisms of perspective-taking: An MEG investigation of agency

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ABSTRACT

According to the embodied cognition framework, sensory and motor areas are recruited during language understanding through simulation processes. Behavioral and imaging findings point to a dependence of the latter on perspective-taking (e.g., first person "I" versus third person "s/he"). The current study aims at identifying possible neurophysiological correlates of perspective in a linguistic context. Twenty healthy participants were measured with magnetoencephalography (MEG) while semantically processing visually presented inflected German verbs in the first- and third-person perspective, simple present tense. Results show that the first-person perspective induces stronger beta (15–25 Hz) desynchronization in the right-hemispheric posterior superior temporal sulcus, ventral posterior cingulate gyrus, and V5/MT+ area; no modulation of sensorimotor cortex emerged. Moreover, a stronger event-related field (ERF) was observed for the first-person perspective at about 150 ms after pronoun-verb onset, originating in occipital and moving to central and left temporal cortical sites. No effect of perspective on sensory gating was found when targeting the N1 component related to tones following the linguistic stimuli. Results indicate an effect of linguistic perspective-taking on brain activation patterns. The contribution of the single brain areas and their role in self-other distinction is further discussed.

Introduction

The embodied (or grounded) cognition theoretical framework has pointed to the role of sensory and motor systems in the processing of concept representation (Barsalou, 2008). These have been proposed to be engaged not only during sensory perception and motor execution, but also during language understanding. Simulation has been suggested as a possible mechanism thereof (Barsalou, 2008; Gallese & Lakoff, 2005) and has been addressed in a number of studies (for a review see Binder & Desai, 2011). A crucial aspect, the neurophysiological mechanisms of which remain to be determined, is the role played by perspective in action simulation. Three different possible perspectives have been suggested (Beveridge & Pickering, 2013): that of an embodied agent, of an embodied patient, and of an embodied observer. Earlier research on sentence comprehension showed that an actor perspective (you/I) versus an external perspective (s/he) were adopted depending on the used pronoun (Brunyé et al., 2009). The authors also found that in the actor condition, the perspective could be further modulated by an introductory sentence, thus suggesting that the discourse context can additionally affect perspective-taking. Modulation of mental simulation using a first- instead of a third-person

perspective leads to higher immersion when reading a story (Hartung et al., 2016). Two factors in particular, transportation into the story world and mental imagery during reading, showed higher scores for first- compared to third-person pronoun stories. Also, the use of a the third-person perspective abolished the Action-sentence Compatibility Effect (ACE) found using the first-person perspective (Gianelli et al., 2011; Van Dam & Desai, 2017). Hereby the pronoun "you" was sometimes used for the first-person perspective instead of "I" (Gianelli et al., 2011; Van Dam & Desai, 2017): it remains to be determined whether the two pronouns are indeed exchangeable, as findings are still inconsistent (Brilmayer et al., 2019; Gianelli et al., 2017). Altogether, behavioral results suggest an advantage of the first-person perspective in linguistically induced simulation processes.

Neuroimaging findings partly confirm these results as sentences in first-person perspective activated cortical areas such as the posterior cingulate area, the occipital cortex, the right superior temporal sulcus (STS), the motor and the somatosensory area more strongly than sentences in third-person perspective (Perrine Ruby & Decety, 2003; Tomasino et al., 2007). However, two fMRI studies using pronoun-verb pairs did not replicate these effects and

found neither a difference in cortical activation (Hartung et al., 2017) nor stronger cortical activation for the first-person perspective in left visual-motion area and pSTS (Papeo & Lingnau, 2015). Moreover, there is evidence for an increased activation of the middle temporal gyrus accompanying third- versus first-person perspective processing (Papeo & Lingnau, 2015; Perrine Ruby & Decety, 2003). The role of the V5/MT in perspective-taking was also addressed by a PET study showing similar activation for the first- and the third-person perspective (P. Ruby & Decety, 2001). The inconsistent findings may depend on different aspects: the method (fMRI versus PET), the stimuli (sentences versus single verbs), their presentation modality (visual versus auditory), the language and the task, which varied broadly across studies. Overall, findings from previous research on verb-related perspective-taking point to the activation of the following areas: the cingulate area, the occipital cortex, the STS, the sensorimotor and the V5/MT area. In particular, the cingulate area was suggested to be activated because of its sensitivity to the sense of self (Tomasino et al., 2007) and its role in the theory of mind (P. Ruby & Decety, 2001). The activation of the medial temporal cortex was instead linked to the activation of episodic memories as well as to processing the subject of an action (Papeo & Lingnau, 2015; Perrine Ruby & Decety, 2003).

In the present study, we aimed to further determine the neurophysiological correlates of perspective-taking using pronoun-verb stimuli and capitalizing on the good time- and space-resolution of magnetoencephalography (MEG). We defined the following ROIs according to results from the available literature on perspective-taking applying verb stimuli: the sensorimotor cortex, the visual motion area V5/MT+, the medial temporal cortex, the STS and the cingular cortex. For all ROIs except the V5/MT+ area we expected first-person perspective pronoun-verb pairs to induce enhanced simulation processes compared to third-person perspective and these to become visible through increased brain activity. The V5/MT+ area and the sensorimotor area were expected to be inversely modulated: while first-person perspective should induce stronger person-centered simulation in the sensorimotor cortex, third-person perspective should more strongly activate the V5/MT+ area compared to first-person due to the related observer perspective.

The current study focused on the oscillatory correlates of linguistic perspective-taking and targeted the beta frequency (15–25 Hz) because of its role in embodiment processes in the motor (Klepp et al., 2015; Moreno et al., 2013; Van Elk et al., 2010) and in the auditory system (Niccolai et al., 2020). These studies together with our previous work on embodiment and brain oscillations in the sensorimotor area (Klepp et al., 2015, 2019; Niccolai et al., 2014) point to the beta frequency (i.e., beta power

suppression) as a good cortical marker of simulation. In the current study we target the beta frequency in order to determine the modulatory effect of perspective-taking on simulation: mentally simulating an action in the first or in the third person might recruit the above-mentioned brain areas with a different intensity. We expected first- vs. third-person perspective to elicit stronger simulation processes due to the "internal" view on the action (vs. a view "from the outside"). Differently, the V5/MT+ area was expected to be more strongly triggered by third-person perspective and thus show increased beta power. To the best of our knowledge, there is only one study pointing to the link between the beta band and perception of the self: here, beta power decrease accompanied selflessness compared to self-awareness (Dor-Ziderman et al., 2013). There is however a lack of research concerning oscillatory processes related to first- versus third-person perspective.

Interestingly, the effect of linguistic perspective-taking was also shown to affect event-related components (ERPs): self- versus other-related possessive pronouns for example, elicited stronger activations in central and parietal sites from 300 to 500 ms after word onset (Shi et al., 2011). Larger positive ERPs for first- versus third-person pronouns emerged in another study in the time-window between 150 and 250 ms (Brilmayer et al., 2019). We therefore expected stronger simulation for first-person actions to become visible in event-related components attributable to semantic processing. Moreover, we hypothesized that this modulation would further influence successive sensory processes by sensory attenuation effects affecting the amplitude of a sensory component, i.e., the N1. Notably, the N1 amplitude is suppressed by self-compared to externally-produced tones; also, spoken language elicits smaller evoked potentials in the speaker than in the listener (for a review see Bendixen et al., 2012; Ross et al., 2017). These effects point to a cortical sensitivity to the agent of an action being detectable also on sensory patterns of activation. Stronger simulation as possibly induced by first-person perspective was thus expected to suppress the N1 amplitude related to a tone following word presentation.

Materials and methods

Participants

Twenty healthy volunteers (12 females) on average 24 years old (SD = 4.2), all monolingual German native speakers, were included in the study. Participants were right-handed (laterality quotient = 84.8; SD = 3.2; Edinburgh Handedness Inventory, Oldfield, 1971). The subjects had normal or corrected-to-normal vision and

none reported neurological or psychiatric disorders. Participants provided written informed consent prior to MEG and received financial compensation for their participation. The study was in accordance with the Declaration of Helsinki and was approved by the local Ethics Committee of the Medical Faculty of the Heinrich-Heine University, Duesseldorf (study number 4814R).

Stimuli and procedure

Word paradigm

Word stimuli were German verbs describing human actions. A total of 80 different verbs were used implying mouth, facial, limb or whole-body actions. For details on word selection and characteristics please refer to Niccolai et al. (2020). Each word was presented twice in the first-person (i.e., "I") and twice in the third-person simple present tense, the latter belonging to the opposite gender of that of the participant ("he" for females and "she" for males): this was aimed at maximizing the difference between self- and other-related simulation processes.

Trials started with a gray fixation point lasting 1 second and turning white 1 second before word onset. Each verb was projected on the screen together with the pronoun and was accordingly inflected in the first- or third-singular person (Figure 1). Each pronoun-verb pair remained on the screen for 600 ms. Thereafter a fixation point was presented for an interval of 600–1000 ms jittered in steps of 100 ms; a 440 Hz-tone lasting 150 ms followed in each trial. To ensure semantic processing participants were required to indicate after each verb either which body part was involved in the action or which pronoun had been presented; the two kinds of prompts were balanced and pseudo-randomized. For the pronoun task, the response prompt showed a first- and a third-person pronoun, one on the left and one on the right half

of the screen. For the body-part task, two body silhouettes were shown on the left and the right half of the screen, with different body parts highlighted in yellow (arms, head, legs, or entire body). The two halves were counterbalanced regarding lateralization of correct responses. Crucially, the pseudorandomisation of the two tasks and the time-line of the paradigm prevented participants from focusing exclusively on one aspect (the semantic or the pronoun-related one). This means that during word presentation participants did not know, which of the two tasks they should have performed afterward and had therefore to process both aspects in order to respond correctly. Participants responded by lifting the right or the left index finger according to the position of the correct answer displayed on the screen. The prompt remained on the screen until a response occurred but for a maximum of 2 seconds. Subjects were subsequently encouraged to blink and after 2 seconds the following trial started. Practice trials were given before starting the measurement.

Data acquisition and analysis

Neuromagnetic brain activity was continuously recorded with a 306-channel MEG system (Elekta Neuromag, Helsinki, Finland) including 204 orthogonal planar gradiometers and 102 magnetometers. A bipolar horizontal and vertical electrooculogram (EOG) was recorded for the offline detection of eye movements. Four coils were attached to the subject's head bilaterally on the forehead and behind the ears. The position of these coils, prominent anatomical landmarks (right and left preauricular points and nasion) and additional points along the subject's head were digitized (Polhemus Isotrak) to map functional MEG data to individual anatomy. MEG data were digitized at 1000 Hz, band-pass filtered from 0.03 to 330 Hz online, and stored on a computer hard disk. MEG data from gradiometers were analyzed with Matlab
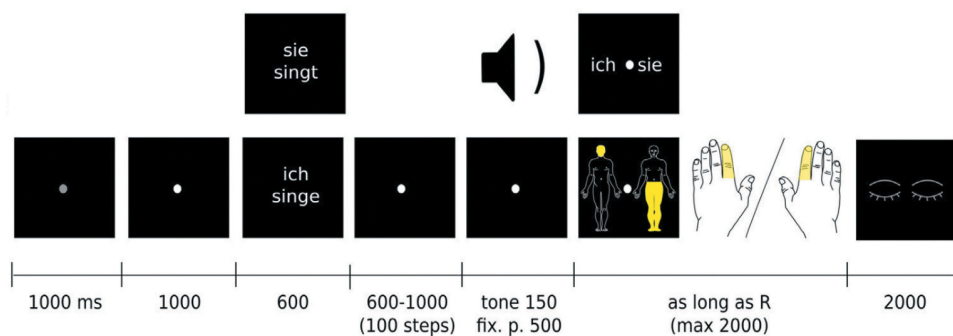

Figure 1. Experimental paradigm. Verbs implying human body-related actions were shown inflected either in the first- or the third-person simple present tense (i.e., "ich singe" = "I sing"; "sie singt" = "she sings"). Participants were required to indicate either the pronoun of the inflection or the body-part mainly involved in the action; fix.p. = fixation point; R = response.

(Mathworks, Natick, MA, USA) and FieldTrip (http://field trip.fcdonders.nl), a Matlab software toolbox for MEG and EEG analyses (Oostenveld et al., 2011).

Epochs from 1 second before onset of a pronoun-verb pair to 1 second after tone onset were collected from the continuous data. Only stimuli followed by correct responses entered the analysis. Sensor jumps, eye-, and muscle-related artifacts were eliminated with semiautomatic and visual artifact rejection. For the analysis of oscillatory activity continuous data were filtered with a high-pass filter of 2 Hz to remove DC drifts and with band-stop filters at 49–51, 99–101, 149–151 Hz; a Butterworth IIR zero-phase forward and reverse filter and a padding of 5 s were used; channels with no or defective signal were replaced with the average of their intact neighbors. Individual coregistered MRI-MEG data were used for analysis of regions of interest (ROIs); one subject (female, 28 years old) with deviant MRI acquisition settings was not included in the ROI analyses. Data from the remaining 19 subjects (11 females, average age = 24 ± 4.38) entered the analyses. The brain volume was discretized to a 3-D grid with 1 cm resolution, grid points were warped to the normalized brain and those belonging to the defined ROIs were determined by means of Brainnetome atlas (Fan et al., 2016). Preprocessed MEG data were projected through an MNI normalized subject-specific linearly constrained minimum variance (LCMV) filter for the selected virtual channels. For the analysis of event-related fields data were additionally filtered with a low-pass filter of 30 Hz and trials were averaged to word onset and tone onset.

Statistical analysis

The following critical ROIs were selected using the Brainnetome atlas integrated into FieldTrip, separately for the two hemispheres: the sensorimotor area (postcentral gyrus area 1/2/3 and precentral gyrus area 4), the lateral occipital cortex V5/MT+, the medial temporal gyrus (caudal and rostral area 21 as well as dorsolateral area 37), the STS (anterior, rostroposterior and caudoposterior superior temporal sulcus), and the cingular gyrus (dorsal area 23, rostroventral area 24, pregenual area 32, ventral area 23, caudodorsal area 24, caudal area 23, and subgenual area 32). A total of 78 virtual channels were included per hemisphere. Considering the multidimensionality of the MEG data, a nonparametric randomization test (Maris & Oostenveld, 2007) was used that effectively corrects for multiple comparisons. First, the power difference between the first-person and third-person perspective was calculated by means of t-values. These were calculated for each virtual channel, frequency bin and time point of

each subject. In a second step, the cluster-based nonparametric randomization approach was used to test significance at group level (Maris & Oostenveld, 2007). For every channel the two conditions were compared across subjects by means of a t-test for dependent samples. All samples with a t-value larger than the threshold (corresponding to p < .05) were selected and clustered with spatially adjacent bins. A cluster-level statistic was then calculated by taking the sum of the t-values of the samples within every cluster. Nonparametric permutation testing, which consisted in computing 5000 random sets of permutations between the two conditions in the sensor space, was used to obtain a distribution of cluster statistics and the significance level of the observed cluster (bidirectional hypothesis, p < .025). The group analysis was run on the virtual channels belonging to the selected areas, on a time-window between 0 and 500 ms after word onset, and on a frequency range between 12 and 25 Hz. According to the null hypothesis, the difference between the two conditions should not significantly differ from zero, that is, t-values should be replaceable by zeros. Thus, resulting t-values of each subject and values from a pseudo-dataset consisting of zeros went through the nonparametric randomization test. Analyses were run separately on logarithmically normalized data of the left and the right hemispheres due to the different role of the two hemispheres in linguistic processing in right-handers (Knecht et al., 2000; Vingerhoets et al., 2013; Willems et al., 2010) and in perspective-taking (Perrine Ruby & Decety, 2003; Tops et al., 2014). Word-related ERF analyses included 20 subjects. ERF data were baseline-corrected (baseline = −300 to −100 ms). The first- and third-person perspective conditions were compared across subjects by means of a t-test for dependent samples in the time-window between 0 and 500 ms after word onset across all channels using the cluster-based nonparametric randomization approach mentioned above. The tone-related ERF analysis in the word paradigm included 19 subjects (12 females, average age = 24 ± 4.05), as no tone was presented to one participant (male, 32 years old) due to a technical issue. The N1-related analysis was run by contrasting the two conditions in the time-window between 100 and 150 ms after tone onset on the average of channels showing the strongest N1 peak amplitude across subjects (three left, two right: see Fig. 5a in Niccolai et al., 2020 for reference). Since we expected N1 amplitude suppression for tones following first-person actions, a monodirectional hypothesis was used.

Results

A behavioral average task accuracy of 94.3% (SD = 7.3) indicated that the presented words were attended to by the participants. The contrast first- vs. third-person verbs on the selected ROIs showed significantly stronger beta power suppression following verbs in the first- person perspective. Three significant negative clusters emerged in single channels belonging to the following areas: the right lateral V5/MT+ area (p = .004), the right posterior ventral posterior cingulate gyrus (CG, A23v; p = .014), and the right pSTS (p = .021). They started shortly after word onset and lasted about as long as visual word presentation (Figure 2). No positive cluster reached significance (p = .550).

An ERF showed a significantly larger amplitude for first-person perspective verbs between 110 and 170 ms after word onset (p = .019; Figure 3(a,b)). This effect started in occipital leads and moved to central and left temporal cortical sites. The comparison between N1 amplitudes for tones following first- and third-person actions resulted in no significant cluster (p = .946).

Discussion

Reading verbs inflected in the first-person perspective ("I") triggered significantly stronger beta power suppression in the right-hemispheric lateral V5/MT+, ventral posterior CG, and pSTS than the same verbs inflected in the third-person perspective ("s/he"). In these brain areas beta power suppression started soon after word onset and lasted about as long as word presentation. Moreover, first-person perspective verbs elicited a larger magnetic field at about 150 ms: this effect started occipitally and broadened to central and finally left temporal cortical sites, suggesting an evolution from perceptual to more semantic stimulus analysis levels.

The increased right pSTS activation for first-person verbs is in line with previous fMRI and PET findings (Perrine Ruby & Decety, 2003; Tomasino et al., 2007). Interestingly, this region was shown to be activated while understanding the meaning of stories and cartoons involving people (Gallagher & Frith, 2003). In addition, biological motion of eyes, mouth, hands and body as well as implied motion like static images of the face and the body activated this area (Allison et al., 2000; Quandt & Chatterjee, 2015). Altogether, these findings point to a sensitivity of the pSTS to body-related action perspective and to its potential role in disentangling the self from the other.

Stronger activation for the first vs. third-person perspective emerged also in the right ventral CG. Analogously, engagement of the posterior cingulate

cortex (PCC) emerged during self-related thinking, that is during the shift of attention from the external to the internal world (Buckner et al., 2008) and deactivated during meditation, a not self-centered mind state (Brewer et al., 2013). Self-related stimuli seem to activate PCC independently from the functional domain (e.g., verbal, spatial, emotional or facial) (Northoff et al., 2006). Hereby, three variables correlated with its activity: personal significance, introspection about one's own mental states, and evoked emotion (Andrews-Hanna et al., 2010). In line with that, PCC was activated by direct appraisals (an individual`s own self-beliefs) more than by reflected appraisals (an individual`s perception of how others view him/her; Ochsner et al., 2008). PCC showed increased activation also when comparing the own versus an avatar perspective in a virtual environment (Vogeley et al., 2004). Finally, although beta power was not modulated by self vs. selflessness in a previous MEG study, findings confirmed a main role of beta oscillations in the activation of the PCC (Lou et al., 2010). Altogether, these and the present findings point to an engagement of PCC in self-consciousness.

The unexpected finding of increased right V5/MT+ activation for first-person perspective verbs may depend on a possible role of this area in processing also self-related motion and may indicate a sensitivity to biological movement from an internal perspective. Interestingly, each of the four retinotopic areas of the V5/MT+ cluster includes substantial fractions of the extrastriate body area (EBA) and this proportion was found to be slightly greater in the right than the left hemisphere (Ferri et al., 2013). According to the authors, this explains the high sensitivity of this area to body, motion, and human-action. Although there are findings showing stronger responses of the right EBA to body parts presented from an allocentric perspective (Saxe et al., 2006), the extrastriate cortex responds also during goal-directed movements of the participant's body parts (Astafiev et al., 2004). In particular, the EBA was shown to distinguish between internal body or action representations and external visual signals (David et al., 2007), thus disentangling one's own from another's behavior. The current results may be explained by an activation of the EBA within the V5/MT+ area; further investigations are needed to disentangle the role of these two areas as for their contribution to perspective-taking.

Our results show a right-hemispheric lateralization, which possibly depends on the experiential mode induced by first-person perspective-taking. This mode has been linked to right-hemispheric activation, whereas left-hemisphere was suggested to be engaged by making meaning of experience and integrating it with a broader context during rumination and reappraisal (Tops et al., 2014). It is also
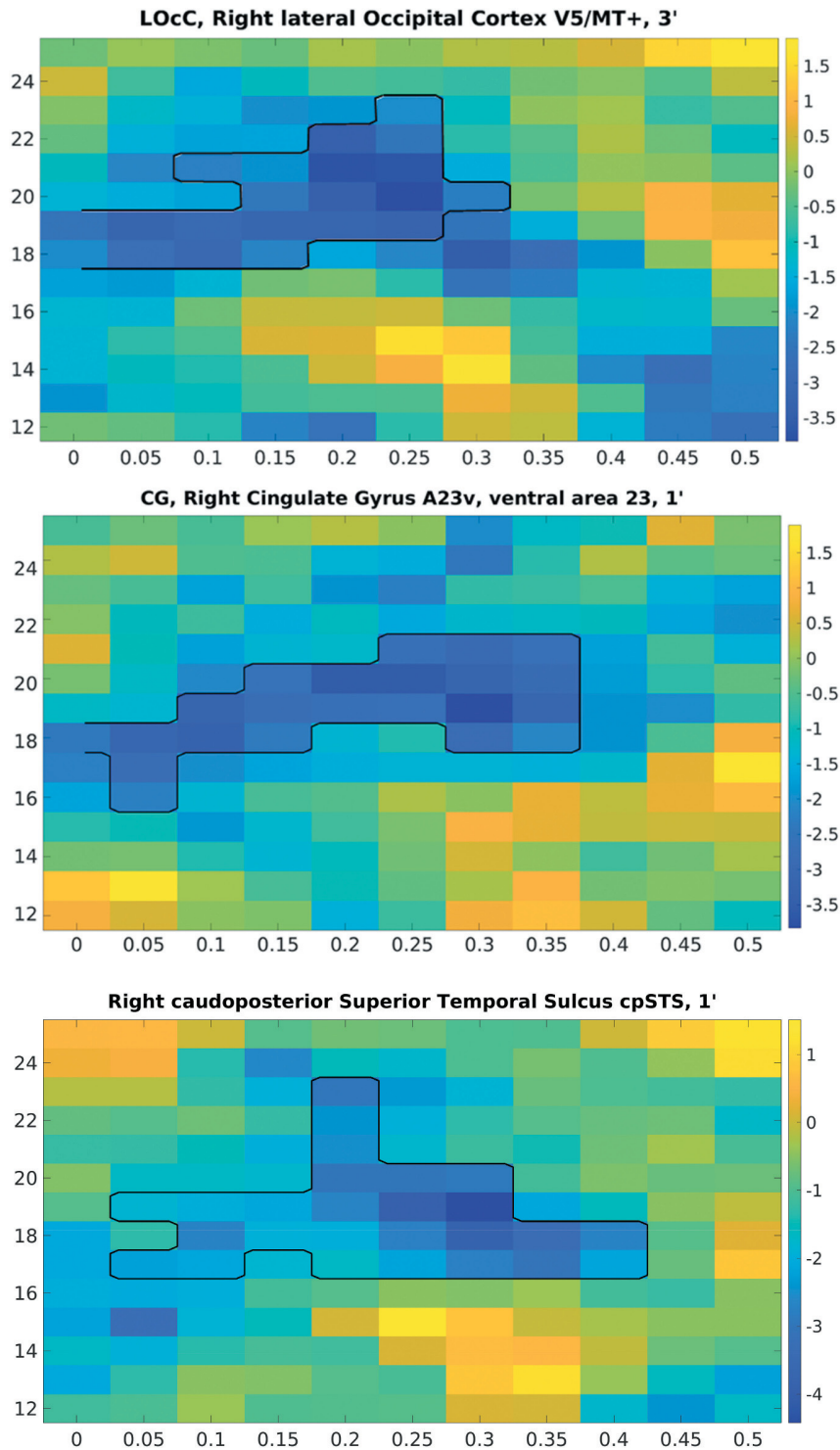
Figure 2. Result of statistical comparisons on ROIs-related virtual channels between first- and third-person perspective (colors represent *t*-values) showing significant stronger beta suppression emerging in the right-hemispheric lateral occipital cortex V5/MT + area, ventral CG, and caudoposterior superior temporal sulcus (pSTS); significant cluster are outlined; channel number is indicated in the plot title).

worth noting that the stimuli used in the current study were action verbs and that the right hemisphere was previously shown to predominantly contribute to action observation-execution matching (Biermann-Ruben et al., 2008). It is therefore possible that perspective on actions is biased by a differential involvement of the two brain hemispheres in motor simulation processes.
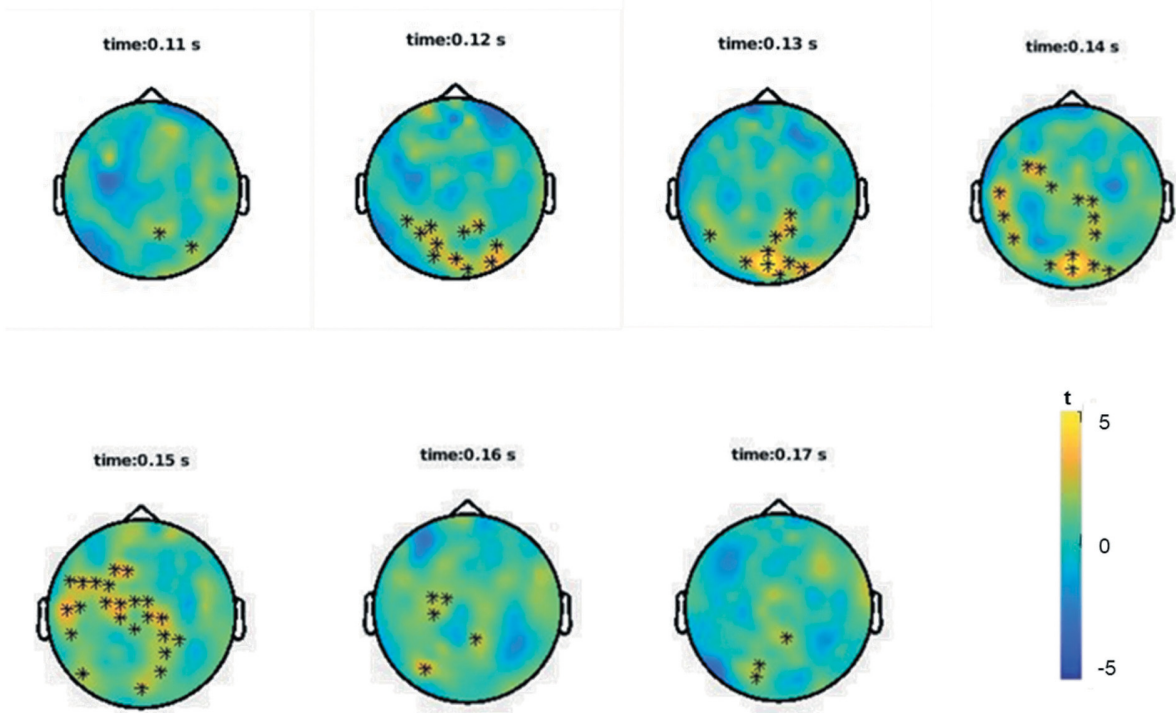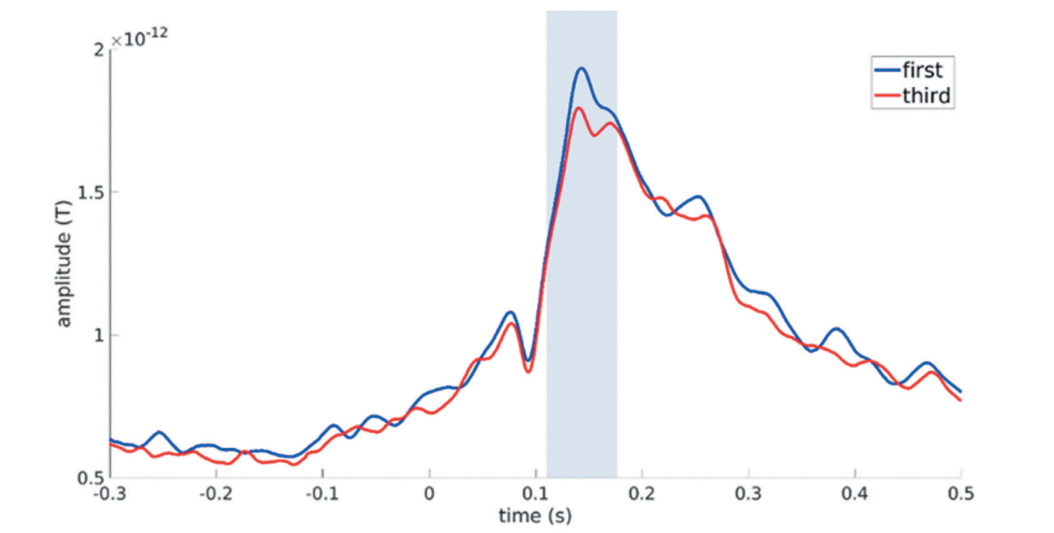
Figure 3. Event related fields: (a) Statistical results from the comparisons between first- and third-person perspective (stars indicate channels showing a significant effect; colors represent *t*-values). (b) Grandaverage of channels (n = 23, corresponding to star symbols in (a) showing a significant effect at 150 ms after word onset.

Differently, the sensorimotor area was not modulated by perspective-taking, a finding also observed in previous fMRI studies applying sentence stimuli (Tomasino et al., 2007) and pronoun-verb pairs (Hartung et al., 2017). The insensitivity of the sensorimotor cortical activation to perspective-taking together with its role in action embodiment (Binder & Desai, 2011) suggest an earlier or a different hierarchical level of this area in simulation processes. Before taking place, perspective-taking might for example require an enhanced details resolution, possibly delivered by the earlier engagement of the sensorimotor area. Alternatively, the sensorimotor simulation might occur in parallel to the activation of areas engaged in perspective-taking; the output of the two networks might be finally merged to one coherent sensation. Further research with suitable study designs is needed to determine the specific roles of these areas in processing actions and perspective-taking.

The current ERF results point to an early effect at about 150 ms after pronoun-verb onset in form of larger amplitudes for first- versus third-person perspective. Analogously, larger ERP amplitudes were observed for first- compared to third-person pronouns in the time-window 150–250 ms in frontal, central, and parietal midline sites (Brilmayer et al., 2019; Shi et al., 2011). Although in Shi et al.'s study the difference reached significance at a later time point (from 300 to 500 ms after word onset), a descriptive difference between conditions was already observable at about 200 ms on parietal sites. Investigation of different levels of self-representation using particular sentence parts such as "a," "his" and "mine" showed both early (200–400 ms) and late (500–800 ms) effects in posterior central sites (Walla et al., 2007). There is a number of studies pointing to short latencies of semantic processes and addressing for example, the mismatch negativity (MMN) (Assadollahi & Rockstroh, 2005; Ortigue et al., 2004; Shtyrov et al., 2004) or semantic coherence (Hauk et al., 2006). The observed ERF activation started in occipital sites, an area that was reported to be more activated by first- than third-person perspective (Perrine Ruby & Decety, 2003). The broadening activation toward central and then left-hemispheric temporal areas indicates an increasing recruitment of areas involved in semantic processing.

Both behavioral and neuroimaging findings seem thus to point to an advantage of first-person perspective, but what can explain this effect? One tentative explanation is that simulation in first-person already occurs at a prereflective level and in a sort of a priori approach to reality. This seems to be the case from a cognitive developmental point of view, as young children are not yet able to imagine a perspective different from theirs (egocentric thinking according to Piaget; three mountains task). This might depend on the immaturity of particular brain structures and also on evolutionary aspects: studies using visuomotor stimuli suggest that information from the first-person perspective facilitates efficient imitative behavior (Watanabe & Higuchi, 2016). Processing events from a third-person perspective implies different possible expectations that not necessarily reflect this a priori personal experience, although they may be strongly biased by it: this together with a smaller sensorial and experiential richness of details may result in a weakened cortical activation.

Interestingly, self-other distinction emerged also in sensory ERPs: the N1 suppression accompanying perception of self- vs. externally produced tones (Timm et al., 2013) demonstrates that despite the constancy of the stimulus, the brain is sensitive to the role of perspective already at an early hierarchical processing stage. In the present study we aimed at targeting this aspect also by looking at a possible modulation of a sensory ERF by semantic perspective, which however did not emerge. Possibly, the auditory sensory modality had an overall weak link to semantic processing of the action or the tone onset latency might have been too long to allow an interference on the related ERF amplitude.

Concluding, the current findings of stronger beta power suppression in the right pSTS, ventral posterior CG, and V5/MT+ are novel neurophysiological findings pointing to mechanisms of perspective-taking during linguistic processing. These cortical areas are likely to play a key-role in simulation processes involving the development of a sense of agency and of self-other distinction.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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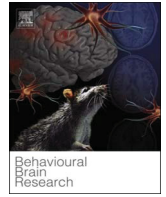
Research report

Body-part specific interactions of action verb processing with motor behaviour

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ABSTRACT

The interaction of action-related language processing with actual movement is an indicator of the functional role of motor cortical involvement in language understanding. This paper describes two experiments using single action verb stimuli. Motor responses were performed with the hand or the foot. To test the double dissociation of language-motor facilitation effects within subjects, Experiments 1 and 2 used a priming procedure where both hand and foot reactions had to be performed in response to different geometrical shapes, which were preceded by action verbs. In Experiment 1, the semantics of the verbs could be ignored whereas Experiment 2 included semantic decisions. Only Experiment 2 revealed a clear double dissociation in reaction times: reactions were facilitated when preceded by verbs describing actions with the matching effector. In Experiment 1, by contrast, there was an interaction between verb-response congruence and a semantic variable related to motor features of the verbs. Thus, the double dissociation paradigm of semantic motor priming was effective, corroborating the role of the motor system in action-related language processing. Importantly, this effect was body part specific.

1. Introduction

The interaction of action language processing with concurrent motor behaviour is assumed to reflect semantic processing in the brain's motor system [1,2]. This motor-language interaction supports the claim of embodied cognition theories [3,4] that conceptual processing is modality-specific. Potentially, the precise conditions under which the processing of verbal material influences specific motor acts (and vice versa) are informative about how motor simulation contributes to language understanding. While neuroimaging and electrophysiological methods showed a body-part specific and early recruitment of several nodes in the motor network during verb processing (e.g. [5–7]), this information does not allow a direct inference about the function of underlying neuronal processes. Since the motor system is not only well characterised neuroanatomically and neurophysiologically, but also generates specific output, i.e. motor behaviour, this offers intriguing research questions with respect to the functional interaction of motor execution and language processing. Research on other features in language processing, such as different sensory properties, has also provided compelling evidence for the characteristics of semantic

processing and embodied cognition [8–10]. Nevertheless, motor language is special due to its link to motor execution, which can be readily studied in behavioural experiments. Here, the general finding is that a certain motor act, requiring the coordinated activation of several muscles, is influenced by reading or hearing and understanding words or sentences with a specific action content. This may imply that parts of the same or connected cell assemblies are active both in the language processing stream and in motor execution, leading to altered reaction times or kinematic parameters [11–14]. Regarding the effects that action language processing and motor behaviour may exert on each other, both faciliation and interference have been reported in different tasks and stimulus-response delays [13,12,15–19].

The present experiments aimed to investigate facilitating language-motor interaction. Stimuli consisted of single German action verbs that described actions performed with the hand or with the foot, as well as abstract verbs. Both experiments used a double dissociation paradigm to investigate body-part specific effects in a within-subjects comparison. The experimental task included a response effector decision to sets of geometrical shapes, to be executed after reading a verb. Thus, the response choice was not determined by the verbal stimuli themselves,

but by a visual target stimulus. The temporal delay between the verb stimulus and the response cue was comparatively long (400 ms). This was expected to lead to facilitation rather than interference effects [16,20,21]. Parts of the motor system that were pre-activated by verb understanding may facilitate motor output when they are engaged by the response [22,23,21]. Studies investigating body-part specific language-motor interaction aimed at either facilitation or interference effects in a within-subject double dissociation paradigm are yet rare. In the context of language-motor interaction research, double dissociations of effects can help to infer the specificity of underlying processes and to generalize across language material. More precisely, this means that one category of verbal stimuli should interact with one type of motor response but not with another response. This second response should in turn interact with a second category of verbal material but not with the first. The current study used hand responses, hypothesized to be facilitated only following hand but not foot verbs, and foot responses, thought to be facilitated by foot verbs. This allows more direct inferences about the motor-relatedness of effects, in this case the association to the body part, than contrasting action verbs and abstract verbs, for instance. In studies using only one kind of response (e.g. [12,13,24]), it is less clear whether effects might be related to uncontrolled differences between verbal conditions. Moreover, conducting a within-subjects experiment further increases the inferential power by excluding the possibility that reverse effects for different responses could be due to different subject samples. The current experiments allowed for this setup by using a priming paradigm where responses where not recorded for the verbs, but for the secondary shape decision task. For tasks where the subjects respond directly to language stimuli, the double dissociation can often only be achieved by testing separate groups of subjects or repeatedly testing the same subjects in different blocks or sessions (e.g., as in [15,25]). In one paradigm for instance, hand, foot, and abstract verbs were presented. Participants had to respond to concrete verbs using their hand and to abstract verbs using their foot in half of the experimental blocks. This mapping was reversed in the other half of the blocks. Body-part specific effects were found, with faster reaction times for matching body parts [26]. Another experiment asked participants to overtly categorise hand and foot verbs by directly responding with the matching body part in one block and the opposite body part in another block. Facilitatory effects were found for the kinematics of the response [14]. A recent MEG study found no behavioural effects, but reduced neuronal activation in congruent conditions when subjects pre-activated the finger in some blocks or the foot in other blocks [27]. In addition to these between-block designs, some reports focused on language-motor interaction in between-subject designs [11,28].

Moreover, the relevance of semantic or deep processing for the detection of language-motor interaction effects on reaction times was investigated. Some previous studies reported an influence only when semantic processing was necessary [13,29], while others found effects even during subliminal processing [30,31]. In the current study, we addressed this issue by either including (Experiment 2) or not including (Experiment 1) a semantic decision task.

Additionally, we included two semantic feature variables into the analysis, which we termed "prototypicality" and "effector-specific movement". High values for prototypicality show that a verb has a strong association with one "prototypical" action, for instance *klatschen (to clap)* or *trampeln (to trample)*. In contrast, low values indicate that there are several associated ways to perform the action described by the verb, such as for *basteln (to do arts and crafts)* or *fliehen (to flee)*. The variable "effector-specific movement" describes the amount of movement in the major executing limb that subjects associate with a given verb. Examples for high effector-specific movement verbs are *rubbeln (to rub)* or *springen (to jump)* while low effector-specific movement was reported for *buddeln (to dig)* or *schleichen (to tiptoe)*. Both of these variables were introduced because they may interact with the expected priming effect in a specific way, for instance by modulating the latency

or strength of motor cortex recruitment during word understanding. This extends previous findings of a modulatory role of imageability [24,32] to more specifically action-related semantic features of the verbs. In line with this idea, increased motor cortex activation or modulations in priming effects of differently operationalised but conceptually similar variables have been reported [33–36].

In short, the current experiments combined responses with two effectors and the respective action verbs in one priming task, presuming facilitation effects and also investigating the influence of semantic processing requirements.

2. Experiment 1

In Experiment 1, hand and foot responses were collected to visual target stimuli preceded by action verbs. If verbal processing includes motor simulation, a differential effect on reaction times would be expected depending on the body part the verb prime refers to. The temporal delay between verb prime onset and target stimulus was 400 ms. This was hypothesised to induce facilitation effects on reaction times. Crucially, there were no requirements to actively read and understand the verb stimuli since responses to geometric shapes were given in all trials independently of verb content. Thus, any priming effects emerging in Experiment 1 would be associated with automatic verbal processing.

2.1. Material and methods

2.1.1. Participants

In both experiments reported in this paper, all participants gave written informed consent prior to beginning the experiment and received course credit. 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). All subjects were native monolingual speakers of German, had normal or corrected-to-normal vision, no formal education in linguistics, no neurological nor psychiatric disorders and were not taking medication affecting the central nervous system. Right-handedness was assessed using the German translation of the Edinburgh Handedness questionnaire [37]. Right hand dominance was further corroborated by the Hand Dominance Test (HDT, [38]), a performance measure consisting of the comparison of right hand and left hand performance on three paper-pencil motor tasks. Another self-report questionnaire, extracted from the Lateral Preference Inventory [39] was used to confirm right-footedness.

One subject was excluded due to uncertain handedness. The final set included 20 participants (10 female, mean age 21.29 years, SD = 1.18).

2.1.2. Stimulus material

Verb stimuli were selected in multi-step rating and matching procedures (compare [40]). The final stimulus set was comprised of 48 German disyllabic hand action verbs, e.g. *greifen (to grasp)*, 48 foot action verbs, e.g. *gehen (to walk)*, and 48 abstract verbs, e.g. *raten (to guess)*. In order to obtain comparable stimulus sets for a number of background variables, verb frequency was determined using a database ([41], Leipzig Corpora Collection, available at http://wortschatz.uni-leipzig.de) whereas body part, verb familiarity and imageability were assessed in separate ratings (each $n = 30$). These values were used to create sets of verbs with some variability within, but as little difference between conditions as possible, unless theoretically justified. Residual differences between the three stimulus categories were found in univariate ANOVAs for group means of imageability ($F(2;141) = 273.302$, $p < .001$), frequency ($F(2;141) = 9.366$, $p \leq .001$) and number of letters ($F(2;123) = 5.231$, $p < .007$), but not familiarity. These differences are accounted for by a lower imageability, higher frequency and smaller number of letters for the abstract verbs. No differences were found between hand and foot verbs using paired t-tests

(all $p > .283$). A further rating study ($n = 25$) was used to obtain measures for the perceived prototypicality as well as the amount of effector-specific movement of the actions described by the verbs. These ratings were collected only for the hand and foot verbs. Prototypicality was assessed on a 6-point rating scale from very low to very high. Hand verbs (mean = 4.362, SD = 0.652) and foot verbs (mean = 4.318, SD = 0.610) did not differ significantly in a paired *t*-test ($t = -0.064$, $p = .950$). Effector-specific movement was assessed using a scale from 0 to 100. Subjects were asked to adjust four sliding bars to the value they felt expressed the amount of hand, arm, foot, and leg movement in the actions the verbs described. The values for the body part rated to have the highest mean amount of movement in the groups of hand and foot verbs were taken to form the variable "effector-specific movement". This turned out to be the amount of hand movement for hand verbs and the amount of leg movement for foot verbs. Thus, "effector-specific movement" captures the amount of motor activity in the major executing limb subjects report for action verbs. For the sake of keeping in line with widely used category labels we retained the terms "hand verbs" and "foot verbs" despite our rating showing that the latter might more appropriately be called "leg verbs". With respect to effector-specific movement, hand verbs (mean = 69.998, SD = 10.194) and foot verbs (mean = 68.672, SD = 11.296) did not differ significantly in a paired *t*-test ($t = -0.597$, $p = .552$). Both prototypicality and effector-specific movement were *z*-transformed for the statistical analysis of the two priming experiments.

In addition, 12 pairs of geometric star-like shapes with either pointed or rounded corners were used. Initially, a total of 52 pairs of shapes had been created. Of these, 14 pairs had five outer corners, 14 pairs had six corners, and 14 pairs had seven corners. Across shapes, the inner and outer corners were equally distant from the centre point, respectively. The matching shape with rounded corners for each pair was formed by using the rounding function in the graphics software on the previously created pointed shapes. Next, a pilot study with six participants was performed. Subjects had to react to pointed or rounded corners with their hand or foot, for two repetitions of the full stimulus set, and the reverse combination afterwards. This procedure was chosen to identify any shapes that might inherently be harder or easier to process, for instance because they might resemble generic star shapes. The 12 shape pairs for the main experiment were chosen from the shapes closest to mean overall reaction time and with less than average standard deviation across pilot participants. Thus, visual properties or basic processing demands of the geometric shape stimuli should not influence the verbal priming experiment.

2.2. Procedure

Each trial started with the presentation of a fixation cross as an attention cue, followed by either a hand verb, a foot verb, or an abstract verb lasting 300 ms (see Fig. 1). Verbs were projected in white letters onto a black background. Participants were asked to fixate the centre of the screen throughout the experiment. After a blank screen presented for 100 ms the geometric target stimulus appeared, thus resulting in a delay of 400 ms between verb and target onset. The geometric shapes were pseudorandomized from the set with pointed or rounded corners, with each shape shown equally often in each verb condition, 24 times in total. The corner type determined whether subjects had to respond

using the fingers of their right hand on the space bar of a standard keyboard or using their right foot on a foot pedal; this was counterbalanced across participants. Each verb was presented twice with each response modality. After the response or after a maximum duration of 2300 ms, the trial proceeded with a blank screen for 1500 ms. Importantly, the choice of the response effector depended only on the shape stimulus, and thus the action verb conditions were not related to the response effector. The instructions did not give any information about the verbs' purpose or semantic information, but simply asked participants to read the verbs and then to perform the shape reaction task as fast and as accurately as possible. The main experiment was preceded by 12 practice trials which could be repeated if the participant wished to do so. The verbs used in the practice trials were different from the main experiment. Furthermore, handedness and footedness were assessed after the main experiment.

2.3. Statistical analysis

Individual trial reaction times exceeding three standard deviations within each subject and response effector were excluded (1.98% of all trials). Linear mixed-effects models were fit for log-transformed reaction times of correct responses using the package lme4 1.1-8 [42] for R version 3.2.2., including crossed random effects for participants and items. The maximal random effects structure justified by the experimental design was used. The fixed effects structure was defined as the 2-level factor verb condition (hand or foot verbs), the 2-level factor response effector (hand or foot), prototypicality (continuous), and effector-specific movement (continuous). The model also included the 2- and 3-way interactions of verb condition with response effector and prototypicality as well as of verb condition with response effector and effector-specific movement. The hypothesized effect, reflecting facilitated motor behaviour after reading congruent action verbs, was the interaction of verb condition and response effector. The random effects structure included random intercepts for items and random intercepts for participants, as well as random slopes for all four main effects by participants. Factors were sum coded to allow ANOVA-like interpretation of main effects. For all models in all experiments, visual analysis showed no violations of homoscedasticity or normality of residuals. Post hoc comparisons were performed with the R package lsmeans version 2.20-23 [43]. In interactions including the factor response effector, post hoc tests were carried out within the levels of response effector. *z*-Ratios assessed the differences of marginal means of one factor of interest at the different levels of another factor. Interactions involving a continuous predictor were followed up in one of two ways, depending on the appropriate research question: To examine the effect of the continuous predictor at different factor combinations, separate models were fit for the respective factor levels. In cases where the research question was not sufficiently answered by investigating the slopes of the continuous predictor at different factor levels, a "spotlight analysis" [44,45] was chosen. In this approach, the *z*-transformed continuous predictor was re-coded once by adding and once by subtracting one standard deviation from each value. With this re-coded data, two separate models were fit, where the value zero of the continuous predictor does not correspond to the mean as it did in the main model, but to the value one standard deviation above or below the mean. This leads to the model's results for the other predictors and their

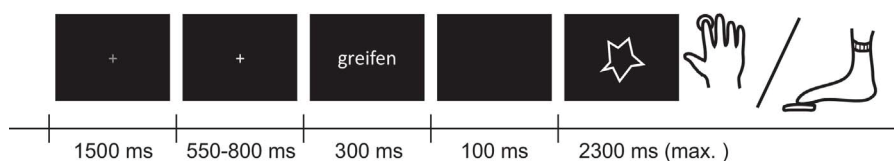
Fig. 1. Experimental procedure in Experiments 1 and 2. The verb prime was followed by a target stimulus of a geometric shape with either pointed or rounded corners. The type of corners determined the response effector, i.e., the right hand or the right foot. In Experiment 1, responses were executed in all trials. In Experiment 2, responses were only required following concrete verb primes.
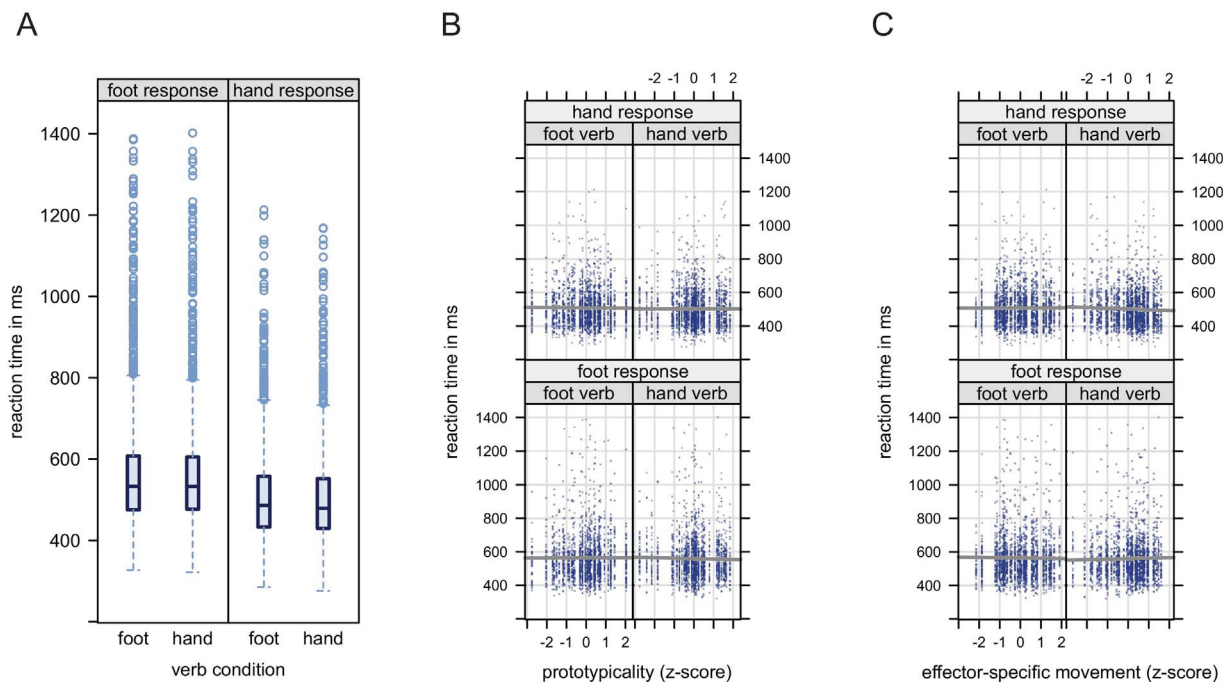
Fig. 2. Experiment 1: Raw un-aggregated reaction time distributions of correct responses in the verb conditions. Panel A: averaged across semantic variables (box-and-whisker plot, boxes mark 25th and 75th percentile, horizontal bars show median, whisker limits are at 1.5 interquartile range.). Panel B: single trials and correlation fit for the distribution of prototypicality. Panel C: single trials and correlation fit for the distribution of effector-specific movement.

interactions being tested at high and low levels of the continuous predictor without dichotomizing the continuous data. Thus, for instance a three-way interaction involving a continuous predictor can be resolved by examining the two-way interaction of the other two predictors involved in the interaction in the two models re-centred at high and low levels of the continuous predictor. The spotlight analyses were also compared with a classical median split approach, with the continuous predictor dichotomised and treated as a factor.

2.4. Results

Raw reaction times and statistical effects are shown in Figs. 2 and 3 while the detailed results of all models can be found in Table A.1. The mixed model showed a significant main effect of response effector ($\beta = 0.051$, $t = 7.48$). Foot responses were slower than hand responses. Moreover, there was a main effect of verb condition ($\beta = 0.005$, $t = 2.06$), with hand verbs overall faster than foot verbs. The 2-way interaction of verb condition and response effector was not significant. Importantly, the three-way interaction between verb condition, response effector, and effector-specific movement also reached significance ($\beta = -0.005$, $t = -2.19$). This interaction was followed up by a spotlight analysis to examine the interaction of verb condition with response effector at high and low levels of effector-specific movement in two separate models. The model for low effector-specific movement revealed no significant interaction. The model for high effector-specific movement showed the interaction of verb condition with response effector to be significant ($\beta = -0.007$, $t = -2.36$). Post hoc test revealed that this reflected a significant difference between hand and foot verbs with high effector-specific movement when responding with the hand ($z = 2.272$, $p < .03$). In this case, hand responses to hand verbs were faster than to foot verbs, averaged across prototypicality. The spotlight analysis was corroborated by a post-hoc follow-up procedure dichotomizing effector-specific movement using a median split. Separate models were then fit for the verbs with levels of effector-specific movement below the median and above the median, respectively. The interaction of verb condition with response effector was significant in the model including above-median effector-specific move-

ment ($\beta = 0.003$, $t = -2.22$), but not in the model including below-median effector-specific movement. For above-median effector-specific movement, hand responses were faster following hand verbs than following foot verbs ($z = 2.231$, $p < .03$).

2.5. Discussion

Overall, foot responses were slower than hand responses. This may partly be due to differences in the response device used, but also due to the motor conduction speed [46]. For instance, the different response devices used to record hand and foot responses may have a different temporal delay, artificially increasing foot reaction times. If, however, this was the case, then a fixed delay in recorded response triggers would not alter the relative difference between experimental conditions. Regardless of the contributions of technical and physiological mechanisms to the difference in overall responses from the two limbs, it implies that direct comparisons should be computed within, not across, response effectors. Generally, the hypothesized priming effect should be found in the contrast between hand and foot verbs for hand responses separately from foot responses.

The main effect of verb condition was not expected and does not yet offer any interpretation in relation to embodied language processing. However, this effect is surpassed by the interaction of verb condition with response effector and effector-specific movement. Here, a priming effect in the sense of faster reaction times for congruent verb-effector combinations was found only for verbs with high effector-specific movement and hand responses. This semantic-to-motor priming may be the result of a pre-activation of neuronal circuits in the hand motor area by processing hand verbs. Parts of the same circuits are subsequently accessed again when the motor choice task requires a hand response. In semantic priming, the partial pre-activation by prime stimuli is assumed to reduce processing demands and decrease response latencies to target stimuli [47], and is associated with reduced neuronal activation compared to unprimed targets [48–50]. The delay between verb onset and response cue in Experiment 1 allowed for verbal understanding to take place before the onset of the response target and continue during response preparation, akin to semantic priming
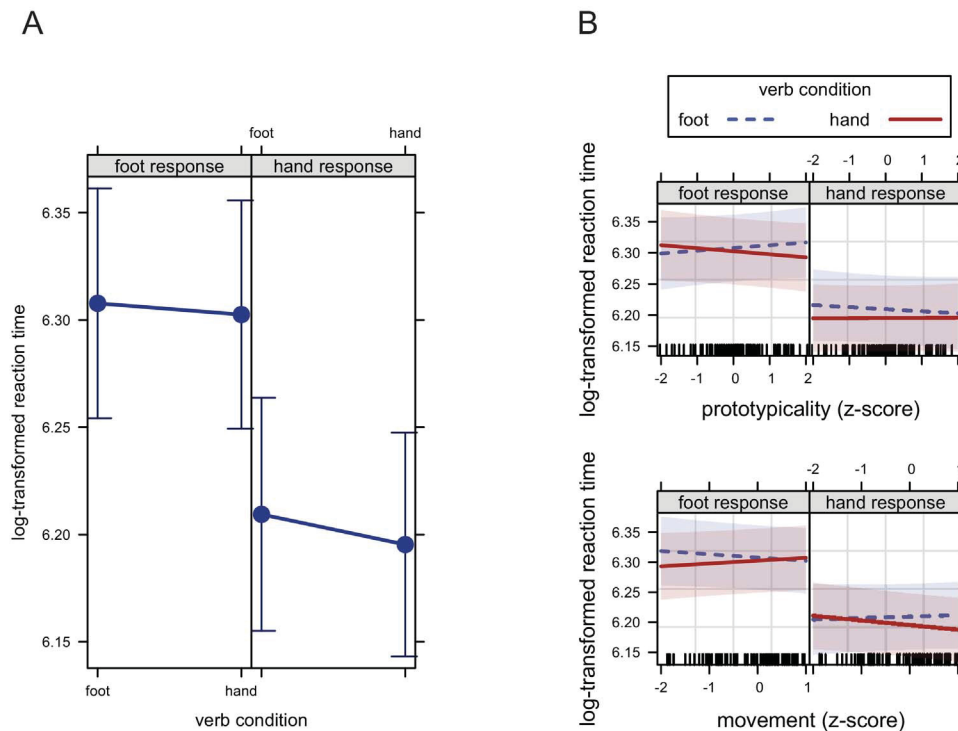
Fig. 3. Experiment 1: Predictor estimates and confidence intervals for the mixed model on log-transformed reaction times. Panel A: effect for the main experimental hypothesis of an interaction of verb condition with response effector (not significant). Panel B: Highest-order effects including prototypicality and effector-specific movement. The interaction of effector-specific movement with verb condition and response effector was significant.

with medium to long SOAs. Thus, the facilitation in congruent responses may be mediated by the processes described in semantic priming, for instance increased cortical excitability combined with reduced processing demands in specific motor circuits following action verb processing.

Crucially, however, the pattern of facilitated responses for congruent verb-effector pairs was only found for hand responses and only for verbs with high effector-specific movement. The latter is particularly interesting to embodied language processing, since this semantic variable directly captures the link between a verb concept to the action it describes.

The three-way interaction also implies that while a priming effect was found for verbs with high effector-specific movement and hand responses, the effect is not robust enough to generalise across verbal material and does not show the double dissociation between response effectors. Interestingly, in this specific experimental set-up the priming effect is found for hand but not foot responses. This could be a consequence of differences in the verbal material in the conditions, of the overlap between verb actions and executed actions, or it could be a consequence of a different relationship between language and motor processing depending on the kind of action language being processed. For instance, hand actions may play a special role since they also form co-speech gestures [51] and have even been argued to link the phylogenetic evolution of communication from gestures to language [52]. The verbs used in the current study, however, generally do not describe actions with a strong communicative function and are often complex hand/arm actions. Nevertheless, hand actions may be more susceptible to subtle language-motor interactions.

The main effects of prototypicality and effector-specific movement were not signficant. This is in line with a shallow processing of verbs in this task, where the access to verbal concepts is not necessary and does not appear to be influenced by the semantic variables. At the same time, this renders the interaction with verb condition and response effector even more interesting. Semantic processing is not required and cannot be assumed to consistently take place, as corroborated by the lack of

modulation by semantic features. Yet, a subtle priming effect emerges, which may be directly related to superficial bottom-up motor simulation during verb stimulus processing even in the absence of conscious, deep semantic processing.

Thus, Experiment 1 shows that language-motor priming can occur even when no active verbal processing is required, albeit only under specific circumstances. This is in line with other studies reporting motor-language interaction or action-feature priming effects for non-semantic tasks and even for subliminal processing [30,31,53–55]. Moreover, silent reading or passive listening was also shown to produce measurable neurophysiological responses in the motor cortex [6,56,33,7,57]. Yet, semantic processing may be a crucial factor to enhance motor cortex recruitment in verbal processing and language-motor interaction, or the ability to empirically observe it. In the interference paradigm in [13], lexical decision was not sufficient to produce an effect, but semantic decision was (see also [58]). Attention to semantics may also generally be important for semantic priming on the behavioural and neurophysiological level [59,60]. Thus, combining our priming paradigm with a semantic task in Experiment 2 was expected to lead to further insights into language-motor interaction and to more robust priming effects.

3. Experiment 2

Experiment 2 used the same priming paradigm set-up as Experiment 1, but also included a semantic Go/No-Go task. The visual target stimuli defined whether a hand or a foot response was required, but the verb primes were used for a semantic decision. Abstract verbs identified NoGo trials, while concrete verbs indicated that the subsequent response choice task should be carried out. Thus, semantic processing and verb understanding were necessary for a successful performance, and we expected priming effects to lead to differential response patterns depending on the congruence of verb body part and response effector.
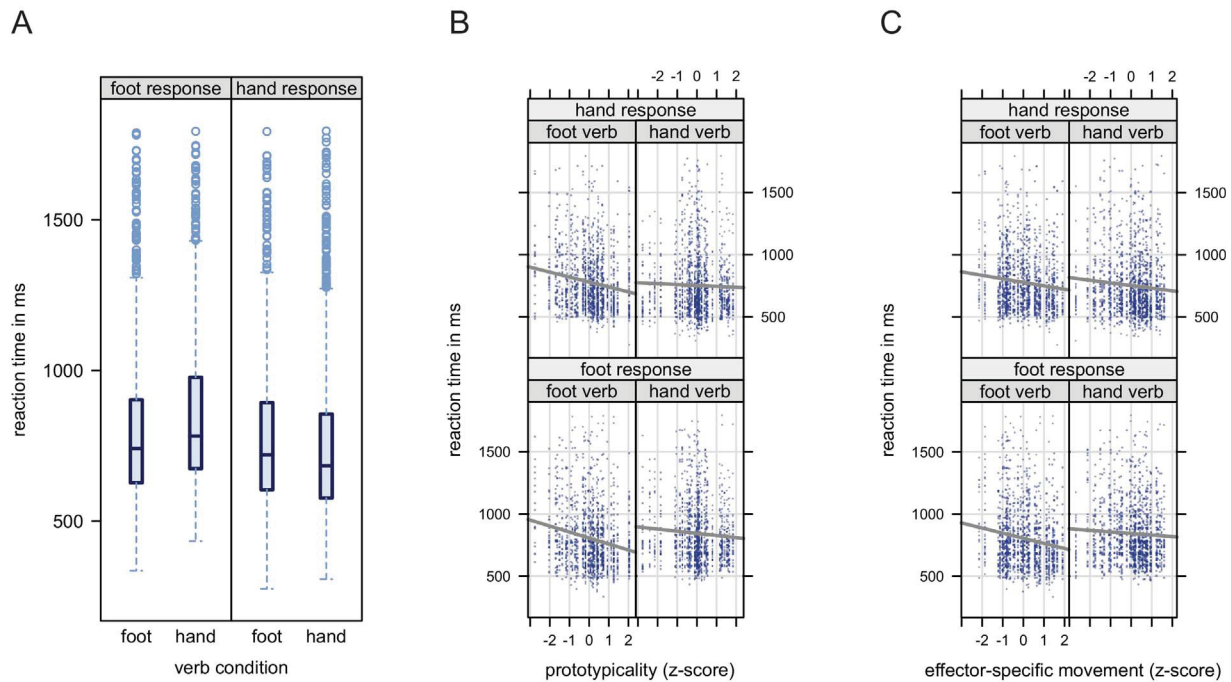
Fig. 4. Experiment 2: Raw un-aggregated reaction time distributions of correct responses in the verb conditions. Panel A: averaged across semantic variables (box-and-whisker plot, boxes mark 25th and 75th percentile, horizontal bars show median, whisker limits are at 1.5 interquartile range.). Panel B: single trials and correlation fit for the distribution of prototypicality. Panel C: single trials and correlation fit for the distribution of effector-specific movement.

3.1. Material and methods

3.1.1. Participants

Fifteen healthy subjects (12 female, mean age 22.79, SD = 3.31) were included in the final analyses. Of the 22 participants who took part in the experiment, four were excluded because of high false alarm rates of > 20%, two due to a high amount of missed responses in all conditions (> 20%) and one because of too many wrong responses (> 15%).

3.1.2. Stimulus material

Experiment 2 used the same stimulus material as Experiment 1, i.e., the same verbs and 12 pairs of geometric shapes.

3.2. Procedure

The experimental task of Experiment 1 combined the shape recognition with a semantic decision task (compare Fig. 1). Thus, participants saw the same visual input as in Experiment 1, but had to perform the shape reaction task only in those trials where concrete verbs had been shown. Two hand and two foot responses were collected for all hand and foot verbs, and participants were not informed about this experimental manipulation. Compared to Experiment 1, while the visual input was the same, verb processing and the conditional responses differed. In Experiment 1, responses were necessary in each trial and verb processing was assumed to be shallow, since the verbs played no role for the successful execution of the experimental task. In contrast, Experiment 2 required semantic processing of verb meaning in order to correctly identify whether the trial was a Go or a NoGo trial, and then to perform the shape decision task similarly to Experiment 1 only following concrete verbs. Handedness and footedness assessment followed the main experiment.

3.3. Statistical analysis

Individual trial reaction times exceeding three standard deviations within each subject and response effector were excluded (1.42% of all trials). Analogous to Experiment 1, linear mixed models were fit with random intercepts for items and random intercepts and slopes for participants using the lme4 package version 1.1-8 [42] for R version 3.2.2. Fixed effects were specified by the factors verb condition (hand or foot), response effector (hand or foot), prototypicality (continuous), effector-specific movement (continuous), the two-way interaction between verb condition and response effector, and the two- and three-way interactions of each semantic variable with verb condition and response effector. Random by-subject slopes included all four main effects, random intercepts for subjects and items were also modelled. All factors were sum-coded, post hoc tests were performed with lsmeans version 2.20-23 [43]. In interactions including the factor response effector, post hoc tests were carried out within the levels of response effector. For interactions involving continuous predictors, separate models were fit for the respective factor combinations or according to the spotlight analysis routine for levels of the continuous predictor. As in Experiment 1, statistical analyses were performed on log-transformed reaction times of correct responses.

3.4. Results

The mixed model revealed a significant main effect of response effector ($\beta = 0.040$, $t = 4.36$), with faster responses executed using the hand compared with the foot. More importantly, a significant interaction ($\beta = -0.023$, $t = -6.98$) between the factors verb body part and response effector showed the body-part specific priming: Post hoc analyses revealed that hand responses were faster for shapes preceded by hand verbs than by foot verbs ($z = 2.643$, $p < .01$). The reverse effect was found for foot responses, which were faster following foot verbs than hand verbs ($z = -3.390$, $p < .01$). This is illustrated in Figs. 4 and 5, showing the raw reaction time distributions and statistical results. Moreover, significant main effects were found for prototypicality ($\beta = -0.028$, $t = -4.04$) and effector-specific movement ($\beta = -0.018$, $t = -2.55$), with faster reaction times associated with higher prototypicality and effector-specific movement. The interaction of verb condition with prototypicality was also significant ($\beta = -0.015$, $t = -2.31$). This was followed up by two separate models for hand
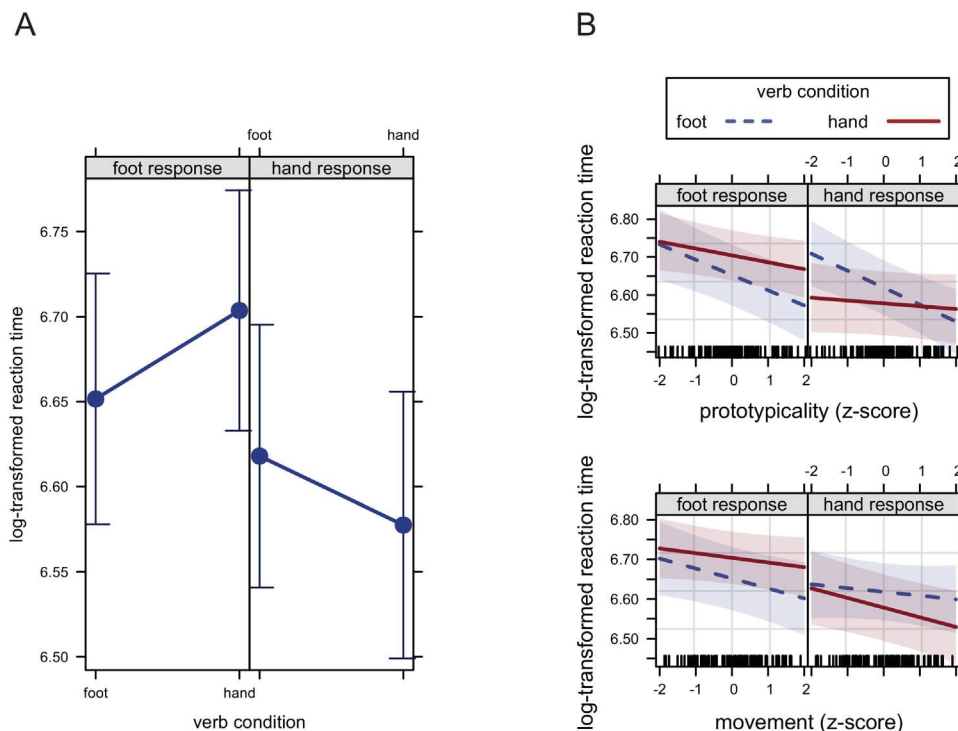
Fig. 5. Experiment 2: Predictor estimates and confidence intervals for the mixed model on log-transformed reaction times. Panel A: effect for the main experimental hypothesis of an interaction of verb condition with response effector (significant). Panel B: Highest-order effects including prototypicality and effector-specific movement. Main effects for prototypicality and effector-specific movement as well as the interaction between verb condition and prototypicality were significant.

verbs and foot verbs, to examine whether prototypicality would show a significant influence on either or both types of verbs, regardless of response effector. In the model for hand verbs only, no such effect was observed ($t = -1.39$), while it was found in the foot verbs model ($\beta = -0.043$, $t = -4.28$). Detailed results for all models can be found in Table A.1.

3.5. Discussion

The main hypothesis was confirmed: When responses to geometric shapes were performed using the hand, reaction times were faster in trials with hand verb primes than with foot verb primes. The reverse effect was also found, i.e., foot responses were faster following foot verbs than hand verbs. Crucially, this effect likely depends on the depth of processing or possibly the strategy of verb processing. Experiment 2 combined the shape recognition with a semantic decision Go/NoGo task, forcing participants to process verb meaning. Thus, semantic processing may recruit the motor cortex in a body-part specific fashion, producing a pre-activation with regard to a facilitated motor execution when the same areas are involved in planning a motor response following language understanding (compare [47,48,22]). This was not reliably found in Experiment 1, where no semantic processing of the verbs was necessary for successful task performance. These results indicate that understanding the meaning of a single verb partly relies on neuronal processes in the motor system [61,4] and that the context of language understanding can recruit sensory-motor areas to a flexible degree [62].

Faster reaction times were associated both with high prototypicality and high effector-specific movement. Note that the facilitating effect for prototypicality was more pronounced for foot verbs than for hand verbs, regardless of response effector. When investigating hand and foot verbs in separate models, the effect of prototypicality was actually too weak to be significant for hand verbs. It is unclear to what extent this lack of effect is due to lower statistical power in the separate models. Nevertheless, the two-way interaction in the main model (see Fig. 5B)

also shows that the effect is stronger for foot verbs. This was an unexpected result. Untransformed prototypicality values are comparable between the verb conditions and the difference in effects should not be due to a difference in prototypicality distributions between hand and foot verbs. While the sets of verbs are largely comparable in prototypicality and further background variables, it can be argued that the overall similarity between the foot verbs is larger than between hand verbs. Even though both sets contain verbs describing a range of different actions but also a few near-synonyms, foot verbs by nature tend to often relate to locomotion actions. Possibly, in the context of this experiment, understanding and reaching a semantic decision about these verbs can profit more from the ease or speed of simulating this action or activating its action schema - as measured by prototypicality - than understanding verbs that are more easily discriminable, such as most hand verbs. It should also be noted that the relationship between prototypicality and effector-specific movement appears to be different for hand and foot verbs: For hand verbs, the two variables correlate with $\rho = 0.18$ ($p = .22$) while for foot verbs this correlation is stronger with $\rho = 0.64$ ($p < .01$). Thus, the stronger prototypicality effect for foot verbs may actually to some extent reflect the effect of effector-specific movement. Taken together, the interpretation of the facilitating effect of prototypicality is difficult. It is conceivable that rather than prototypicality, effector-specific movement is the more interesting variable, not only because its effect was clearer in Experiment 2 but also because it interacted with a priming effect in Experiment 1. In contrast to Experiment 1, there was no interaction between effector-specific movement and the verb-motor facilitation effect in Experiment 2. This could be the result of more conscious and complete semantic processing, where the robust body-part specific effects cannot be further modulated by semantic features. The temporal association of verb processing and motor behaviour is crucial in language-motor interaction research, to the extent that either interference or facilitation can be detected depending on the temporal course of experiments. At the same time, semantic processing tends to produce more robust effects [13], while some experiment have also found interactions with

lexical or even subliminal processing [30,55]. In the current experiments, timing and task are to some extent confounded due to the instruction. While the delay between verb and shape onset was the same, reaction times were about 300 ms slower on average for Experiment 2. This is not surprising because a second, semantic task had to be performed and presumably this was more difficult and more effortful. However, it is possible that this difference in the time course of internal processing and the robust priming effect may have masked any additional modulations of effector-specific movement. Note also that the regression slopes do indeed show a pattern in line with stronger priming for higher effector-specific movement, but the three-way interaction was associated with a *t*-value of -1.84, which does not exceed the threshold of -2 or 2 set to accept an effect as significant.

High prototypicality as well as high effector-specific movement seem to generally facilitate access to verb concepts. Rather than specifically facilitating congruent responses at the motor preparation stage, high prototypicality and high effector-specific movement appear to facilitate the semantic decision stage. The semantic decision may be faster for verbs scoring high on the two semantic variables because they are more easily distinguishable from abstract verbs. It is conceivable that this is also directly related to facilitated motor simulation for these verbs, especially since the semantic variables directly capture motor features, but the data do not exclude the possibility that other processes in conceptual access might play a role. Still, it is interesting that the understanding of action verbs, necessary for the decision of whether a verb described a concrete or an abstract action, was facilitated by high effector-specific movement and also high prototypicality. In Experiment 1, verb understanding was not required for successful task performance. Nevertheless, it can be presumed that verbal stimuli even without an explicit task elicit at least a shallow understanding process, as also indicated by studies showing effects for silent reading or passive listening [6,56,33,7,57]. Thus, the current results show a subtle priming effect in the absence of a semantic task, which would have been undetectable in the current setup and for these action verbs without the inclusion of effector-specific movement. With a semantic task, in contrast, the semantic variables - effector-specific movement and prototypicality - appear to modulate the understanding process itself and the semantic decision, rather than the priming as an interaction between this understanding and the response.

4. General discussion

A body-part specific facilitation effect emerged in Experiment 2, which required semantic processing. When concrete verb primes referred to the same body part as the subsequent response, reaction times to subsequent target stimuli were faster than in the cases where the verb was unrelated. This facilitation effect was only observed for verbs with high effector-specific movement when responding with the hand in Experiment 1, where semantic processing of the action verbs was not required. The process underlying the facilitation effect may be the motor resonance of verbal processing as predicted by the embodied cognition hypothesis [23,3]. Generally, semantic priming effects are assumed to reflect reduced processing demands for target stimuli and reduced neuronal activation in areas that have been pre-activated by a semantically related prime stimulus [48,49,47,63]. This directly depends on the task set, where even subliminal priming is modulated by attention to semantic content [59,60]. Facilitation effects of action language on reaction times were reduced in patients with early Parkinson's disease [64]. Neurophysiological responses associated with priming were reduced when processing hand verbs after rTMS to the hand motor cortex [19]. Thus, language-motor priming is associated with similar neuronal mechanisms as in other types of priming, while the motor system plays a specific role in the processing of action-related language. This is in line with the body-part specific effect found in the double dissociation paradigm of the current study.

The body part association itself is unlikely to be the direct

mechanism on which language-motor facilitation operates, since the congruence of language and response at least partly depends on the paradigm and experimental manipulation. This is evident in experiments where motor-language facilitation was found for compatible mappings within one body part, based for instance on the specific hand shape implied by action language and the response or implied movement direction [65,1,66–68,2,53,64]. Other studies investigated semantic information that is not directly connected to an action description, such as emotional content or spatial properties, also with facilitating effects for congruent feature-response mappings [31,69,70]. All of these studies together with the current findings of a body-part specific interaction between verb and motor processing support the claim of grounded and embodied cognition theories, which stress a flexible semantic system in interacting modality-specific processing areas [4,3,71,62]. Current theories of semantic memory and conceptual processing often describe multilevel networks including both modality-specific, sensory-motor nodes as well as supramodal hubs or convergence zones and argue that neither fully embodied nor fully disembodied accounts can explain the accumulating findings of language and conceptual processing [72–74]. The contribution of modality-specific systems to cognition is regarded differently in these theories, ranging from non-essential interaction between sensory-motor and conceptual brain areas [75,76] to sensory-motor grounding as an important mechanism in concept acquisition and retrieval [3,77]. Indeed, the body of empirical evidence can be summarised as showing that sensory-motor contributions to language understanding can occur, but they do not do so automatically under all circumstances and in all contexts (for a review, see [62]). Thus, there is a need for further characterising the way in which sensory-motor areas are recruited during language understanding and how semantic and motor processing interact in order to understand when and how these interactions occur and how specific they are. The results of the current study may contribute to this discussion, showing that the task context and a requirement of semantic processing is essential for robust language-motor priming to occur, but that subtle effects may also be seen for a non-semantic task. Importantly, the double dissociation paradigm analysed here may offer a clearer interpretation of results compared with studies that use between-subject designs, compare one type of concrete to abstract verbs or nouns, or make a body-part manipulation explicit. In these experiments, caution is necessary regarding the influence of the specific set of subjects, the desired contrast of experimental conditions potentially confounded by grammatical class or unobserved differences between language stimuli, and the changes in processing strategies associated with salient body part features, respectively.

One limitation in the current experiments is the not strictly controlled temporal dimension of semantic processing. The delay between verb onset and response cue was set to 400 ms, the classical time window associated with semantic processing [78]. Average reaction times were about 600 ms. Thus, it is not entirely clear to what extent the observed effects are mediated by early semantic processing in the motor system, which has been found already at around 200 ms after stimulus onset [5,40] and even earlier [57]. There may be more and higher level contributions, for instance by prefrontal areas, where priming operates on the (possibly verbalised) shape-response mapping.

Another interesting finding from the current series of experiments concerns the influence of semantic features of verbs. Both the prototypicality of the action described by the verbs and the amount of movement of the specific body part in this action appear to play a role. The variable prototypicality aimed to capture how clearly a verb invokes an associated action. The rationale behind this was that motor system recruitment may be stronger for verbs that have a highly prototypical action compared with verbs that have weaker associations to several diffuse ways to execute an action. This idea is related to the distinction between basic and subordinate verbs in one experiment [34]. There, subordinate verbs, which describe a very specific motor

program, enhanced activity in parietal motor system areas more strongly than basic verbs, which refer to more general motor programs. Moreover, one study compared verbs representing actions with low degrees of freedom – i.e. actions typically performed by specific actors in definite contexts, such as *to water* – with verbs with high degrees of freedom, i.e. actions that can be performed in many different ways such as *to recycle*. Verbs with low degrees of freedom, conceptually similar to our verbs with high prototypicality, were associated with faster processing [35]. The variable that we called effector-specific movement may be even more directly related to the relationship between verb processing and motor system recruitment. The rationale behind this was simple: the portions of the motor cortex associated with a specific body part may be more involved in understanding a verb that describes an action involving a lot of movement with the same effector compared with one that describes an action with some, but less movement of the same effector (and even less for a verb with very little or no movement of that effector, for instance in verbs relating to a different body part). Previous studies found a modulatory role for body relatedness, where higher importance of bodily experience decreased reaction times in lexical decision [36] and where hand ratings correlated with fMRI activation in the motor system [33]. Our approach is similar but focuses specifically on the amount of movement with the most relevant body part. Here, a generally facilitating influence was found in Experiment 2, while an interaction with verb type and response effector was seen in Experiment 1. This indicates that verbs describing highly prototypical actions or actions with a lot of movement with specific effectors are more easily accessed or processed. This is an important issue because it directly links motor features with conceptual processing. Similar results were obtained when comparing basic and subordinate verbs [34], action verbs with high or low degrees of freedom [35] or the relative importance of bodily experience [36]. Note also that correlations between the values for the different motor-related variables with each other and with imageability and familiarity are between $\rho = 0.25$ and $\rho = 0.45$, while for instance the correlation between imageability and familiarity is stronger with $\rho = 0.8$. Therefore, effects for prototypicality and effector-specific movement are not just mediators for other unspecific influences of variables which were not modelled at the same time. On top of this, prototypicality as well as effector-specific movement seem to directly influence motor simulation. This interaction is especially interesting in Experiment 1, where a subtle priming effect for verbs with high effector-specific movement was observed for hand responses. Thus, motor features of verbs may have general as well as specific effects on action verb processing.

Taken together, the present series of experiments shows that when language-motor interaction is invoked, it can be body-part specific. This is in line with the claim of embodied cognition theories, postulating a recruitment of the motor system when understanding language describing actions. With a comparatively long delay, motor system recruitment may function as a pre-activation as described for semantic priming, thus leading to faster or less effortful access to body-part specific motor areas. Moreover, the amount or reliability of motor cortex activation is modulated by the depth of semantic processing with processing strategies defined by task requirements.

Acknowledgement

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bbr.2017.04.002.

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Semantic discrimination impacts tDCS modulation of verb processing

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Motor cortex activation observed during body-related verb processing hints at simulation accompanying linguistic understanding. By exploiting the up- and down-regulation that anodal and cathodal transcranial direct current stimulation (tDCS) exert on motor cortical excitability, we aimed at further characterizing the functional contribution of the motor system to linguistic processing. In a double-blind sham-controlled within-subjects design, online stimulation was applied to the left hemispheric hand-related motor cortex of 20 healthy subjects. A dual, double-dissociation task required participants to semantically discriminate concrete (hand/foot) from abstract verb primes as well as to respond with the hand or with the foot to verb-unrelated geometric targets. Analyses were conducted with linear mixed models. Semantic priming was confirmed by faster and more accurate reactions when the response effector was congruent with the verb's body part. Cathodal stimulation induced faster responses for hand verb primes thus indicating a somatotopical distribution of cortical activation as induced by body-related verbs. Importantly, this effect depended on performance in semantic discrimination. The current results point to verb processing being selectively modifiable by neuromodulation and at the same time to a dependence of tDCS effects on enhanced simulation. We discuss putative mechanisms operating in this reciprocal dependence of neuromodulation and motor resonance.

The assumption that cognition is grounded in simulation processes[1,2] implies a cross-talk between action-related language and neurophysiological motor mechanisms. Cortical motor engagement accompanying the processing of verbs and action-related sentences has indeed been detected by means of blood-oxygen-level dependent (BOLD) signal[3–5], event related potentials/fields (ERPs)[6–8], and neural oscillatory activity[9,10]. Also, behavioural measures of verbal-motor interaction such as priming and interference effects consistently hint at shared brain resources between linguistic and motor processes (for a review see[11]). Complementary neurophysiological investigations confirm that priming and interference exert a modulatory effect on cortical motor activation[12–14]. Yet, some studies on cortical motor lesions point to a lack of impairment in action word processing and to a possible involvement of other brain areas[15,16] thus raising questions on the causal relevance of cortical motor activation for action-related linguistic understanding.

To tackle this issue, a number of studies have applied transcranial magnetic stimulation (TMS) of the motor cortex while participants processed action verbs and sentences. Overall, results point to a word-dependent modulation of cortical motor excitability as measured with motor evoked potentials (MEPs) and reaction times. Interestingly, abstract action knowledge as elicited by motor-related pictures[17] and athletes' surnames[18] can also affect response latency and cortical MEPs in the primary motor cortex. While there may be a dissociation between cortical motor excitability elicited by abstract action knowledge and observation of real actions[18], results from TMS studies indicate an instrumental role of the motor cortex in language understanding. However, an inconsistent scenario concerning the direction of this modulation emerges. Some investigations showed decreased MEPs and/or longer reaction times suggesting inhibited cortical motor activation[19–22], while others showed increased MEPs and/or shorter reaction times[23–25] indicating cortical motor facilitation. As for inconsistencies among single pulse TMS studies, these may depend on whether MEP recording accompanied word onset[19,24,26] or took place at subsequent time-points (i.e., between 170 and 500 ms after word onset[22,25]. Although other methodological differences such as types of protocols (e.g., repetitive versus single pulse TMS) and stimuli may also to some extent explain inconsistencies, opposite TMS effects have been observed despite applying the same paradigm and

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stimuli[19,26]. To clarify the role of increased versus decreased cortical excitability in verbal processing an alternative approach can be applied that bi-directionally manipulates cortical motor excitability.

Transcranial direct current stimulation (tDCS) induces changes in the membrane permeability and accomplishes a moderate shift of cortical excitability[27]. This technique offers some advantages over TMS. First, it allows the investigation of bi-directional effects of stimulation by depolarising and hyperpolarising the cellular membrane. Anodal and cathodal stimulation of the hand-related motor area led to motor cortical excitation and inhibition respectively[27,28]. Significant reduction in gamma-aminobutyric acid (GABA) concentration corroborates the excitatory effect of anodal stimulation of the hand-related cortical motor area[29]. In the context of linguistic processing, tDCS has often been applied to frontal, parietal and temporal areas (see[30,31] for reviews). By contrast, tDCS of the cortical motor area has seen applications in motor observation[32]. As for tDCS application to the motor cortex in linguistic paradigms, only a few studies were conducted[33–35]. The present study aimed at filling this gap by determining the bi-directional modulatory effect of stimulation on the verbal-motor interface in healthy individuals and thus further characterizing the functional contribution of the motor system to linguistic processing.

An important characteristic of tDCS is that, differently from TMS, it modulates spontaneous cortical activation instead of disrupting it[36]. Although it induces cortical noise like TMS, the dependent neural activity is strongly influenced by the state of the system, which is mainly determined by the task[36,37]. Anodal tDCS induces firing of neurons that are near threshold: if neurons are not influenced by the task, they will be far from the threshold and will less likely discharge[37]. This makes tDCS particularly suited to address the role of semantic processing for cortical motor activation. In general, when semantic access is irrelevant for task completion, hand related expressions do not induce significant motor resonance[11]. Conversely, motor activation seems to depend on deeper understanding of action verbs as required by a semantic task[38]. Results from studies on abstract action knowledge based on the relationship between personal names and athletes' motor skills suggest that the strength of the association between name and motor content needs to rise above some level of consolidation for the process of embodying in the motor system to take place[39]. By varying task requirements, the depth of semantic processing was shown to affect verbal-motor interference[40] and priming[41], possibly by modifying the amount of recruitment of the motor system. In the current study we addressed the synergies between tDCS and semantic processing depth, defined as the individual accuracy in a verb categorization task. Both the effect of cortical motor stimulation on verb processing and the role played by semantic processing depth in tDCS-induced modulatory effects on reaction times were examined. A dual, double-dissociation task was applied in which a) a verb had to be semantically categorized as concrete versus abstract and b) in case of a concrete verb, hand/foot responses had to be given to a verb-unrelated prompt (a shape with rounded or pointed corners). This priming paradigm has the advantage of disentangling hand from foot-related verbal and motor contributions: responses from both effectors follow the same stimuli thus allowing the attribution of possible differences to priming. On the other hand, this task does not allow direct measure of response latencies to verb presentation: responses are prompted by the shape and not by the verb thus precluding contrasts in reaction time between different verb categories (e.g., concrete versus abstract verbs, or hand versus foot verbs). Online tDCS of the left hemispheric hand knob was expected to selectively affect processing of hand- but not foot-related verbs. As tDCS does not seem to affect simple motor hand reactions[42,43], no tDCS effect on hand reaction times was anticipated. Capitalizing on the stronger reliability of the sham stimulation in tDCS compared to TMS paradigms[44–46], we applied it as a control condition in a double-blind cross-over design. Planned comparisons between verum and sham stimulation were expected to result in opposite effects of anodal and cathodal tDCS on behavioural measures.

Methods

Participants. Twenty monolingual German native speakers (10 females, mean age = 23.8 ± 6 SD) took part in the study. The sample size was based on a previous investigation with the same paradigm showing that behavioural effects emerged already with 15 participants[41]. All subjects were right-handed, with an average laterality quotient of 92.3% (SD = 16.2%; Edinburgh Handedness Inventory[47]); 15 subjects were right-footed, 4 showed no clear side preference and 1 was left-footed (Lateral Preference Inventory[48]). The subjects had normal or corrected-to-normal vision and none made use of neuro-modulatory medications. Exclusion criteria were history of serious medical, neurological, or psychiatric illnesses, severe head trauma, personal or family history of epilepsy, metal implant in the head/neck region, pacemaker implantation and pregnancy. Participants provided written informed consent prior to each measurement and received financial compensation for their participation. The study was in accordance with the Declaration of Helsinki and was approved by the local ethics committee of the Medical Faculty at the Heinrich Heine University in Duesseldorf (study number 3400).

Materials. German disyllabic infinitive verbs describing actions executed with the upper extremities (hand verbs), with the lower extremities (foot verbs), and actions in which no body part was involved (abstract verbs) were visually presented. The three conditions underwent a matching procedure for the parameters word length, frequency, imageability and familiarity to properly select stimuli. Word familiarity and imageability were assessed by means of two rating scales (each n = 30, see[8,9] for further details) and word frequency was derived by the Leipzig corpora collection[49]. Each condition finally included 48 verbs, which were also used in previous studies[8,9], repeated twice. Hand and foot verbs did not differ in familiarity, length, imageability and frequency (all p > 0.283).

The prompt stimulus consisted of 12 different star-like shapes, each of which could have rounded or pointed corners (further details in[41]). Presentation software (version 14.9, Neurobehavioral Systems, Albany, California, USA) was used to display the stimuli. The space bar of a standard computer keyboard and a foot-pedal (Foot Switch SW3-M, PCsensor) were used as hand and foot response device, respectively.
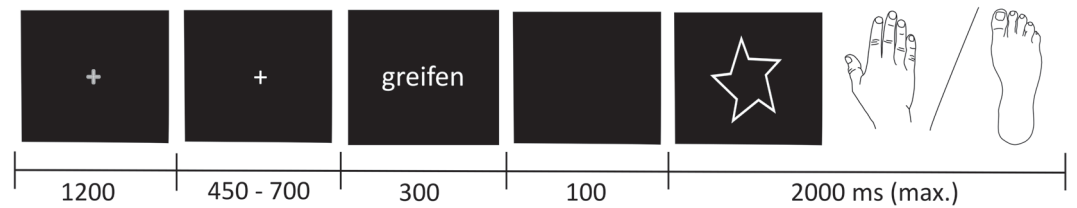
Figure 1. Task design. In the case of a concrete verb (e.g.,"greifen" = "to grab"), participants had to respond to a shape by pressing a hand button or a foot pedal depending on the shape's corners (here: pointed corners).

Procedure. The experimental design consisted in a double-dissociation paradigm based on a Go-NoGo task that required semantic processing. For each verb presentation, participants were required to identify whether the verb was concrete or abstract: concrete verbs defined the Go-condition and participants had to respond later on with the right hand or with the right foot depending on the type of corners of a prompt shape (rounded/pointed, Fig. 1) as soon as the prompt occurred. Abstract verbs represented a NoGo cue. Each verb was followed once by each prompt type. The association between the shape's rounded/pointed corners and the response effector was counterbalanced across subjects and kept stable across three sessions (see below). Each trial began with a central fixation cross displayed on a black background for a jittered interval between 1200 and 1700 ms. Then a word in white font appeared centrally and remained on the screen for 300 ms followed by 100 ms black screen. Afterwards, a shape with either rounded or pointed corners was centrally presented for a maximal time of 2 s. Hand or foot responses ended the shape presentation and initiated the following trial. The experiment was split into two blocks each including 144 trials; a break lasting one minute separated the two blocks. Overall the measurement lasted about 18 minutes and each subject underwent three sessions on three different days; the sessions were one week apart and generally at the same time of the day. A total of 18 stimuli different from those of the main study were used in practice trials preceding the main experiment and each word was randomly followed by both types of shapes. The training lasted about 4 minutes in the first session and 1 minute in the following two sessions. Participants were not informed about the aim of the experiment being related to hand and foot verbs.

TMS. Transcranial magnetic stimulation was applied to localise the hand-related primary motor cortex of the left hemisphere by determining the individual resting motor threshold. After about 10 minutes of relaxed sitting, participants received single pulse TMS, delivered by a standard eight-shaped coil (MC-B70) connected to a stimulator (Medtronic MagPro, Minneapolis, USA). This was tangentially placed on the scalp of the participant, with the handle pointing backwards and laterally at about 45 degree away from the midline. The target site was marked with a marker pen on the skin of the participant's head.

tDCS. Two saline-soaked sponge electrodes were placed on the head of the participants after locally cleaning the skin surface with alcohol and applying scrubbing gel (Abralyt HiCl). One smaller tDCS electrode (3×3 cm) was positioned on the left hemispheric hand motor cortex and the other larger electrode (7×5 cm) was located on the contralateral supra-orbital region. The use of a smaller electrode was aimed at narrowing the stimulated area around the hot spot[50]. A current intensity of 0.75 mA was applied using a battery-driven stimulator system (NeuroConn, Ilmenau, Germany) and impedance was kept below 11 kOhm. Stimulation parameters were in accordance with current safety guidelines of transcranial brain stimulation[45,51]. Online anodal, cathodal or sham stimulation was applied during the main experiment, starting after the practice trials. Stimulation was pseudorandomly delivered to the participants in a double-blind, cross-over design so that each subject received each type of stimulation once (anodal, cathodal, and sham). To mimic the sensation of verum stimulation in the sham condition the current was ramped up for 10 seconds and then immediately ramped down for 10 seconds. At the end of each session a debriefing questionnaire was administered to assess the participant's blindness to the type of stimulation. On average each subject correctly guessed only one session out of three, i.e. guessing was at chance level and thus indicated effectiveness of the blinding procedure. 31.5% of the subjects correctly guessed the anodal and the sham condition and 36.8% the cathodal condition. Data from the cathodal condition of one subject and from part of the sham condition of another subject were not available due to technical problems.

Analysis. Log-transformed reaction times for correct responses and shape-response task accuracy were analysed using linear mixed models[52]. This method is advantageous due to its sensitivity to differences among individual subjects, robustness to unequal sample sizes (unbalanced designs can be analysed without eliminating or replacing data-points), and for reducing variance by accounting for item-related differences in performance[53], which optimizes generalization over participants and word samples. To capture accuracy related to word processing the discrimination parameter d-prime (d') was assessed for the single sessions of each participant. This specifically referred to the accuracy of the first (semantic) part of task, where concrete versus abstract verbs had to be identified; the accuracy of responses to shapes was not concerned. d' was calculated as a difference between the normalised rate of hits to concrete words (i.e., responses from any effector following concrete words) and the normalised rate of false alarms to abstract words (i.e., responses from any effector occurring although they should have been inhibited). In the cases of perfect accuracy, which results in infinite d' values, the accuracy was estimated as half way between the best value of the corresponding tDCS condition and 100% accuracy to preserve the order of the subject performance ranking. Reaction times exceeding two standard deviations within each session
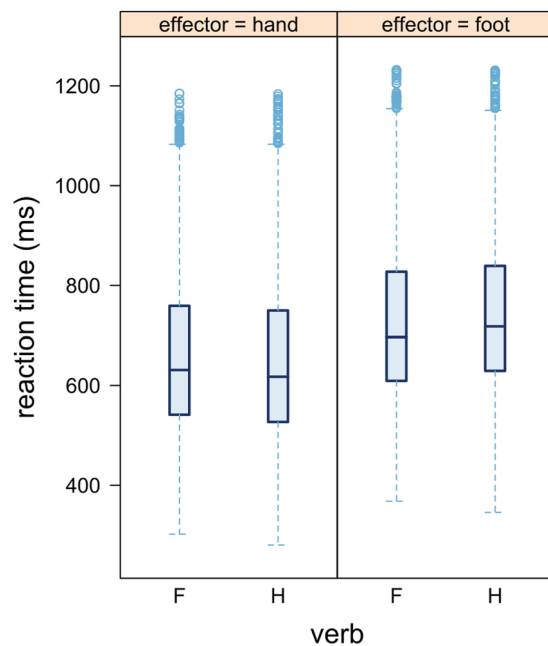
Figure 2. Averaged raw reaction times for each response effector following hand (H) and foot (F) verbs; the horizontal line shows the median, the box indicate the 25th and 75th percentile and whisker limits are at 1.5 interquartile range.

and response effector were eliminated. This was motivated by the effect that learning and responses with different body parts have on reaction times[54] and accuracy[14]. Data points from one session of one subject were excluded because the related d' value exceeded two SD across all d' values.

For reaction time analysis, the following four factors were employed in the linear mixed model using the package lme4[55] run on R[56]: tDCS condition (anodal, cathodal, and sham), response effector (hand, foot), verb type (hand, foot) and semantic discrimination performance expressed as median split d' values (high, low). High and low d' indicated higher and lower performance, respectively. d' values were calculated per subject and per single session, so each subject could score differently depending on the performance in each of the three sessions. As literature evidence shows inconsistencies in the presumed opposite modulatory effects of anodal and cathodal stimulation (see Discussion section), we opted for the sham condition as a neutral and more adequate control condition. We a priori sum contrasted all fixed effects, thus resulting in the following planned comparisons for the tDCS factor: anodal versus sham and cathodal versus sham stimulation. The main effects and interactions of the four factors were specified in the model as fixed effects. Crossed random effects for participants and items were applied. Random effects for participants included random intercepts and random slopes of the four main effects and their interactions starting with a maximal, design-driven random effects structure[57]. The converging model with the maximal random effects structure included random intercepts for participants and items as well as random slopes of the four main effects for participants. P-values were computed via Wald-statistics approximation. Post-hoc contrasts of verb type by effector interactions were done for each effector separately to exclude an influence of the different latency of hand versus foot responses. The post-hoc tests were performed with lsmeans[58] adopting the Tukey method for multiple comparisons; the confidence level was set at 0.95.

For shape-response accuracy analysis, main effects and interactions between tDCS condition, response effector, and verb type were specified as fixed effects in a binomial logit model[59]; random effects for participants included random intercepts. As the logit model predicts the probability of a particular outcome, only correct responses for concrete verbs were included in the analysis.

Results

Subjects correctly performed the semantic categorization task as indicated by an average accuracy of 91.1% (SD = 9.05) in inhibiting responses after abstract verbs and of 93.7% (SD = 10.49) in responding after concrete verbs.

Response effector showed a significant main effect consisting in faster hand than foot responses ($p < 0.001$; Table 1). Semantic discrimination as measured for each participant in each session showed a main effect consisting of significantly faster responses for high versus low verb discrimination accuracy (d'; $p = 0.045$). A significant interaction between verb type and response effector indicated a facilitation effect consisting in shorter reaction times for congruent verb-effector pairs ($p < 0.001$; Figs 2 and 3a). Yet, post-hoc analysis did not result in significant differences between reaction times for hand versus foot verbs (all $p > 0.883$). Importantly, there was a significant interaction between cathodal versus sham stimulation (c-tDCS), verb type and semantic discrimination ($p = 0.006$). To disentangle this 3-way interaction, data subsets for high and low semantic discrimination were created. The main effects and the interactions between tDCS and verb as well as between verb and effector were specified in the model as fixed effects. Random effects for participants included random intercepts and random

Formula: log-rt ~ DCS*verb*effector*d' + (1 + verb + tDCS + effector + d'|subject) + (1|item)			
Fixed parts	*Estimate*	*Std. Error*	*p-value*
(Intercept)	6.521	0.028	**<0.001**
a-tDCS	0.003	0.015	0.828
c-tDCS	0.000	0.017	0.991
verb	−0.001	0.006	0.830
effector	−0.060	0.010	**<0.001**
d'	−0.034	0.017	**0.045**
a-tDCS × verb	0.002	0.003	0.554
c-tDCS × verb	0.002	0.003	0.389
a-tDCS × effector	−0.001	0.003	0.703
c-tDCS × effector	0.001	0.003	0.844
verb × effector	0.009	0.002	**<0.001**
a-tDCS × d'	0.018	0.011	0.079
c-tDCS × d'	−0.013	0.013	0.316
verb × d'	0.001	0.003	0.642
effector × d'	−0.000	0.003	0.951
a-tDCS × verb × effector	0.002	0.003	0.353
c-tDCS × verb × effector	0.001	0.003	0.624
a-tDCS × verb × d'	−0.001	0.003	0.611
c-tDCS × verb × d'	0.008	0.003	**0.006**
a-tDCS × effector × d'	0.004	0.003	0.198
c-tDCS × effector × d'	−0.002	0.003	0.512
verb × effector × d'	0.001	0.002	0.777
a-tDCS × verb × effector × d'	−0.002	0.003	0.541
c-tDCS × verb × effector × d'	−0.001	0.003	0.716

Table 1. Formula and statistical results from the mixed model analysis of reaction times (a-tDCS = anodal vs. sham; c-tDCS = cathodal vs. sham). P-values are computed via Wald-statistics approximation and significant p-values are shown in bold.

Formula: log-rt ~ tDCS*verb + verb*effector + (1 + tDCS + verb*effector|subject) + (1|item)						
	high d'			**low d'**		
Fixed parts	*Estimate*	*Std. Error*	*p-value*	*Estimate*	*Std. Error*	*p-value*
(Intercept)	6.532	0.034	**<0.001**	6.532	0.031	**<0.001**
a-tDCS	0.004	0.012	0.748	−0.031	0.027	0.257
c-tDCS	−0.013	0.020	0.506	0.048	0.034	0.158
verb	−0.003	0.007	0.627	−0.001	0.006	0.911
effector	−0.045	0.010	**<0.001**	−0.070	0.011	**<0.001**
a-tDCS × verb	−0.001	0.004	0.753	0.003	0.004	0.490
c-tDCS × verb	0.012	0.004	**0.003**	−0.005	0.004	0.190
verb × effector	0.009	0.004	**0.023**	0.008	0.003	**0.011**

Table 2. Formula and statistical results from the mixed model analysis of reaction times in the subsets with high (left) and low (right) semantic discrimination (d′). P-values are computed via Wald-statistics approximation and significant p-values are shown in bold.

slopes, starting with a maximal random effects structure. The converging model with the maximal random effects structure included random intercepts for participants and items as well as random slopes of tDCS main effect and of verb-effector interaction for participants (Table 2). A significant main effect of response effector (p < 0.001) and a significant interaction of verb with effector pointing to a priming effect were confirmed in both data subsets (p = 0.023 and p = 0.011; Table 2). Crucially, while the cathodal versus sham planned contrast interacted significantly with verb in the high semantic discrimination subset (p = 0.003), it did not do so in the low semantic discrimination subset (p = 0.190). This significant interaction between cathodal versus sham stimulation and verb type consisted in faster responses to prompts following hand verbs in the cathodal compared to the sham condition (Fig. 4) independently from response effector, while no tDCS effect was observed for foot verbs.

For shape-response task accuracy, a significant interaction of verb with effector (p = 0.004) showing higher accuracy for congruent verb-response pairs pointed to a facilitation effect (Fig. 3b, Table 3). Post-hoc analysis resulted in significantly more accurate hand responses for hand verb primes (p = 0.028) and a trend for
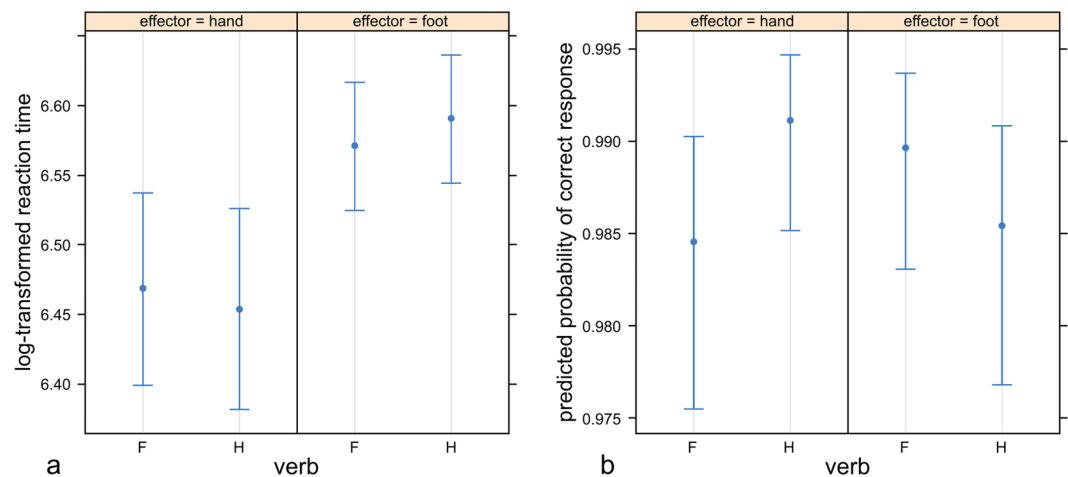
Figure 3. Priming effect across tDCS conditions on reaction times (**a**) and shape-response accuracy measures (**b**). Estimates and confidence intervals for verb type (H = hand, F = foot) and response effector.
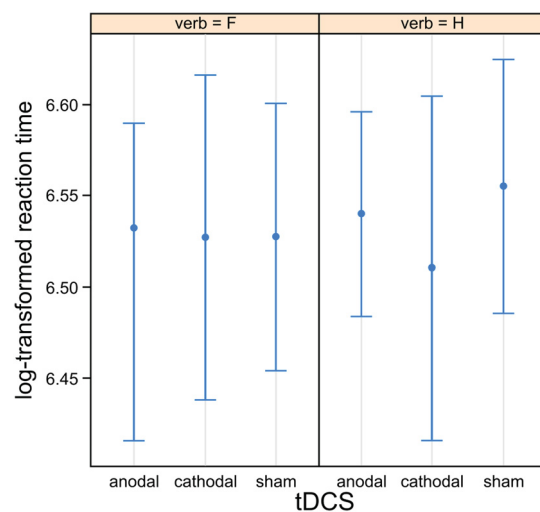

Figure 4. Estimates and confidence intervals for tDCS and verb type (H = hand, F = foot) on logarithmically transformed reaction times for the subgroup with high semantic discrimination.

significantly more accurate foot responses for foot verb primes (p = 0.059). Also, the interaction between cathodal versus sham tDCS, verb type, and response effector approached significance (p = 0.050). To follow up this interaction, models including the main effects and the interaction of verb with response as fixed effects and random intercepts for participants were separately applied to the cathodal and the sham condition: while the interaction remained significant in the sham condition (p = 0.003), it was not significant in the cathodal condition (p = 0.987) indicating a loss of the priming effect regarding accuracy (Fig. 5). Follow-up analysis showed the presence of a significant priming effect also in the anodal condition (p = 0.013), with p-values surviving post-hoc Bonferroni multiple comparisons correction.

Discussion

Beyond a predictable advantage of hand over foot reaction times likely due to nerve conduction speed[54] and to practice, a priming effect of verb type on response latency and accuracy emerged, whereby the latter was statistically mainly expressed by hand verb primes. Together with previous results showing limb-specific facilitation in response latency with a similar task paradigm[60], the present findings indicate a somatotopically localised engagement of hand and foot motor cortices in processing body-related verbs as hand/foot-verbs seem to recruit the related hand/foot motor area in a faster and more accurate way. Motor simulation[1,2] appears a plausible mechanism underlying this facilitation effect. Crucially, in case of high semantic discrimination cathodal stimulation of the hand motor cortex accelerated responses for hand but not for foot verb primes.

Previous studies have shown interference effects to precede facilitation effects by varying the time-lapse between verb presentation and action onset. A systematic review of studies focussing on hand-related expressions showed that single word presentation of hand verbs delays hand responses in early time-windows (up to 400 ms)

Formula: accuracy ~ tDCS*verb*effector + (1|subject)			
Fixed parts	*Odd ratios*	*Std. Error*	*p-value*
(Intercept)	82.080	0.209	**<0.001**
a-tDCS	1.156	0.114	0.204
c-tDCS	1.194	0.116	0.128
verb	1.055	0.078	0.499
effector	1.024	0.078	0.767
a-tDCS × verb	0.967	0.114	0.766
c-tDCS × verb	0.982	0.115	0.876
a-tDCS × effector	1.072	0.114	0.544
c-tDCS × effector	0.981	0.115	0.869
verb × effector	1.254	0.078	**0.004**
a-tDCS × verb × effector	1.145	0.114	0.236
c-tDCS × verb × effector	0.798	0.115	0.050

Table 3. Formula and statistical results from the mixed model analysis of shape-response accuracy. Significant p-values are shown in bold.
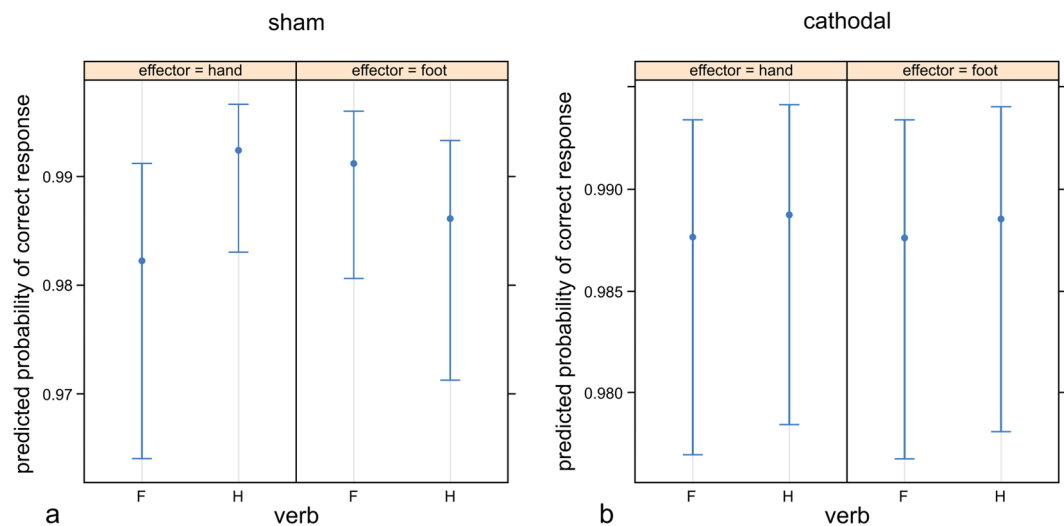

Figure 5. Estimates and confidence intervals for verb type and response effector in the sham (left) and cathodal (right) condition. Note the absence of priming in accuracy measures with cathodal stimulation.

and subsequently facilitates them between 450 and 750 ms[11]. This agrees with the neurocomputational perspective that the time-window up to half a second after verb onset is accompanied by neuronal decrease of firing rate in the premotor cortex, whereas a facilitation time-window from half a second to about a second is related to more rapid neural reaction[61]. Early interference and subsequent facilitation thus constitute a temporal dynamics with which online stimulation as applied in the present study interacts.

A plausible mechanism underlying faster responses for hand verb primes is that the cortical inhibitory effect of cathodal stimulation (see Introduction) selectively decreased cortical motor activation induced by hand verb processing and by hand response preparation. Although the present task design does not provide direct measures of interference, task timing and reaction time improvement suggest reduced interference between verb processing and motor preparation as triggered by concrete words. Differential engagement of hand and foot motor areas in concrete versus abstract verb processing has already been found around 200 ms after word onset[9], thus conceivably leading to early response preparation in the present design. From a neurophysiological perspective, concurrent linguistic and motor (preparation) processes appear to compete for common neural resources. This is suggested by reduced cortical excitability[19] and decreased motor-related activity accompanying the overlap between hand/foot-related word processing and congruent limb action execution/preparation[12–14,62]. Accordingly, a cathodally induced decrease in cortical excitability may have reduced competition by shifting activation dependent on hand verb processing and hand response preparation to a below-threshold state. Reduced interference thus possibly led to an earlier onset of priming and faster hand responses. In line with our findings, the application of theta burst TMS to the left hemispheric hand-related motor cortex, a technique known to reduce cortical excitability[63], shortened hand reaction times to hand verbs compared to right hemispheric stimulation[64].

Altogether, results suggest that externally-induced decline in cortical excitability may disrupt verbal-motor interference and allow faster cortical recovery processes.

Cathodal stimulation and improved semantic discrimination also resulted in faster foot responses to hand verbs, thus impairing priming on reaction time. One possible explanation is that reduced activation of the hand-related motor cortex liberated the foot motor cortex from lateral inhibition[65,66]. Also, results show a significant inverse relationship between semantic discrimination and response latency: while a causal relationship cannot be directly deduced, increased verb categorization accuracy accelerating responses appears a more plausible interpretation than shorter response latencies improving semantic accuracy. Faster foot responses to hand verbs may thus depend on a combination of beneficial cathodal stimulation effects on hand verb processing and improved semantic discrimination performance.

Effects of transcranial direct current stimulation are highly dependent on the state of the subject during stimulation[67]. It has been proposed that tDCS interacts with the level of excitation of the system, driven by the task to shape the final result[37]. The present paradigm required discriminating between concrete and abstract verbs, which likely implicates internal simulation of motor behaviour, as confirmed by the presence of priming. Enhanced cortical motor recruitment for concrete compared to abstract verbs[9,22,24,68] hints at stronger simulation processes accompanying the former. Improved semantic discrimination between concrete and abstract verbs may thus reflect inherent enhanced simulation. Although it may be argued that other parameters can influence discrimination accuracy (e.g., attention), it cannot be excluded that they do so by modulating simulation processes. Our finding of a dependence of cathodal effects on semantic discrimination suggests that simulation needs to be strong enough to allow down-modulation. Interestingly, cathodal tDCS has been shown to decrease MEP amplitude of about 30% at rest and of 50% during motor imagery[69]. Also, cathodal stimulation of the left motor cortex improved coherent motor perception in a complex but not in a simple movement perception condition[36]. These task conditions likely differ in amount of cortical motor recruitment. Altogether, enhanced cortical activation induced by stronger simulation processes (i.e., better versus worse semantic discrimination) may thus boost the effect of cathodal stimulation.

Cathodal stimulation eliminated priming in accuracy measures and, concomitantly to improved semantic discrimination, impaired it on reaction times (compare $p = 0.023$ in the high d' subset model versus $p < 0.001$ in the main model). Dissociation between the impact of stimulation on response accuracy and latency emerged also in other studies focussing on action-related words. Cortical motor cathodal stimulation reduced accuracy of associations between novel words and the appropriate action-related information, whereas it had no impact on reaction time[33]. Cortical premotor repetitive TMS eliminated semantic priming on accuracy for hand verbs while it only reduced priming on reaction time[70]. While these results suggest stronger susceptibility of accuracy measures of priming to neuromodulation, the reasons for that remain to be determined.

No effect of anodal compared to sham stimulation was observed. The polarity effect of tDCS on direct cortical excitability measures like MEP amplitudes appears to fade on behavioural measures[71]. The presence of cathodal but not of opposite anodal effects was previously reported in action word learning[33] and motor imagery[69] using the same electrode montage as in the present study. One reason for the lack of anodal influence in the current study may be an induced ceiling effect in cortical excitability preventing further modulation by cognitive processes. The interplay between tDCS and a linguistic task may affect performance measures in a different and more complex way than cortical stimulation alone, thus disrupting tDCS polarity effects.

One limitation of the present study is the lack of objective measures such as MEPs, which renders the interpretations concerning the state of cortical excitability speculative; MEP recording, however, would have not been possible without interfering with the tDCS protocol. Also, tDCS over the foot motor cortex might have well complemented the present double-dissociation paradigm, although at the cost of a resulting 5-way interactions with difficult interpretability. While a more homogenous right-foot lateralization across subjects would have been desirable, the inclusion of response effector as random slope per subject in the mixed linear model (see Methods section) in part mitigates this as it allows the effect of response effector to vary across subjects. Finally, while the categories of hand and foot verbs were matched according to length, frequency, imageability and familiarity, the abstract verb category could not be completely matched except for familiarity. Although this might imply that the effects found are not unequivocally dependent on performance in semantic discrimination, Supplementary Fig. S1 suggests that neither word frequency nor word length were reliable criteria for the distinction between abstract and concrete verbs, which argues for the adequacy of the semantic discrimination task design.

To conclude, the present study shows that cathodal stimulation of the hand-related motor cortex can specifically modulate hand-verb processing, whereby the strength of internal simulation processes appears to further affect this modulation. Verbal-motor interaction has typically been investigated by means of tasks focussing on the lexical/literal/syllabic versus semantic/syntactic dimension. However, our results hint at action comprehension being not an all-or-none phenomenon[72] and point to the determinant role of an additional dimension such as semantic processing depth. Assessing individual effective motor simulation may result in finer tests of linguistic grounding theories and may provide information on the impact, rather than complementarity, of motor resonance on linguistic understanding. Facilitatory effects of tDCS, which is not aimed at virtually lesioning the cortex, are indicative here and possibly applicable to aphasia[73] in a supportive and preventive therapeutic approach.

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Author Contributions

V.N., A.K., A.S. and K.B.R. conceived the study. V.N., A.K., P.I. and K.B.R. contributed to the study design. V.N. and A.K. implemented the study, data collection and data analysis. V.N., A.K. and K.B.R. interpreted the results. V.N. drafted the manuscript, which was critically revised and approved by A.K., P.I., A.S. and K.B.R.

Additional Information

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