Neurophysiological investigations on action word processing

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Anne Klepp
aus Coburg

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Aus dem Institut für Klinische Neurowissenschaften
und Medizinische Psychologie
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Every representation of a movement awakens in some degree the actual movement which is its object

William James (1890)

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Glossary

ALS	amyotrophic lateral sclerosis
BA	Brodmann Area
BOLD	blood oxygenation level dependent
DICS	dynamic imaging of coherent sources
DTI	diffusion tensor imaging
ECD	equivalent current dipole
EEG	electroencephalography
EMG	electromyography
ERD	event-related desynchronisation
FDI	first dorsal interosseus
fMRI	functional magnetic resonance imaging
GABA	gamma-aminobutyric acid
MEG	magnetoencephalography
MNI	Montreal Neurological Institute
MNS	mirror neuron system
MRI	magnetic resonance imaging
PD	Parkinson's disease
PET	positron emission tomography
PSS	perceptual symbol systems
SQUID	superconducting quantum interference device
TMS	transcranial magnetic stimulation

1 Summary

The present thesis investigated the neurophysiological processing of action verbs and the contributions of the motor system. Classical theories of language processing, semantic memory and brain function in general are based on the idea that anatomical brain areas form distinct functional modules. This modularisation is supported by clinical and experimental evidence. Lesions in specific brain areas cause predictable functional deficits, and activation in a certain brain region can be shown to correlate with a specific behaviour using neuroimaging methods. For language processing, the visual word form area, Wernicke's area in the superior temporal cortex, and Broca's area in the frontal cortex have been shown to be of particular relevance. However, a number of theories called embodied cognition or grounded cognition challenge this structure-to-function mapping of the domains of perception, cognition and action. They claim that on the one hand a cognitive function such as conceptual and language processing may not be as strictly located in certain brain areas as most 20th century theories postulate. On the other hand, they argue that a certain brain region is not only involved in one function or one domain of functions. More specifically, this implies that distributed modal networks in the sensorimotor system form the basis of cognitive functions, of concept acquisition and semantic memory activation as well as language processing. Concepts are not merely associated with their sensory and motor features. Rather, neuronal circuits in the sensory and motor areas actually create the formation of conceptual knowledge through their activation during learning in body-environment interactions. These same circuits are activated by the principle of Hebbian learning when concepts are accessed.

While there is accumulating empirical support for the major claims of embodied cognition theories, a lot of open questions remain and differences in methods and experimental designs make studies difficult to compare. This thesis provides a series of experiments with identical language stimulus material and magnetoencephalographic recordings which allow a better understanding of different aspects of embodied cognition. In particular, this thesis investigated neural activation reflecting motor system involvement in verb processing regarding its spatial localisation, its time course, and its functional mechanisms in interaction with motor behaviour using magnetoencephalography (MEG).

In a first study, participants silently read verbs describing actions performed with the hands, with the feet, and abstract verbs that did not contain an action. Despite the absence of any movement in this task, individual neuromagnetic sources that had been derived from a separate movement execution task were active during action verb reading. Moreover, this activity was somatotopic, i.e. sensitive to the effector of the verbs, with hand motor sources showing a stronger peak for hand than foot verbs and vice versa.

Crucially, activity peaked around 200 ms after word onset, which is strong evidence that motor system activation in language processing is part of the access to meaning in semantic memory and not a post-lexical effect.

Complementary to these findings in evoked brain responses, a second study investigated oscillatory brain dynamics in the same paradigm. Neuronal oscillations are thought to be an important mechanism in neuronal communication, and different frequency bands have been shown to play distinct functional roles in certain brain areas. For the sensorimotor system, oscillations in the alpha (8-12 Hz) and beta (13-30 Hz) frequency bands are most characteristic and show typical patterns of modulation before, during, and after movement execution. Here, a suppression of oscillatory power with respect to baseline – also described as desynchronisation – is associated with neuronal activation. Silent reading of action verbs was sufficient to lead to power suppression in the alpha and beta frequency range. This suppression was stronger for hand verbs than abstract verbs in a hand motor channel selection. It was also stronger for foot verbs than abstract verbs in a foot motor channel selection. These effects started around 200 ms after word onset for the beta band and 375 ms for the alpha band, corroborating the notion of a semantic access contribution by motor system activation.

A third study directly investigated the interaction of verb processing with a simultaneous motor task. The aim was to draw conclusions about the functional specificity of the motor cortex activations seen during language processing, and to directly link behavioural reaction time effects with neurophysiological measures. This was operationalised using a semantic decision paradigm that required a right index finger button press in response to both hand and foot action verbs. Only for hand verbs the match between verb and response effector was expected to produce interference while foot verbs served as the control condition. With regard to the MEG measures, of particular relevance were again neuronal oscillations in the beta frequency band in the time window of concurrent verb processing and response preparation. Language–motor interactions were only found for action verbs with high imageability. High imageability verbs are those for which it is particularly easy to mentally depict the associated action, implying that the motor system involvement may be stronger in high imageability verb processing. Here, reaction times were slower for hand verbs, i.e. when verbs described an action with the same effector as used in the motor task. This was accompanied by weaker motor preparatory power suppression in the beta frequency band.

Taken together, this thesis tested the embodied cognition hypothesis of motor cortex involvement in language in a series of MEG experiments on single action verb processing. This is important because despite mounting evidence supporting this claim, comparability between studies is hampered by differences in methods and design. A comprehensive investigation of the spatial and temporal characteristics of motor system contributions using MEG and simple language stimuli had as yet been lacking. This thesis thus provides important groundwork for future research in the field focusing on other detailed aspects of embodied language processing such as context effects and more complex language material. The three studies show that motor cortex contributions to verb processing are individually specific and somatotopic, that they recruit neuronal oscillations in the beta and alpha frequencies, and that interactions with motor execution occur behaviourally and neurophysiologically.

2 Zusammenfassung

Die vorliegende Doktorarbeit befasst sich mit den neurophysiologischen Prozessen bei der Verarbeitung von Handlungsverben unter Beteiligung des motorischen Systems. Klassische Theorien der Sprachverarbeitung, des semantischen Gedächtnisses und von Gehirnfunktionen im Allgemeinen begründen sich auf der Idee, dass anatomische Hirnregionen unabhängige funktionelle Module bilden. Für diese Modularisierung gibt es klinische Evidenz, wenn nämlich Läsionen in bestimmten Bereichen vorhersagbare funktionelle Defizite verursachen. Die Annahme einer Modulasierung wird zudem experimentell durch bildgebende Verfahren unterstützt, die beschreiben, wie die Aktivität einer Hirnregion mit Verhalten korreliert. Für die Sprachverarbeitung wurde diesbezüglich gezeigt, dass eine besondere Relevanz der visuellen Wortform-Region (*visual word form area*), dem Wernicke-Areal im superioren temporalen Kortex und dem Broca-Areal im frontalen Kortex zukommt. Im Gegensatz dazu sieht eine Reihe an Theorien, die sogenannten Embodied–Cognition– oder Grounded–Cognition–Theorien (in etwa *verkörperte/verankerte Kognition*), diese Struktur–Funktion–Zuordnung der Domänen von Wahrnehmung, Kognition und Bewegung kritisch. Sie besagen einerseits, dass kognitive Funktionen wie Konzept- und Sprachverarbeitung nicht so strikt in einem bestimmten Hirnareal lokalisiert seien wie die meisten Theorien des 20. Jahrhunderts postulieren. Andererseits seien auch bestimmmte Gehirnregionen nicht nur an einer Funktion bzw. einem Bereich von Funktionen beteiligt. Dies bedeutet, dass verteilte modale Netzwerke des sensomotorischen Systems die Basis kognitiver Funktionen bilden, vom Erwerb von Konzepten und dem Zugriff auf das semantische Gedächtnis bis zur Sprachverarbeitung. Konzepte sind nicht nur einfach mit ihren sensorischen und motorischen Eigenschaften assoziiert. Tatsächlich sind es neuronale Schaltkreise in sensorischen und motorischen Arealen, die die Bildung von konzeptuellem Wissen durch ihre Aktivierung während des Lernens in der Körper-Umwelt-Interaktion erst erlauben. Dieselben Schaltkreise sind nach dem Prinzip des Hebb'schen Lernens auch beim Abruf von Konzepten aktiv.

Während die empirische Unterstützung für die Thesen der Embodied-Cognition-Theorien zunimmt, bleiben eine Reihe offener Fragen. Unterschiedliche Methoden und experimentelle Pläne erschweren zudem den direkten Vergleich zwischen Studien. Diese Dissertation umfasst eine Reihe Experimente, die unter Verwendung des gleichen sprachlichen Stimulusmaterials und mit Hilfe magnetenzephalographischer Messungen darauf abzielen, die verschiedenen Facetten von Embodied Cognition besser zu charakterisieren. Insbesondere untersuchte diese Dissertation die Beteiligung des motorischen Systems an der Verbverarbeitung hinsichtlich dessen räumlichen Verortung, des Zeitverlaufs und der funktionellen Interaktion mit motorischem Verhalten unter Verwendung der Magnetenzephalographie (MEG).

In einer ersten Studie lasen die Probanden still Verben, die Tätigkeiten mit den Händen oder mit den Füßen beschrieben, und abstrakte Verben, die keine Tätigkeit beinhalteten. Trotz der Abwesenheit jeglicher Bewegung während dieser Aufgabe waren neuronale Quellen aktiv, die in einer gesonderten Bewegungsausführungsaufgabe motorische Prozesse abbildeten. Darüber hinaus war diese Aktivität somatotop, also sensitiv für den Effektor der Verben. Motorische Quellen der Hand wiesen ein höheres Aktivitätsmaximum für Handverben als für Fußverben auf und umgekehrt. Von zentraler Bedeutung ist hierbei, dass die Aktivität ihr Maximum ca. 200 ms nach Wortbeginn erreichte, was ein deutlicher Hinweis darauf ist, dass die Aktivierung des Motorsystems bei der Sprachverarbeitung Teil des Bedeutungszugriffs ist und kein postlexikalischer Effekt.

In Ergänzung zu diesen Ergebnissen bei evozierten Gehirnantworten untersuchte eine zweite Studie die oszillatorische Dynamik im gleichen Paradigma. Es wird angenommen, dass neuronale Oszillationen einen wichtigen Mechanismus neuronaler Kommunikation darstellen, wobei unterschiedliche Frequenzbänder eine spezifische funktionelle Rolle in bestimmten Hirnarealen spielen. Im sensomotorischen System sind Oszillationen im Alpha-Frequenzband (ca. 8-12 Hz) und Beta-Frequenzband (ca. 13-30 Hz) charakteristisch, die ein typisches Modulationsmuster vor, während und nach der Ausführung einer Bewegung zeigen. Hierbei ist eine Unterdrückung des oszillatorischen Leistungsspektrums (*power*) in Bezug zur Baseline, auch Desynchronisierung genannt, mit neuronaler Aktivierung assoziiert. Die Studie zeigte, dass stilles Lesen von Handlungsverben ausreichend war, um zu solch einer Unterdrückung des Leistungsspektrums im Alpha- und Beta-Bereich zu führen. Diese war stärker für Handverben im Vergleich zu abstrakten Verben in einer Kanalauswahl für das motorische System der Hand. Gleichzeitig war sie stärker für Fußverben im Vergleich zu abstrakten Verben in einer Kanalauswahl für das motorische System des Fußes. Diese Effekte zeigten sich ca. 200 ms nach Wortbeginn im Beta-Band und ca. 375 ms nach Wortbeginn im Alpha-Band, was die Hypothese der Beteiligung des motorischen Systems am semantischen Zugriff unterstützt.

Eine dritte Studie untersuchte direkt die Interaktion zwischen Verbverarbeitung und einer gleichzeitig stattfindenden motorischen Aufgabe. Ziel der Studie war, Rückschlüsse auf die funktionelle Spezifität der Aktivierungen des Motorkortex während der Sprachverarbeitung zu ziehen und eine direkte Verbindung zwischen Reaktionszeiteffekten im Verhalten und neurophysiologischen Maßen herzustellen. Dies wurde durch ein semantisches Entscheidungsparadigma operationalisiert, in welchem durch einen Knopfdruck mit dem rechten Zeigefinger sowohl auf Hand- als auch auf Fußverben geantwortet wurde. Nur für die Handverben wurde angenommen, dass die Übereinstimmung zwischen dem Effektor des Verbs und der Antwort zu einer Interferenz führen würde, während die Fußverben als Kontrollbedingung dienten. Bezüglich der MEG-Maße waren wiederum die neuronalen Oszillationen im Beta-Frequenzband im Zeitfenster der gleichzeitigen Verbverarbeitung und Antwortvorbereitung von besonderer Bedeutung. Sprache–Motorik–Interaktion fand sich nur für Handlungsverben mit hoher Vorstellbarkeit. Hohe Vorstellbarkeit besitzen solche Verben, die leicht ein mentales Bild der Tätigkeit hervorrufen, was darauf hinweist, dass die sensomotorische Beteiligung an der Verarbeitung dieser Verben stärker sein könnte. Hier waren die Reaktionszeiten auf Handverben langsamer, d.h. dann, wenn die Verben eine Tätigkeit mit dem gleichen Effektor wie die Antwort beschrieben (in diesem Fall mit der Hand). Dieser Verhaltenseffekt wurde von einer schwächeren Unterdrückung des Leistungsspektrums im Beta-Band während der Bewegungsvorbereitung begleitet.

Zusammengefasst untersuchte diese Dissertation die Hypothese von Embodied Cognition am Beispiel der Beteiligung des Motorkortex an der Sprachverarbeitung mit einer Reihe von MEG-Experimenten zur Verarbeitung einzelner Handlungsverben. Dieses Vorgehen ist deshalb von großer Bedeutung, da trotz zunehmender Hinweise, die diese Embodied-Cognition-Hypothese unterstützen, die Vergleichbarkeit zwischen Studien durch deren unterschiedliche Methoden und Studiendesigns erschwert wird. Eine zusammenhängende Untersuchung der räumlichen und zeitlichen Charakteristika der Beteiligung des motorischen Systems mit Hilfe von MEG und einfachen sprachlichen Stimuli lag bisher noch nicht vor. Diese Dissertation ergänzt daher wichtige Grundlageninformationen für zukünftige Forschung in diesem Feld, die sich auf andere detaillierte Aspekte der verkörperten Sprachverarbeitung fokussieren kann, wie z.B. Kontexteffekte und komplexeres Sprachmaterial. Die drei Studien zeigen, dass die Beteiligung des motorischen Systems and der Verarbeitung von Verben individuell spezifisch und somatotop ist, dass sie auf neuronale Oszillationen im Alpha- und Beta-Frequenzband zugreift, und dass Wechselwirkungen mit auszuführenden Bewegungen im Verhalten und neurophysiologisch sichtbar sind.

3 Introduction

This thesis used magnetoencephalography (MEG) to investigate action verb processing in the brain's motor system. This phenomenon is predicted by the embodied cognition hypothesis, which will be described regarding its theoretical basis and empirical evidence in the introduction, following a short overview of language processing in general. MEG and the analysis of MEG data as used in this thesis will be addressed briefly afterwards.

3.1 Language processing in the human brain

In the 19th century, the study of neurological patients showed discrete brain lesions to be associated with specific subfunctions of language by the type of aphasia they produced. Expressive aphasia often followed lesions in the left-hemispheric inferior frontal lobe (Broca, 1861, 1865). This brain region, now called Broca's area, was assumed to be especially important for language production (despite recent magnetic resonance imaging of the two original and never dissected brains showing much more extensive medial lesions, see Dronkers et al., 2007). Similarly, lesions in a superior temporal cortex region, now called Wernicke's area, were shown to produce sensory aphasia and thus taken to be crucial to language understanding (Wernicke, 1874). The popular model of language processing that was developed from these early accounts assumes separate sensory (superior temporal) and motor (inferior frontal) language core regions, linked by the arcuate fasciculus (Geschwind, 1970). Modern theories of language processing place a stronger emphasis on interconnected networks (Chang et al., 2015). An overview of the brain regions involved in auditory and visual language processing according to recent network models is shown in Fig. 1 (adapted from Bernstein and Liebenthal, 2014). These theories describe dorsal and ventral pathways, where the ventral pathways are mainly involved in different stages of semantic processing, while the dorsal pathways are recruited for syntactic processing (Dick et al., 2014; Friederici and Gierhan, 2013). The white matter fiber tracts connecting these networks could be successfully described using diffusion tensor imaging (DTI; Turken and Dronkers, 2011). Generally, deriving meaning from spoken language involves structuring the auditory input into sound units, syllables and words, and linking these with semantic memory. Reading follows the same principles, with the analysis of visual features and letters that make words, which then activate lexical-semantic representations and possibly phonology as well (Carreiras et al., 2014). Apart from early visual areas, the visual word form area in the left fusiform gyrus is thought to play a crucial role in orthographic language processing (Cohen et al., 2002). Superior temporal areas have been found to be involved in semantic processing for both visually and auditorily presented language (Vartiainen et al., 2009). In line with the interactive anatomical models of language pro-

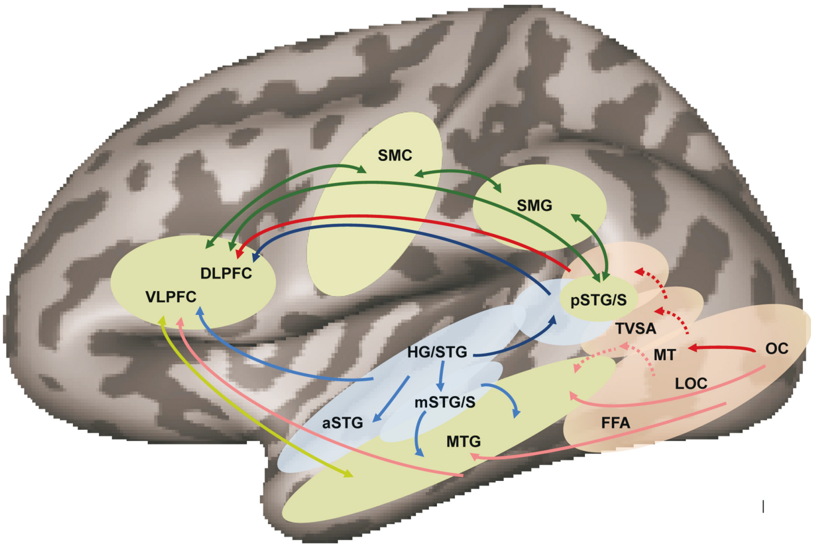

Figure 1: Adapted from Figure 1 in Bernstein and Liebenthal (2014). Brain regions involved in audiovisual speech perception. Visual areas (red shade) and auditory areas (blue shade) project to amodal middle temporal cortex (green shade) via the ventral pathways (light red and blue arrows) that terminate in ventrolateral prefrontal cortex (VLPFC). The dorsal pathways from the auditory (dark blue arrows) and visual (dark red arrows) areas terminate in dorsolateral prefrontal cortex (DLPFC). Multimodal or amodal areas are connected bi-directionally via ventral (light green arrows) and dorsal (dark green arrows) pathways. (HG/STG: Heschl's gyrus/superior temporal gyrus; aSTG: anterior superior temporal gyrus; mSTG/S: middle superior temporal gyrus and sulcus; pSTG/S. posterior superior temporal gyrus and sulcus; MTG: middle temporal gyrus; OC: occipital cortex; FFA: fusiform face area; LOC: lateral occipital complex; MT: middle temporal area; TVSA: temporal visual speech area; SMG: supramarginal gyrus; SMC: somatomotor cortex; VLPFC: ventrolateral prefrontal cortex; DLPFC: dorsolateral prefrontal cortex).

cessing, functional interactions were also found for meaning understanding, where both bottom-up and top-down processes influence semantic access (Woodhead et al., 2014).

Taken together, language processing comprises a range of very different functions, from sensory feature analysis to word identification, syntactical analysis and discourse memory, engaging a network of visual and auditory sensory areas, temporal lobe and also parietal and frontal lobe regions. This thesis is concerned with the subfunction of semantic access to meaning in visually presented single words, and the contributions of motor cortex regions to verb understanding.

3.2 Embodied Cognition

The embodied cognition framework describes semantic memory activation as a modality-specific simulation of past bodily experiences (Barsalou, 2008). This challenges the classical view of the brain's functional organisation into different specialized modules such as the language system or the motor system (Fodor, 1983). Embodied cognition accounts have been developed in the fields of linguistics, philosophy, cognitive psychology and neuroscience. In fact, modal representations as the core or at least as a part of cognition have been described by philosophers such as Aristotle to Heidegger and Wittgenstein, spanning the course of the history of philosophy (Barsalou, 2010). In contrast to this, the cognitive revolution of the 20$^{\text{th}}$ century and the rise of research in artificial intelligence (compare Turing, 1950) resulted in a different view of language and cognition which was assumed to comprise amodal and symbolic representations, and to follow computational rules (Caramazza et al., 1990; Chomsky, 2002; Fodor and Pylyshyn, 1988). For instance, the Language of Thought Hypothesis states that thinking takes place in a mental language that is a symbolic system and akin to natural language in that it uses combinatorial semantics and syntax to operate on representations (Fodor and Pylyshyn, 1988). Perception and action are regarded as largely independent from each other and from the higher processes of cognition, as illustrated by the vivid metaphor of the sandwich model, with cognition as the filling, wedged between perception and action (Hurley, 1998). Another omnipresent axiom since the rise of neuroscience and neuroimaging is the view of the modularised brain. The observation of lesions in specific brain areas producing predictable behavioural deficits and, more recently, neuroimaging studies linking brain function with anatomy, support the Modularity of Mind Hypothesis. This states that cognitive abilities are organised in independent domains or modules (Fodor, 1983) and can be located in the brain.

Embodied and grounded cognition theories challenge these views and instead postulate modal simulations or representations at the basis of cognitive processes. The different accounts can be grouped into embodied cognition theories on the one hand and grounded cognition theories on the other hand, but the distinction is subtle. The former theories put a focus on the role of the body in situated action and the interaction of bodily states with cognitive states, challenging the need for a representational system itself (e.g. Chemero, 2009; Wilson and Golonka, 2013). The latter theories acknowledge the importance of the brain–body–environment–interaction, but do not dispense of the brain as the major organ of interest for studying cognition, and rather focus on modal and simulation processes within the brain (e.g. Barsalou, 1999; Jeannerod, 2001). They stress the Hebbian learning based mechanisms to acquire concept representations through experience (Pulvermüller et al., 2001; Ursino et al., 2010). In this context, the Hebbian learning principle of increasing synaptic strength between cells that repeatedly fire at the same time (Hebb, 1949) can explain how sensory, motor and word form cell assemblies create the core of concepts in semantic memory. Some grounded cognition theories acknowledge also multimodal semantic representation as a consequence of sensorimotor grounding (Pulvermüller and Garagnani, 2014). This thesis is not drawing its hypotheses strictly from one of the embodied/grounded cognition theories, and therefore the terms will be mainly used interchangeably.

There is an ongoing debate especially in the philosophy of mind about the constitutive versus associative nature of sensorimotor simulation of conceptual processing, or even the necessity of a representational system at all (Thelen et al., 2001; Wilson and Golonka, 2013). In essence, this debate revolves around the potential for paradigm shifting consequences derived from radical embodied theories (Chemero, 2009). Criticism concerning the weak embodiment theories states that they only flesh out existing representation-based views of cognition. On the other hand, the radical embodiment theories are criticised for not being supported by empirical evidence that would show that, for instance, action semantics are necessarily and sufficiently constituted by the motor system. In fact, as the following section will describe in more detail, empirical evidence is most strongly in favour of moderate embodied cognition theories. These claim a crucial role for sensorimotor processes in the acquisition of conceptual knowledge and a facilitating and only partly necessary role in access to once acquired concepts. This idea is reflected in the most recent accounts of neuroscience-driven embodied/grounded cognition accounts. They attempt to reconcile embodied and disembodied views of semantic memory and stress the interdependency between modal and multimodal processing (Andrews et al., 2014; Pulvermüller, 2013; Zwaan, 2014).

The perhaps least radical of the grounded cognition accounts that is directly supported by the research in this thesis (while it does not contradict other theories) is the model of perceptual symbol systems (PSS, Barsalou, 1999) as a cognitive simulation theory. This theory accepts the symbolic functionality of classic theories but proposes a novel way to implement it in the brain: simulation and dynamic systems (Barsalou, 2008). Crucially, PSS proposes that re-enactment of episodes that activated perceptual and motor circuits allows the access to conceptual knowledge, see Fig. 2. Apart from PSS theory, this thesis draws its hypotheses primarily from the neuroscience-based theoretical accounts developed to explain the mechanisms behind grounding cognition in sensorimotor systems on the level of neuronal circuits, and to articulate testable hypotheses (Pulvermüller et al., 2014, 2005; Zwaan, 2014).

Embodied cognition and language theories possess explanatory power on many levels. Phylogenetically, embodied language processing may be seen as an extension of the processes leading to the development of the human mirror neuron system (MNS), and founded in the strong connection between speech and gestures (Arbib et al., 2014; Gallese and Lakoff, 2005). Mirror neurons, i.e. cells that fire both when executing and observing an action, have first been found in the monkey premotor cortex (Di Pellegrino et al., 1992). In humans, a similar function of the inferior frontal cortex as well as parietal areas is assumed. Particularly the role of Broca's area, BA 44, for both mirror neuron and language processing provides an interesting link between interpersonal communication and conceptual understanding (Gallese, 2008).

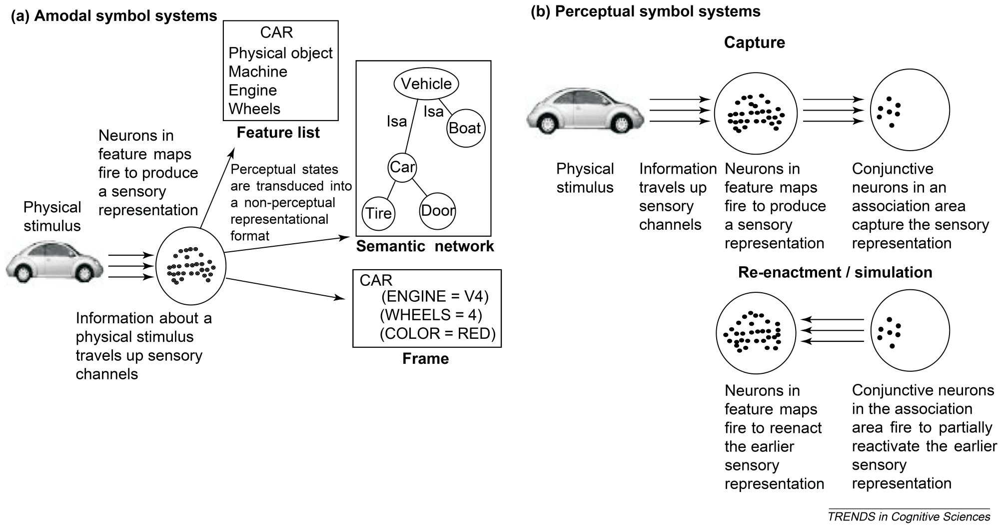

Figure 2: Adapted from Figure 2 in Barsalou et al. (2003). a: Classical models of semantic memory, where sensory input needs to be converted into an amodel representation format. b: Perceptual symbol systems model, where sensory input is not transformed, but rather re-activated during semantic memory recall.

Along these lines, the body specificity hypothesis (Casasanto, 2011) focuses on interindividual differences that arise in neuronal and conceptual representations due to different kinds of bodies by which individuals experience their environment. This interesting approach can directly show the connection between individual concept acquisition during ontogenetic development and access to semantic memory content.

For verbs and sentences describing events as well as for action observation, the relation to action and motor representations is straightforward. Similarly, noun concepts as well as objects in the environment are assumed to be represented not only regarding their perceptual appearance, but crucially also including the interactions they allow with the individual. The so-called affordances (Gibson, 1979) are automatically activated possible actions and interactions with the environment, thus directly linking perception and action. For instance, upon seeing a cup, the possible action of grasping it at the handle is automatically activated, while a chair would elicit the action of sitting down (e.g. Chemero, 2003; Turvey, 1992). While the idea of affordances is usually used to describe the situated activation of action dispositions (a tree might only activate climbing actions when positioned nearby and not far away), Hebbian learning also allows affordances to play a role in object knowledge and noun processing in the motor system.

Embodiment may also be a key factor for novel ways to characterise representations of concepts in frame formalism with the help of functional recursive attribute-value structures (Barsalou, 1992). This is a promising attempt to form a common ground for different disciplines, allowing the distribution of ideas between for instance computational neuronal modelling, cognitive neuroscience, psycholinguistics, philosophy of mind, and neurorobotics, thus fostering overall increase of knowledge.

3.3 Empirical evidence for embodied cognition

The domain of language is especially interesting to investigate, since it is by nature symbolic and arbitrary (but see also accounts of the non-arbitrariness of linguistic symbols as demonstrated by iconicity in sign language and onomatopoeia in spoken language, e.g. Perniss and Vigliocco, 2014). There is evidence for embodied cognition from multiple non-linguistic approaches such as conceptual object knowledge complimenting findings using linguistic material. Since the present thesis investigated language processing, this section will focus on empirical research concerned with embodiment and language, and briefly describe the most important findings from other domains. Similarly, evidence from developmental psychology and artificial intelligence will be sketched concisely since it is not central to the current thesis but fundamentally important for the general claims of embodied cognition.

3.3.1 Artificial intelligence and self-organising principles

An intriguing line of research comes from artificial intelligence and robotics, with more theoretical implications also picked up in the cognitive sciences and philosophy of mind (Brooks, 1991; Varela et al., 1991). Recent developments turn away from symbolism and complex rule manipulations, and teach robots how to interact with the environment, with feedback based action–perception learning replacing a priori sets of behaviour programmes. Like for living organisms, possessing and being in control of a body is seen as the only way to flexibly solve problems with the potential to do so in a self-organising fashion. Embodiment principles are used in building robots that can learn hand–eye–coordination and navigate difficult terrain – the Mars explorer but one example – and even learn social behaviour and object names (for a review see Chemero, 2009). Another implication of this is that behaviour that seems to require abstract and complex rules may be the result of much simpler processes. For instance, in the so-called didabot experiment, the only rule provided to a group of robots was to turn away whenever an obstacle was encountered (Maris and te Boekhorst, 1996). This simple rule led to behaviour where clusters of cube obstacles in an arena were formed in a seemingly organised way, with observers typically describing what the robots were doing as tidying the cubes or clearing the space. Similar accounts of simple rules guiding complex behaviour have been described for social insects, cricket mating behaviour, wolf pack hunting strategies and herding animal as well as migrating bird group formation (Barrett, 2011). These are examples for the relevance of body-environment interactions for the shaping of behaviour. Moreover, they show how these interactions can in fact account for seemingly complex behaviour without necessarily relying on higher order cognitive processes. This implies that for all kinds of organisms including humans, behaviour may be guided by subconscious sensorimotor loops to a greater amount than previously assumed (Arbib et al., 2014).

3.3.2 The embodied body

Another important line of research concerning embodied cognition focuses on the body and bodily states in reciprocal interaction with brain states (Wilson and Golonka, 2013). This is not the focus of the present thesis, but it is fundamentally relevant to embodied cognition theory if its novelty and explanatory power is taken seriously, and its potential for replacing classical accounts is acknowledged. It is driven by the idea that the living organism interacting with its environment is not separate from cognitive processes in the brain. Along these lines, a range of experiments employed a variety of manipulations of bodily states and assessed their direct influence on cognitive tasks.

Temporally immobilizing the left hand for 24 hours modulated the learning effect in a mental hand rotation paradigm. Mental rotations of numbers as well as mental rotations of right hand images improved from pre- to post-session but mental rotations of left hand images did not (Meugnot et al., 2014). This implies that short-term alterations in body characteristics have the power to influence conceptual processing, which seems to partly rely on simulations and interactions with the current bodily state. Even a simple experimental manipulation causing subjects to slightly shift their body posture to the left or to the right influenced performance in cognitive task (Eerland et al., 2011). While unknowingly leaning to the left, participants underestimated quantities, compared with leaning to the right. The authors attribute this to embodied mental representation of numbers along a line with increasing numbers from left to right. Similarly, wearing a specific kind of clothing may influence performance in an attention task (Adam and Galinsky, 2012). These examples show that online feedback from body–environment–interaction can influence cognitive states and seemingly unrelated behaviour. The underlying mechanisms work on a short time scale and can be presumed to go largely unnoticed.

3.3.3 Embodiment for knowledge acquisition

Evidence for knowledge acquisition through embodiment at work, by grounding in sensorimotor experiences, can be seen in studies from developmental psychology. For instance, infants between 6 and 12 months of age show a curious error. After learning to retrieve a toy repeatedly hidden in location A the toy is suddenly hidden in location B. In around 70-80% of the cases, the infant will continue to reach for the toy in location A despite eye movements to location B indicating a mismatch between reaching and visual exploration behaviour. Crucially, the so-called A-not-B-error is not an example of developing conceptual object knowledge. Rather than drawing on object representations, this phenomenon can be shown to purely arise from learning about sensorimotor interactions with the environment in a cause and effect manner (Thelen et al., 2001). Similarly, the type of sensorimotor interactions with new objects modulates categorisation processes in infants (Smith, 2005). For older children and adults, a parameter quantifying sensorimotor experience influenced a word naming task (Wellsby and Pexman, 2014). A classic example from non-human animal research is the failure of kittens to develop certain visual processing capacities if they only passively gained visual experiences and were not allowed to actively explore the environment (Held and Hein, 1963).

Acquisition of new knowledge in adults following embodiment principles is also compelling evidence supporting embodied cognition. Studies in this domain investigate how conceptual information about novel objects or linguistic material is shaped by sensorimotor interactions. For instance, when participants learned function knowledge about novel objects, brain responses differed from only visually explored objects (Bellebaum et al., 2013; Weisberg et al., 2007). Similarly, training to associate novel words with observed action gestures interacted with alpha power suppression at fronto-central electroencephalography (EEG) electrodes (Fargier et al., 2012). Behaviourally, interference of an effector-specific motor task during the acquisition of functional object knowledge was found (Paulus et al., 2009), with similar effects in verbal working memory (Shebani and Pulvermüller, 2013). These results show that the claims of embodied cognition concerning sensorimotor simulations in knowledge acquisition and recall can effectively be demonstrated in an experimental setting.

3.3.4 Sensorimotor contributions to embodied language processing

Any activity in sensorimotor brain areas during the access phase to semantic memory during language processing can be taken as evidence for modal and embodied processing, associative/correlational or constitutive/causative in nature. For instance, reading words associated with a specific smell or taste like cinnamon or salt activated olfactory or gustatory brain areas (Barrós-Loscertales et al., 2012; González et al., 2006), while reading sound-associated words activated auditory brain areas (Kiefer et al., 2008). An especially interesting approach to the embodied language hypotheses is to investigate action-related language processing in sensorimotor brain areas. In contrast to purely sensory modalities, the motor system is also associated with a specific output, i.e. movement, which

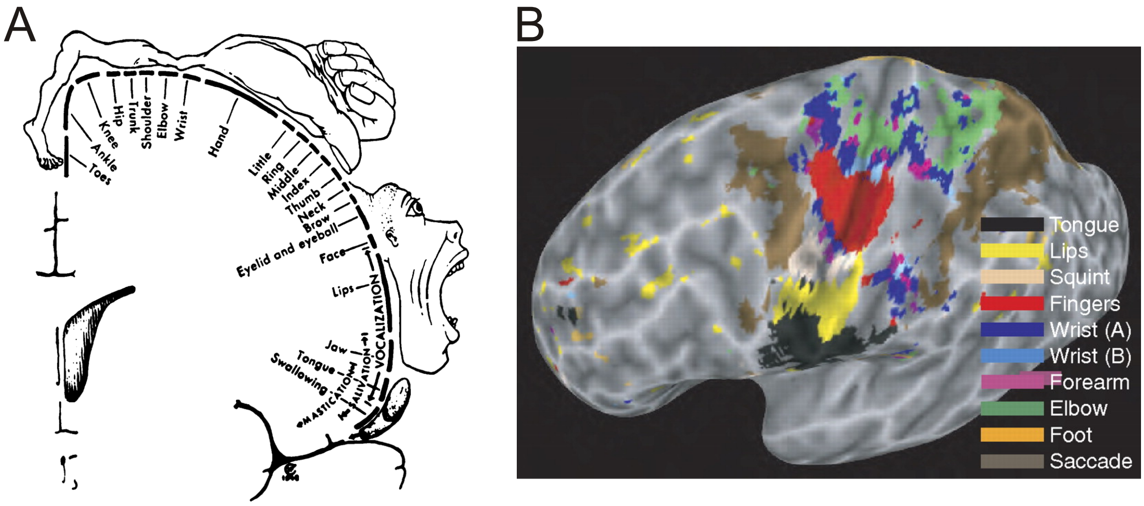

Figure 3: A: Extracted from Figure 2 in Schott (1993) after Penfield (1950). Schematic coronal slice showing the primary motor cortex and the presumed body parts represented in each portion of the motor strip. This model is based on electrophysiological stimulation during neurosurgery and often called the *motor homunculus*. B: Extracted from Figure 3 in Meier et al. (2008). Single-subject high-resolution functional magnetic resonance imaging showing sensorimotor brain areas associated with movement of different body parts. The spatial configuration on single-subject level is largely in line with the somatotopy model.

experiments can capitalise on in language-motor interaction studies (see section 3.3.6). Moreover, the human motor cortex is organised somatotopically. This means that different body parts are represented in distinguishable patches of the motor strip, as shown in Fig. 3A in a schematic model and in Fig. 3B from real single-subject recordings. The subdivision into anatomically and functionally separable regions associated with the different body parts allows inferences about the specificity of activations. This adds information about the level of detail of language processing in sensorimotor areas when activations are recorded from effector-specific areas for matching linguistic material. Fig. 4 illustrates the predictions for neurophysiological recordings during language processing depending on the type of language material. Moreover, neurodegenerative diseases specifically affecting the motor system such as Parkinson's disease (PD) or amyotrophic lateral sclerosis (ALS) lead to conclusions about the causal role of the motor system in language processing (Grossman et al., 2008; Herrera et al., 2012, see section 3.3.8).

3.3.5 Specificity and somatotopy

A number of neurophysiological studies addressed the issue of specificity and somatotopy in embodied language processing. These are aimed to describe the conditions under which sensorimotor activations are found, how precisely they are expressed, and at which level motor simulation can be inferred to take place. When using functional magnetic resonance imaging (fMRI) to directly compare the somatotopy of activation in the left motor cortex

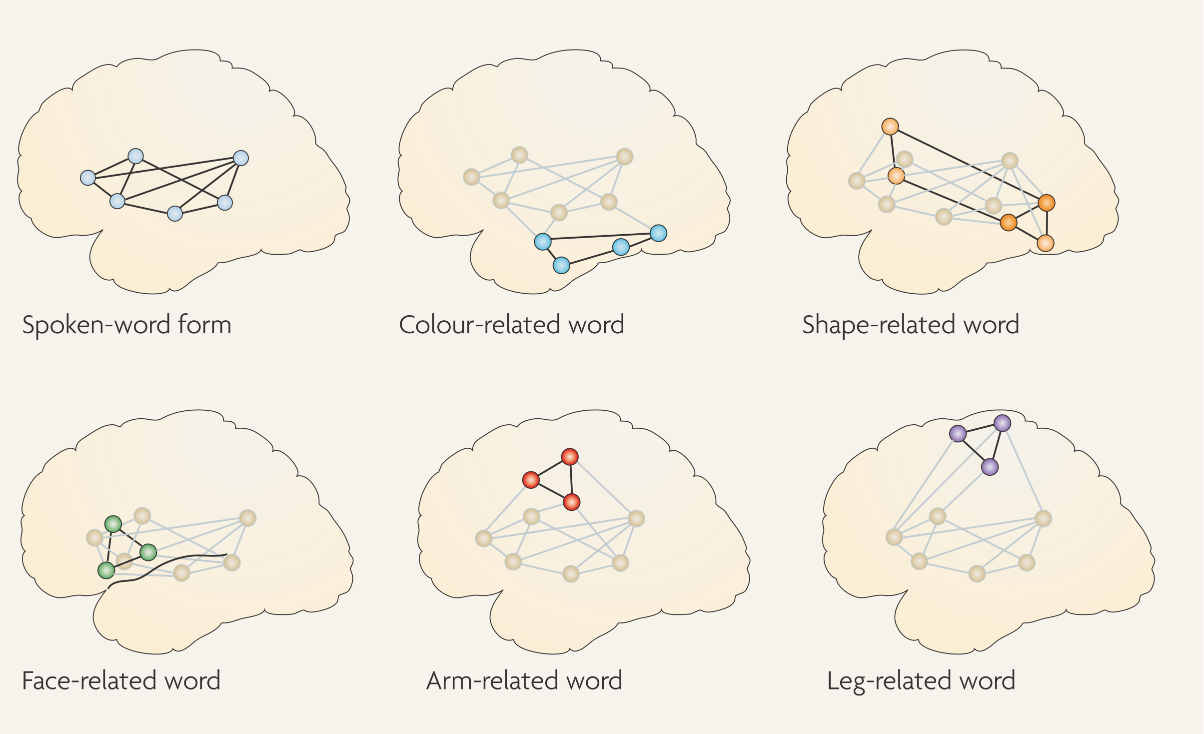

Figure 4: Adapted from Box 2 in Pulvermüller and Fadiga (2010). Model showing how core language areas are recruited together with modal areas depending on the type of language material. For action language referring to different body parts, the somatotopy of the motor cortex helps to predict different activation foci. These range from the most dorsal/medial regions for foot-related language to more lateral regions for hand-related language to most inferior regions for face-related language.

for executing hand, foot, and mouth actions with reading single hand, foot, and mouth verbs, a partial overlap was found (Hauk et al., 2004). For both action execution and verb reading, activations followed a medial-to-lateral distribution along the motor strip, with foot conditions being located most medial, hand conditions more lateral, and mouth conditions even more lateral/inferior. For all verb conditions, activation was also found in the inferior frontal gyrus. This pattern of results is in line with the model described in Fig. 4. Similarly, in the premotor cortex a correspondence of activations during observing hand, foot, and mouth actions and reading phrases describing hand, foot, and mouth actions was reported (Aziz-Zadeh et al., 2006). Somatotopical effects were also found for auditorily presented sentences containing hand, foot, and mouth actions, contrasted with abstract sentences (Tettamanti et al., 2005). In addition to these neuroimaging experiments, transcranial magnetic stimulation (TMS) studies showed that processing action verbs activated the effector-related part of the motor system (Buccino et al., 2005; Repetto et al., 2013).

However, there are concerns about the interpretation of results showing only partial overlap of action execution and verb processing areas, about adequate control conditions, about non-exclusivity of activations, and about null findings in attempts to replicate effects. In most neuroimaging studies, activity in effector-related motor areas was stronger for matching effector verbs, but not exclusive to these conditions. Action verbs related to different effectors (Hauk et al., 2004) and abstract verbs (Rüschemeyer et al., 2007) also recruited these areas. This is not a direct contradiction to embodied language processing theories, but needs further investigation. Similarly, brain regions may be sensitive to the grammatical class of verbs rather than action features. This seems to be the case for the posterior lateral temporal cortex, where effects disappeared when contrasting action verbs with abstract verbs rather than concrete nouns (Bedny and Caramazza, 2011). Despite compelling evidence in line with embodied cognition theories, there are some studies that failed to detect sensorimotor activation during language processing (Papeo et al., 2011; Postle et al., 2008). One reason for this may be the combination of language material, tasks and methods used. For instance, syntactic processing did not lead to modulations in motor-evoked potentials using TMS (Papeo et al., 2011). Generally, there is sufficient evidence from fMRI studies showing motor system involvement in action language processing to support embodied cognition theories (for a meta analysis see Jirak et al., 2010).

Other studies investigated the activation of object affordances in the sensorimotor system. For instance, priming a hand shape typically used to interact with an object influenced reaction times in semantic sensibility judgements (Klatzky et al., 1989), while the affordances of objects prime the response execution grip shape (Glover et al., 2004; Tucker and Ellis, 2004). Object nouns are also associated with a characteristic distribution of activations in the motor system (for a review see Carota et al., 2012).

The timing of motor system contributions has been studied using EEG and MEG, and often effects emerge within 150-350 ms after stimulus onset (Boulenger et al., 2012; Moreno et al., 2013; Moseley et al., 2013; Pulvermüller et al., 2001; Shtyrov et al., 2004). This is important because semantic access is assumed to take place within 400 ms of stimulus onset (Kutas and Hillyard, 1984). The spatial specificity in these studies is usually not as good as in the fMRI studies, partly depending on the method (especially for EEG), but also because somatotopy was not always directly investigated.

The body specificity hypotheses (Casasanto, 2011) was often studied by comparing left- and right handers. While the majority of left-handers still show left-hemispheric dominance for language processing – like right-handers – the hemisphere involved in unimanual actions such as writing is the right hemisphere for left-handers and the left hemisphere for right-handers. The question that arises from this is whether motor cortex contributions to language processing are localised to the left, language-dominant hemisphere, or whether they differentiate between left- and right-handers, with each group activating the hemisphere of their dominant hand, as predicted by the body specificity hypothesis. Several studies found inconsistent results. For instance, in silent reading of single uni- and bimanual verbs, only small differences between handedness groups were observed, arguing for a left hemisphere dominance also in embodied language processing (Hauk and Pulvermüller, 2011). On the other hand, a clear difference between handedness groups was also reported, with lateralisation of premotor activation to the dominant hemisphere, supporting the body specificity hypothesis (Willems et al., 2010).

Generally, there is accumulating evidence that motor system contributions to language processing are functional, that they are specific as shown by somatotopical effects, and that they occur in a relevant time window for semantic access. However, the heterogeneity of the language material and the tasks in different studies as of yet prevent conclusive evaluations of embodied language processing. Moreover, the methods most commonly used in neuroscientific research have inherent properties that allow them to focus on either spatial localisation (fMRI) or temporal extent (EEG), while necessarily not being able to make strong claims about the other domain. This is why the MEG studies described in this thesis provide valuable insight into both the somatotopy and specificity of motor cortex contributions to language processing by analysing neuronal sources and oscillations. Importantly, the use of single verbs rather than more complex language stimuli is a relevant step to establish the groundwork, describing basic word processing. Since all studies in this thesis used the same language material and complementary tasks and data analyses, comparisons between the different studies allow conclusions that comparisons between previous studies mostly do not.

3.3.6 Interactions of action execution and language processing

Behavioural and neurophysiological experiments both show that online interactions between processing action-related language in the motor system and concurrent action execution or preparation take place. On the one hand, this is relevant to the question of the functional mechanism of action simulation: If it interacts with action behaviour, then it is likely that similar neuronal mechanisms underlie both processes. On the other hand, it is informative for the presumed detail of action simulations. Experimental designs often contrast effector-specific conditions, but this may not be the level of detail that is simulated. Perhaps action language elicits a very specific simulation of action schemata down to the muscle commands that would be involved in the action, as suggested from the action observation literature (Fadiga et al., 1995; Strafella and Paus, 2000). Possibly, however, the conceptual processing is not that fine-grained but rather similar for large groups of action verbs. Furthermore, apart from the effector-relatedness, other features of the action verbs such as goal-directedness or semantic class may be activated, as indicated by fMRI studies on hand action verbs with different semantic components such as tool use, contact, or change of state (Kemmerer et al., 2008). In fact, neuroimaging results suggest that motor system activation reflects also the specificity of action verbs in a subordinate vs. superordinate comparison (van Dam et al., 2010). These issues can be addressed by investigating the circumstances and conditions under which language and motor processing interact, and in what way they interact.

A series of experiments found hand action kinematics to be altered depending on the temporal relation between hand action verb onset and behaviour onset (Boulenger et al., 2006, 2008; Nazir et al., 2008), and one study showed the sentential context to influence hand verbs' impact on continuous grip force (Aravena et al., 2012). In a verb-picture-matching task, reaction times were longer for pairs that did not match when both stimuli referred to the same effector, indicating that it is harder to reject same-effector pairs due to partly overlapping motor simulations; pure semantic similarity could not explain the effect (Bergen et al., 2010). Using the hand or the foot to respond to hand and foot action sentences resulted in slower response times with the matching effector, in a between-subjects design (Buccino et al., 2005). This interference was also found for single verbs, with longer response latencies for button press responses or arm reaching movements when subjects performed semantic but not lexical decisions (Mirabella et al., 2012; Sato et al., 2008). Neurophysiological correlates of language-motor interaction were found in EEG readiness potentials, but in a task contrasting manual and abstract verbs (Boulenger et al., 2008). The patterns of facilitating or interfering language-motor cross talk seem to depend on stimulus timing, language material, and task requirements (Diefenbach et al., 2013; Vega et al., 2013). This can be explained in detail by a model describing chained activation of the motor acts involved in action schemata. These overlap to a different extent between the action chains activated by verbs and the action chains recruited for a certain effector-specific behaviour (Chersi et al., 2010). Crucially, the mere effector-relatedness is not in itself an explaining parameter, but only operationalised as the relevant variable in experiments manipulating conditions of verbs with different effectors. What interacts with motor behaviour is the (in)compatibility between verb action and executed actions. This is corroborated by results from studies using verbs only from one effector - in this case the German verbs *öffnen* (to open) and *schließen* (to close). There was a a clear match/mismatch with the response action which was either a hand opening or hand closing motion. Again, the incompatible condition showed interference, i.e. responding by a closing motion to *öffnen* and an opening motion to *schließen* (Liepelt et al., 2012). Another kinematic study argues in favour of the activation of the complete motor program associated with an action verb. This would be the most habitual action associated with the verb, even when different readings suggest very different motor programs, as in the case of to write, an action which can be executed using a pen or using a computer keyboard (Dalla Volta et al., 2009).

This thesis also contains one study investigating language-motor interactions (Study 3). In contrast to most previous studies, both behavioural and neurophysiological measures were analysed in the same experiment, allowing conclusion about the underlying mechanisms.

3.3.7 The role of abstract concepts

Since embodied cognition postulates the sensorimotor grounding of abstract concepts through processes like metaphor (Lakoff and Johnson, 1999), they should also be partly processed in the sensorimotor system. This indicates that on the level of single words as well as for figurative or idiomatic phrases using both concrete and abstract verbs, sensorimotor activation can also be expected. At the same time, abstract concepts and words were shown to have more emotional content than concrete concepts, and their acquisition is assumed to rely also on interospective and linguistic cues (Kousta et al., 2011). Studies investigated either abstract words or sentences forming abstract meaning but containing concrete words. For instance, action verbs can be used in literal sentences as in *to kick the ball* as well as in metaphorical sentences as in *to kick the bucket*. Some fMRI and MEG studies could show motor system activations during non-literal language processing (Aziz-Zadeh and Damasio, 2008; Boulenger et al., 2009). Similarly, both concrete and abstract transfer sentences (*I give you the pizza* vs. *I give you the idea*) led to the same interference effects with the execution of movements that were incompatible with transfer direction (Glenberg and Kaschak, 2002). These results imply that in sentence understanding, decomposing meaning at the level of word constituents, the presence of a concrete word is sufficient to elicit sensorimotor activation. The understanding of the concrete verb seems integral to the meaning of more abstract phrases based on the verb. This decomposition of meaning might also be expected on the level of complex verbs with a motor stem. For instance, the German verb *greifen* (to grasp) can form derivatives like *begreifen* (to understand), while these complex abstract verbs can also have abstract bases like *erkennen* (to realize). These three groups of verbs were compared in a lexical decision fMRI experiment, where the concrete simple verbs elicited stronger activity in the primary motor and somatosensory cortices as well as premotor areas than complex verbs, regardless of their base (Rüschemeyer et al., 2007). All verb groups, however, activated the frontal mirror neuron areas, ventral premotor cortex and inferior parietal lobule similarly. This is evidence for both a grounding of abstract language in sensorimotor processes and for preferential processing of concrete language specifically in primary sensorimotor areas. In the context of a lexical decision task, complex verb decomposition does not lead to processing comparable to the base verbs, even though German complex verbs could be shown to be decomposed by default in behavioural priming tasks (Smolka et al., 2014). At the same time, if abstract language is also partly processed in the sensorimotor system this raises the need for adequate control conditions to investigate embodied language processing.

3.3.8 The causal role of embodied language

Generally, embodied cognition theories state that sensorimotor activation during language processing is not epiphenomenal or post-lexical, but constitutive of semantic access and essential for language comprehension. There is evidence both for and against this notion.

Studying patients with deficits in the sensorimotor system shows that even severe motor symptoms and motor cortex dysfunction do not completely erase any ability to understand and process action-related language. Like neurophysiological data, this shows that sensorimotor areas are not exclusively processing action language, but that a network of brain areas is involved. Spared areas in patients can maintain some level of function regarding action-related language processing. This is not predicted by the strong embodiment hypothesis, but in line with more moderate or weak embodied cognition accounts. Nevertheless, relative impairments have repeatedly been observed in patients suffering from motor system disease. More importantly, these deficits are selective for action-related language (and often also non-linguistic action processing or action-related object recognition) and not a confound of generally impaired language processing. Among the studied patient groups are cases of ALS (Bak and Hodges, 2004; Bak et al., 2001; Grossman et al., 2008) and PD (Boulenger et al., 2008; Fernandino et al., 2012; Herrera et al., 2012). Deficits could be found in a range of tasks, from picture naming to masked priming, and in one study the magnitude of deficits depended directly on the motor content in verbs (Herrera et al., 2012). A caveat in interpreting verb processing deficits after motor system disease or lesions is, as for neuroimaging studies, the adequacy of the control condition. Often, verb processing performance is compared to noun processing performance (e.g. Daniele et al., 1994) without distinguishing between categories of verbs. Moreover, heterogeneous patient groups and co-occurring neurological deficits such as aphasia exacerbate general conclusions (Bak et al., 2001).

Apart from patient studies, the causal role of motor system involvement in action-related language processing can also be deduced from the time course of activation. Lexical-semantic access has classically been described to occur several hundred milliseconds after stimulus onset and to be linked to the N400 component in EEG and MEG (Kutas and Hillyard, 1984). More recent investigations reported effects of semantic memory access already earlier, around 200 ms following stimulus onset (Rabovsky et al., 2012). This is an important benchmark because any activity following the understanding of meaning cannot necessarily be attributed to be directly related to this understanding. If, then, the motor cortex is already active at 200 ms after stimulus onset, this is an indicator of semantic access rather than post-lexical imagery and therefore supports the notion of a causal role. This is precisely what was found in a number of studies using EEG and MEG (Boulenger et al., 2012; Moseley et al., 2013; Pulvermüller et al., 2001). The time course of motor system contributions to language processing was also the focus of the studies in this thesis.

3.4 Measuring brain activity using Magnetoencephalography

Analogous to the scalp electric potentials measured by EEG, MEG measures the magnetic fields emitted by electric potential shifts during neuronal activity. The magnetic field is not susceptible to volume conduction issues related to the skull and scalp, permitting a better spatial resolution compared to EEG in source reconstruction approaches (Hämäläinen et al., 1993). In contrast, other neuroimaging measures such as fMRI and positron emission tomography (PET) do not measure neuronal activity directly but use its metabolic correlates in oxygen or glucose concentration in blood vessels located near brain matter. While this allows good spatial resolution, especially in the case of high-field MRI, the temporal resolution is worse than for electrophysiological measures. The BOLD (blood oxygenation level dependent) response, for instance, only peaks several seconds after an event, rendering event-related analysis with a certain temporal uncertainty. Thus, MEG combines the high temporal resolution in the millisecond range of a direct measure of neuronal activity with a reasonable spatial resolution that can reach 2-3 mm on the cortical surface under optimal circumstances (Hämäläinen et al., 1993; Hari and Salmelin, 2012). Concerning the neuronal origin of MEG signals, it is assumed that they mainly result from post-synaptic potentials at the apical dendrites of pyramidal cells (Hari and Salmelin, 2012). The biomagnetic fields that can be measured with a strength of about 10^{-15} Tesla are the correlate of these electric potentials occurring simultaneously in tens of thousands of active neurons. For optimal signal sensitivity in MEG, the electric current flow is tangential to the skull. Given that pyramidal cell dendrites are oriented in parallel, and perpendicular to the cortex surface, maximum signal can be recorded from neurons within the sulci (Hämäläinen et al., 1993).

The order of magnitude of surrounding (electro)magnetic noise with the earth's magnetic field at 10^{-5} Tesla or electrical devices at 10^{-7} Tesla requires that MEG measurements take place in a magnetically shielded room. Further noise sources from within the body (heartbeat and eye movements) need to be considered during data analysis. For this thesis, the MEG system of the University Clinic Düsseldorf was used, a 306 channel whole head Elekta Neuromag system. The MEG sensor type used for the analyses in the present thesis, the 204 first order planar gradiometers, uses superconducting quantum interference devices (SQUIDs) in order to measure smallest changes in magnetic flux. The superconduction is achieved by cooling the sensors to near 4 Kelvin by means of filling the insulated dewar that holds the sensor array with liquid helium.

3.5 Evoked activity and dipole sources

Multiple occurrences of a stimulus or event of interest allow the averaging of neuronal magnetic signals to identify so-called evoked activity, most often in reference to a baseline period. This works on the premise that random noise is cancelled by the averaging procedure, since it either enhances or reduces the signal amplitude randomly for each time point. Thus, specific average waveforms associated with sensory, motor, and cognitive processes have been described. Based on a sufficient amount of trials they can be found for most subjects. For instance, in the visual system, a flashing light is followed by an activation peak around 100 ms after stimulus onset in posterior sensors, termed the N100m as the magnetic equivalent of the N100 measured by EEG (Hämäläinen et al., 1993).

To localise neuronal sources in the individual brain, equivalent current dipoles (ECDs) can be fitted (for a review, see Hari and Salmelin, 2012). This procedure attempts to solve the inverse problem of mapping MEG signals to their neural origin, which by definition has no unique solution since different neural activation patterns may produce the same field distribution across the spatially arranged MEG sensors. The dipole fitting procedure requires a volume conduction model. For the purpose of this thesis a simple spherical model was used, since hypotheses concerned the motor system, and the sphere's curvature can successfully represent the shape of the pericentral cortex (Biermann-Ruben et al., 2012). The dipole fitting is a semi-automated procedure, with manual inspection of successive field patterns across time to determine the occurrence of a clear bipolar distribution as the first step. A selection of MEG sensors corresponding to this bipolar pattern then allows fitting of an ECD at the centre of gravity of this field distribution, corresponding to a location in the individual anatomical MRI. For a given point in time, an ECD is described by its spatial coordinates (x, y, z), its magnitude (typically 2-100 nAm) and its orientation, which corresponds to the intracellular current flow (Hari and Salmelin, 2012). A value for the goodness of fit determines how much of the magnetic signal is explained by the ECD. It is possible to use the spatial and orientation information to describe the amount of signal variance explained by the ECD over time. This also allows an estimate of the ECD's activation strength even in a separate experimental paradigm, which is a procedure also used in the present thesis (Study 1).

3.5.1 Single equivalent current dipoles in the sensorimotor system

For this thesis two movement-related evoked components are of interest: the motor field (MF) and the movement-evoked field (MEF). They reflect motor processes that can successfully be modelled by a single ECD (e.g. Kristeva-Feige et al., 1994). The motor field is a waveform associated with motor preparatory processes. It follows the readiness potential during the planning of voluntary movements (Cheyne and Weinberg, 1989). In source localisation its origin is found in the precentral motor cortex (Biermann-Ruben et al., 2012; Kristeva-Feige et al., 1994). The MEF, on the other hand, has a maximum shortly after a movement execution (Cheyne and Weinberg, 1989; Salmelin et al., 1995). It is localised in the postcentral sensorimotor cortex, and is thought to reflect the sensory feedback of a movement. The spatial resolution of magnetic ECDs fitted for actions performed with different muscles across the body is fine-grained enough to reflect the somatotopical organisation of the motor strip (e.g. Cheyne et al., 1991).

3.5.2 Single equivalent current dipoles and language processing

Investigations of evoked responses during semantic memory processing using single ECD modelling have been driven by the well-described effects of the N400 in EEG recordings (Kutas and Hillyard, 1984). This component plays a role in processing deviations from expected meaning and is proposed as a strong correlate of semantic memory operations. Several studies successfully localised the cortical source of the N400m, the magnetic equivalent of the EEG N400, by an ECD in the auditory temporal cortex (Helenius et al., 1998; Levelt et al., 1998). ECD modelling is also a useful tool in investigations of language processing or production disorders (Biermann-Ruben et al., 2005).

3.6 Neuronal oscillations

Fluctuating levels of synchronous activity in neuronal populations can be measured and described by oscillations. One of the first empirical accounts of neuronal oscillations originates from the studies by Hans Berger in 1929. He measured electrical potentials on the scalp surface and found an occipital waveform, for which an oscillation of about 10 Hz was stronger when the subjects had their eyes closed versus when the eyes were open (Berger, 1929). This later became known as the visual alpha band, with the robust effect of alpha power enhancement during closed eyes conditions, and alpha power suppression during attention, easily measurable using both surface EEG and MEG. Neuronal oscillations are most importantly characterised by their frequency, power (across time, squared amplitude) and phase (at a given point in time, cycle phase). Different frequency bands are associated with different neuronal origins as well as certain behaviours or processing demands. Classically, the following frequency bands are described: delta (3-5 Hz) with an important role during sleep, theta (5-8 Hz) which plays a role for e.g. memory and executive functions, alpha (8-12 Hz) which is crucially involved in attention, beta (13-30 Hz) with a presumed function in motor control, and gamma (30-100 Hz), which is assumed to arise from local processing in visual and motor systems.

To analyse neuromagnetic oscillations, preprocessed and artefact-free MEG data is decomposed into its frequency components using a Fast Fourier transform. This decomposition of the signal into its frequency components is performed repeatedly for a specific short time window which is shifted along the time axis in the so-called sliding window approach. This results in a time-frequency representation, allowing conclusions about the modulations of power across time. Temporal and spectral smoothing depends on the analysis parameters and can be used to focus on certain frequency bands or to achieve good temporal resolution. These methods were also used in the present thesis (Studies 2 and 3).

The localisation of neuronal oscillations to cortical sources can for instance be achieved by means of a beamformer approach in the frequency domain. Beamforming methods sequentially apply spatial filters to the frequency-transformed MEG data (beamforming methods for the time domain also exist but were not used in this thesis) with a searchlight analogy, maximally passing signals from a certain brain region while suppressing signals from other areas (Gross et al., 2001; Hari and Salmelin, 2012). Like the ECD method and other source analysis procedures, beamforming source analysis suffers from the inverse problem, i.e. the non-unique solution to the mapping of MEG signals to neuronal currents.

3.6.1 Neuronal oscillations in the sensorimotor system

For the sensorimotor system, neuronal oscillations in the beta frequency range seem to be most important, and this thesis focuses on investigating beta and to a minor extent also alpha oscillations. A characteristic pattern of beta and alpha power suppression before and during movement execution, followed by a power rebound exceeding baseline level, is seen for voluntary and externally triggered movements (Pfurtscheller and Lopes da Silva, 1999). A similar pattern of power suppression, also called event-related desynchronisation (ERD), and rebound was shown for action observation (Hari et al., 1998; Koelewijn et al., 2008) and motor imagery (de Lange et al., 2008; Pfurtscheller et al., 2006; Schnitzler et al., 1997). Beta oscillations are assumed to originate in the primary motor cortex and to be directly related to motor planning and execution, while alpha oscillations are thought to have a post-central, somatosensory origin, and to reflect the sensory consequences of action (Salmelin et al., 1995).This has also been shown for beta and alpha oscillations in motor imagery (Brinkman et al., 2014). The functional role of oscillations in the beta band is described as beta synchrony reflecting the status quo of the maintained motor or cognitive state (Engel and Fries, 2010). The power suppression before and during movement is the deviation from this status quo and initiation of a new motor state. Generally speaking, oscillations are assumed to be a key mechanism for dynamic and effective neuronal communication. Their phasic cycles define and structure periods of local cortical excitability, parsing synaptic input and concerting assembly output (Buzsáki, 2007). For instance, the interaction between the phase of slow theta oscillations with fast gamma oscillations and neuronal spiking is a well-described phenomenon in rodent spatial memory formation and activation (Colgin, 2015). The alpha rhythm has been the focus of models describing how their role in attention allows the brain to switch between fluctuating states of excitability, where alpha synchrony is thought to reflect active inhibition (van Dijk et al., 2010).

The physiological origin of neuronal oscillations in the beta frequency band has been linked to inhibitory interneuronal processes mediated by GABA (gamma-aminobutyric acid) in the motor system (Jensen et al., 2005). This in turn is supported by the beta frequency sensitivity to modulations in GABA levels induced by pharmacological intervention in humans and measured by MEG (Hall et al., 2010; Muthukumaraswamy et al., 2013), and also shown in vitro (Yamawaki et al., 2008). Inhibitory GABAergic networks can be described in a computational model, with inhibitory rather than excitatory postsynaptic currents associated with beta synchrony (Jensen et al., 2005). Generally, neuronal oscillations can be an emergent property of cell assemblies with excitatory and inhibitory components. The relevance of oscillatory dynamics in neuronal communication lies in their ability to structure excitability and spiking, and to do so in functional local and long-range networks (Buzsáki, 2007).

3.6.2 Neuronal oscillations and language processing

Oscillations seem to play a role in continuous natural language processing, partly due to the phasic structure of the word and syllable input itself (Giraud and Poeppel, 2012). Thus, a lot of research investigated sentence and discourse processing rather than single words (Lewis et al., 2015). Intracortical recordings of speech processing in the auditory system reveal a bottom-up role for gamma oscillations, with delta to beta frequencies more attributed to top-down processes (Fontolan et al., 2014). Beta oscillations in inferior frontal-temporal networks have also been associated with the N400m response (Wang et al., 2012). Modulations in oscillations with about 20 Hz in frontal and premotor areas can also be linked to language production or language understanding combined with response preparation in word reading tasks (Salmelin et al., 2000).

For sentences describing hand actions, stronger alpha and/or beta rhythm desynchronisation was found than for abstract sentences at frontocentral EEG electrode sites (Alemanno et al., 2012; Moreno et al., 2013; van Elk et al., 2010), with similar results for bilingual speakers using action and abstract single words (Vukovic and Shtyrov, 2014). This is the most central background for the studies focusing on neuronal oscillations in this thesis, indicating that processing hand action sentences activates frontocentral brain regions more strongly than abstract sentences. However, it does not provide clear somatotopic results since only one type of action language was contrasted with abstract language. It is conceivable that neuronal oscillations are involved in action language processing in a specific, somatotopic fashion. In conceptual processing, they may be directly dependent on individual experiences. This is supported by evidence from action observation (Orgs et al., 2008).

Generally, the role of neuronal oscillations in language processing is not fully understood. Beta and alpha oscillations may play a special role in action semantics, as also investigated in this thesis. In addition to language-specific processes, more general binding functions, memory-related processes, maintenance and prediction are also important during language tasks and associated particularly with theta, alpha and beta oscillations (Bastiaansen and Hagoort, 2006; Weiss and Mueller, 2012).

4 Aims and Hypotheses

The aim of this thesis was to investigate the processing of action-related single verbs in the brain's motor system using complementary neurophysiological techniques. Motor cortex involvement in language processing is an indicator of integrative and modal neuronal processing as described in the embodied cognition framework. The core questions of embodied action language processing could not satisfactorily be answered thus far:

- Which parts of the sensorimotor system contribute to action language processing?
- Is this activation early enough to reflect the access to semantic memory?
- Is this activation only context-driven or automatic?
- How do action language processing and motor behaviour interact?

Study 1

Study 1 investigated the activation of limb-specific neuronal dipole sources related to movement preparation and execution in response to verb processing. To this end, healthy subjects silently read single verbs describing actions with the hand, with the feet, and verbs not related to action (abstract or non-body verbs). Real executed movements of the right and left hands and feet served to determine motor-related dipole sources. They were modelled right before movement onset and have been described to be of primary motor origin (motor field, MF) and shortly after movement onset with probably more sensory components (movement-evoked field, MEF). These sources were transferred into the verb reading paradigm in order to test how much variance of neural activation they explained in each of the verbal conditions. Activations were expected to be most pronounced in the matching source-condition pairs (hand-hand and foot-foot), in a time window sensitive to lexical-semantic processing.

Study 2

Study 2 used the same experimental data as Study 1 to investigate neuronal oscillatory activity in the beta and alpha range. Spatially, the analysis was restricted by a selection of MEG channels based on cortico-muscular coherence during executed movements. This spatial selection was less sensitive than the dipole source approach in Study 1, while the focus on the motor-related alpha and beta oscillations was neurophysiologically more specific than the evoked signals in Study 1. These putative functional correlates of motor activity during language processing were expected to be associated with stronger alpha and beta suppression in the matching channel-condition combinations.

Study 3

Study 3 addressed the behavioural and neurophysiological interactions between overt motor execution and action language processing in a dual task setting. Here, participants responded by an index finger button press to concrete verbs (i.e., hand and foot verbs) but gave no response to abstract verbs. The simultaneous semantic processing of hand verbs was expected to interfere with motor preparatory processes for the hand reaction. This would lead to prolonged reaction times and altered beta oscillations before and during the response, originating in the cortical hand area. Such a language-motor interference can be taken to indicate the functional relevance of the motor cortex activation observed during language processing. If it interferes with motor behaviour and neurophysiology through shared processing resources or neuronal inhibition, this alleviates concerns about possible epiphenomenal or wrongly localised motor system activations.

Taken together, this thesis aimed to extend the knowledge about motor cortical activations during action language processing. The different experimental approaches capitalised on the strength of MEG in the spatial source modelling and the functional oscillatory analysis.

5 Stimulus material collected for all studies

Action verbs in the context of this thesis are verbs that describe some kind of bodily action. Strictly speaking, activity verbs in linguistic definitions of verb classes according to lexical aspect or *Aktionsart* are only a subgroup of this, i.e. verbs that describe durative atelic activities such as *to run*. Telicity refers to whether an action has an inherent end point as for *to eat*, where the end point is reached when the foodstuff is fully consumed. Other verb classes have different properties regarding telicity and duration (Comrie, 1976). For both the English and the German language, much finer-grained verb classifications are also widely accepted in linguistics. Here, semantic and syntactic information about meaning components and argument structure group verbs into for instance the put group, the carry group, verbs of contact by impact, or verbs of exchange (Levin, 1993). While these accounts were initially also considered for stimulus selection in the studies comprising this thesis, the more relevant information was directly derived from a series of rating studies. The rationale here is that majority ratings allow a direct focus on the operationalisations to be manipulated experimentally rather than rely on linguistic classifications.

Finding appropriate language material to be used as stimuli in psycholinguistic or neuroscientific research is a non-trivial matter. The experiments in this thesis all used visual presentation of single words. Surface characteristics like the number of syllables or letters as well as the visual angle occupied by each word during the experiment play an important role. Moreover, a wide range of semantic variables can influence the ease and speed of word processing. These need to be identified and matched between stimulus conditions. For instance, high word frequency and familiarity are general factors facilitating the access to word meaning (Connine et al., 1990), and are important variables to be regarded in all language processing studies. More subtle semantic properties of words such as imageability can also play a role in the kind of experiments used in this thesis. To define valid and coherent sets of stimulus conditions, the state of the art procedure is to either use databases to extract values for each candidate word on certain variables, or to perform rating studies with average ratings of human participants providing the values on the tested variables.

Like many studies in the field of embodied cognition, this thesis compared categories of verbs describing actions performed with different body parts. These categories were a priori chosen to be hand action verbs, foot action verbs, and abstract (or non-body) verbs. Before conducting Study 1, a careful multi-step procedure was used to find the appropriate stimulus material to be used in the three studies described in this thesis. 339 candidate words for the three conditions of hand, foot, and abstract verbs entered a first computerised rating study with 30 participants aimed to determine the body part involved in the action described by each word. Verbs with at least 80% congruent ratings in the categories hand/arm, feet/legs/whole body, and no body were subjected to a second rating study in which word familiarity and imageability were rated by another 30 participants. These values along with database word frequency and number of letters were used to match the stimulus sets, resulting in 48 verbs per condition. An overview of all stimuli is shown in Table 1, while further stimulus characteristics such as imageability and familiarity are listed in the respective tables in Studies 1, 2, and 3 in the Appendix.

Table 1: Stimulus material collected for the three studies.

hand verbs		foot verbs		abstract verbs	
German	English	German	English	German	English
angeln	to fish	eilen	to hurry	achten	to respect
basteln	to tinker	fliehen	to flee	ähneln	to resemble
binden	to tie	flitzen	to dash	ahnen	to suspect
boxen	to box	flüchten	to escape	bangen	to fear
buddeln	to dig	folgen	to follow	bessern	to improve
falten	to fold	gehen	to walk	büffeln	to swot
fassen	to grab	grätschen	to straddle	bürgen	to vouch
feilen	to file	hasten	to rush	büßen	to atone
flechten	to plait	hinken	to limp	denken	to think
fuchteln	to wave	hocken	to squat	dulden	to tolerate
greifen	to grasp	hoppeln	to lollop	ehren	to honor
häkeln	to crochet	hopsen	to skip	eignen	to suit
kehren	to sweep	humpeln	to hobble	folgern	to conclude
klatschen	to clap	hüpfen	to hop	fügen	to comply
kneifen	to pinch	joggen	to jog	glauben	to believe
kneten	to knead	kicken	to kick	gönnen	to grant
knoten	to knot	knien	to kneel	grämen	to grieve
melken	to milk	latschen	to traipse	grübeln	to brood
nähen	to sew	laufen	to run	hadern	to quarrel with
paddeln	to paddle	radeln	to cycle	hassen	to hate
pellen	to peel	rasen	to rush	herrschen	to govern
pflücken	to pick	rennen	to run	hoffen	to hope
rubbeln	to scour	scharren	to scrabble	irren	to err
rütteln	to shake	schleichen	to creep	meinen	to mean
schälen	to peel	schlendern	to saunter	meistern	to master
scheuern	to rub	schlittern	to slither	merken	to notice
schlagen	to beat	schlurfen	to scuffle	mogeln	to cheat
schleifen	to whet	schreiten	to stride	mögen	to like
schleudern	to hurl	skaten	to skate	plagen	to afflict
schneidern	to tailor	springen	to jump	planen	to plan
schnipsen	to flick	sprinten	to sprint	raten	to guess
schnitzen	to carve	spurten	to spurt	schätzen	to estimate
schnüren	to lace	stampfen	to stomp	schulden	to owe
schreiben	to write	stapfen	to trudge	schummeln	to cheat

Table 1: Stimulus material collected for the three studies.

hand verbs		foot verbs		abstract verbs	
German	English	German	English	German	English
schrubben	to scrub	stehen	to stand	sehnen	to yearn
spitzen	to sharpen	steigen	to climb	sinnen	to ponder
stapeln	to pile	steppen	to tap-dance	streben	to aspire
stochern	to stoke	stolpern	to stumble	täuschen	to fool
stopfen	to stuff	strampeln	to struggle	trauen	to trust
stricken	to knit	stürmen	to storm	träumen	to dream
stupsen	to nudge	tänzeln	to prance	trotzen	to defy
tippen	to tap	torkeln	to stagger	wagen	to dare
trommeln	to drum	trampeln	to trample	werten	to assess
wedeln	to waggle	treten	to kick	wissen	to know
wickeln	to wrap	trotten	to trot	wundern	to marvel
winken	to wave	wandern	to hike	wünschen	to wish
zerren	to drag	watscheln	to waddle	zaudern	to tarry
zupfen	to pluck	wippen	to seesaw	zweifeln	to doubt

6 Study 1

Study 1 (Appendix 1) investigated the contribution of individual somatotopical sensorimotor dipole sources to action verb processing. Previous studies using fMRI showed a somatotopical partial overlap between cortical activations in the premotor and primary motor regions (Aziz-Zadeh et al., 2006; Hauk et al., 2004). This provides good evidence for a spatially specific correlate of action-language processing in the motor system, but cannot determine the exact latency of effects due to the slow BOLD response, and results might therefore be post-lexical and reflect imagery. Studies using methods with a better temporal resolution such as MEG and EEG claim that sensorimotor activations already occur around 150-300 ms after word onset, which strongly argues in favour of these effects as reflecting lexical-semantic access (Boulenger et al., 2012; Pulvermüller et al., 2001; Shtyrov et al., 2004). However, these studies may have to be interpreted with caution because they can suffer from sub-optimal spatial resolution (Pulvermüller et al., 2001), very small stimulus sets (Shtyrov et al., 2004), or problematic control conditions (Boulenger et al., 2009). The mapping of electrophysiological or neurometabolic activation to the brain anatomy is usually based on averaging information about the activation time course and warping individual brains onto a template such as the Montreal Neurological Institute (MNI) standard brain. Thus, information may be distorted to some extent regarding the precise location and, more importantly, regarding the individual functionality of these regions. Study 1 used an approach where first, sensorimotor dipole sources were fitted to the individual brain of each participant performing hand and foot movement tasks. This information was then used to explain activation during verb reading.

Recent studies also highlight the importance of linguistic context (Aravena et al., 2012; Schuil et al., 2013; Tomasino et al., 2010) for embodied language processing effects, while the task may also play a role (Sato et al., 2008). This is an interesting line of research, but there is still a lack of insight into the precise mechanisms of embodied language processing in isolation, aimed to identify the processes elicited automatically by word reading. Study 1 investigated the very basic single word processing setting by using silent reading trials interleaved with a low-level lexical decision task.

6.1 Methods

Fifteen healthy subjects performed a silent verb reading paradigm with 20% distractor lexical decision trials. Responses in the lexical decision task were not given by the usual finger button press but by saccadic horizontal eye movements with pseudorandomised target directions. This procedure was chosen to prevent any expectancy or task set effects resulting in low-level motor preparatory processes that might spill over to the 80% trials of interest, mainly affecting one of the effectors of interest (right hand). Lexical decision trials were not further analysed.

The verbs were comprised of three categories: hand action, foot action, and non-body verbs. After completion of the verbal task, each subject performed 5 minutes of alternating left and right brisk hand flexions/extensions and 5 minutes of alternating left and right foot flexions/extensions. For the averaged movements as defined by electromyographic (EMG) recordings from each extremity, dipole sources describing the MF and MEF of each limb were fitted for each subject. The interactive procedure of the dipole fitting was performed for a selection of sensorimotor MEG planar gradiometer channels and restricted to time windows around movement onset. Peak latencies approximately reflecting the MF and MEF were chosen manually, and an automated dipole fitting procedure taking into account 20 ms before and after this manually defined peak latency was used, separately for right and left hands and feet, as well as separately for MF and MEF. For each condition and component, the equivalent current dipole (ECD) with the best goodness of fit was chosen. The resulting dipole sources were then localised in the individual anatomical MRI images. The spatial information and field orientation information from the individual dipoles was transferred into the verb reading paradigm to test whether MF and MEF sources would also be recruited in the language task. Grand-averaged peak amplitudes of the dipole source strength for each condition were compared statistically using repeated-measures ANOVA and planned comparisons between hand and foot verb conditions.

6.2 Results

The lexical decision task was performed successfully (Mean = 89.4%, SD ± 6.2%), showing that subjects were attentive. The movement execution task resulted in eight ECDs to be fitted for each participant: left and right hands and feet, MF and MEF for each extremity. This procedure was overall successful for 10-15 subjects, depending on the effector and component. On average, ECD locations were in line with the expected patterns. MF sources were located more anterior than MEF sources, the former mostly in precentral regions and the latter in postcentral regions. Moreover, hand ECDs were located more laterally than foot sources. For the grand-averaged time course of activation in MF sources, the typical pattern of a slowly rising activation strength with a maximum shortly before movement onset was observed. Similarly, grand-averaged MEF sources showed the expected peak shortly after movement onset.

When transferring the ECD information into the verb paradigm, no effects were found for the somatosensory MEF. For the MF, however, activation during verb reading was observed, and hypotheses were confirmed: While all verbal conditions showed an activation peak around 200 ms after verb onset, peak amplitudes for hand MF dipoles were significantly larger in the hand verb condition than in the foot verb condition. For foot MF dipoles the effect was marginally significant, numerically larger in the foot MF condition than in the hand verb condition. Activation peaks were also found for the abstract verbs, but with no modulation between different sources. Peak latencies did not differ between conditions, but peaks in right hand sources located in the left hemisphere were significantly earlier than in left hand sources.

6.3 Discussion

The main hypothesis was confirmed: Activation strength of motor dipoles was maximal during the processing of action verbs describing actions with the identical body part as compared with the non-matching body part. Regarding the motor dipole sources on which the analyses were based, MEFs with their larger peak were easier to identify, and only the left foot MEF could not be found for one subject. MF fitting was successful for 10-13 subjects in the different conditions, reflecting the fact that MF sources are often harder to identify since their peak is not as pronounced as for the MEF (Endo et al., 2004; Kristeva-Feige et al., 1994), and they also often have a worse goodness of fit (Biermann-Ruben et al., 2012). Moreover, some of the foot sources were not strictly lateralised, possibly due to the anatomy of the foot region reaching into the lateral fissure as shown before (Endo et al., 2004).

The latency of MF activation during verb reading confirms earlier EEG and MEG studies reporting somatotopical differences to emerge between 150 and 300 ms after word onset (Pulvermüller et al., 2001; Shtyrov et al., 2004). This is especially noteworthy since this time window precedes later motor imagery based processes and precedes the lexical-semantic integration around 400 ms post word onset (Kutas and Hillyard, 1984). Therefore, the results found in Study 1 presumably reflect early semantic access (compare Pulvermüller et al., 2001).

The latency effect of earlier right hand MF source peaks than left hand source peaks implies a differential involvement of the two hemispheres in embodied language processing. While it is not the case that the left hemisphere is exclusively recruited, as indicated by previous studies (Hauk and Pulvermüller, 2011), the left hemisphere may play a more immediate role for language processing. Since the set of hand verbs used in Study 1 comprised both uni- and bimanual action verbs, it remains unclear whether the earlier peaks in the left hemisphere are the result of the body-specificity of the simulated actions (Willems et al., 2010) or of a special role of the left hemisphere (Gallese, 2008).

Interestingly, non-body verbs also elicited pronounced activity. However, this activity was not spatially selective like the action verb activity. One possible explanation is that abstract verbs recruit neuronal sources in a more medial location such as the anterior cingulate cortex, and that these are oriented in a way that they are also picked up by the motor dipoles. Alternatively or additionally, the sensorimotor activation for abstract verbs may originate from emotional components in non-body verbs (Kousta et al., 2011), or from a pattern search strategy in the current experimental setting. Previous results also show a pattern similar to Study 1, with abstract verbs eliciting activity comparable in strength to action verbs of the matching effector (Moseley et al., 2012). Notably, the activation for non-matching action verbs also showed a peak with the same latency but smaller amplitude, in line with previous studies (Aziz-Zadeh et al., 2006; Hauk et al., 2004; Moseley et al., 2012), and seems to be a general finding in embodied language research. This implies that motor system activations are not a binary operation and exclusive to some instances of conceptual processing, but respond in a graded fashion in several neuronal assemblies at the same time. Related to this, it is not entirely clear what relation the motor dipole sources derived from very simple hand and foot movements bear to the neuronal circuits involved in the more complex actions described by the verbs. From the fact that the motor ECDs explain activation in the word processing task it cannot be directly concluded that the same neuronal assemblies are active in both tasks. Nevertheless, recruitment of cortical patches involved in the different more complex motor acts underlying the action verb meaning would also, in most cases, encompass the correlates of the simple movements used here. This may be precisely the mechanism by which the motor system can informatively contribute to language processing. Thus, the results of Study 1 argue in favour of the embodied cognition accounts postulating that semantic memory access is (partly) constituting sensorimotor simulation (Barsalou, 2008).

6.4 Conclusion

Going beyond what could be shown in earlier fMRI and EEG experiments, Study 1 showed individual functionally relevant motor sources to become active during action verb processing. This was the case without context or semantic processing, and with a strict procedure to exclude any underlying movement of the hands or feet. The simple reading of action verbs was sufficient to elicit motor system activation, implying that it is a universal processing principle. The somatotopy of effects indicates a functionally specific recruitment of the motor system in language processing. Moreover, the early latency of effects suggests that this recruitment is part of the access to semantic memory during word understanding.

7 Study 2

Study 2 (Appendix 2) addressed the neuronal oscillations in effector-specific areas of the motor cortex during simple silent reading of action verbs. This is a complementary approach to the insights gained from Study 1, and the same data was used for this different type of analysis. While Study 1 had its focus on the precise and individually defined location of sources of hand and foot movement tasks in the brain that were tested for their involvement in the silent verb reading task, Study 2 capitalised on the well-described functional role of neuronal oscillations in the alpha and beta rhythm. These frequency bands are associated with patterns of power suppression (or desynchronisation) during motor preparation, execution, imagery and observation (e.g. Koelewijn et al., 2008; Pfurtscheller and Lopes da Silva, 1999; Schnitzler et al., 1997). Some studies have also addressed their role in sentence or word processing within the framework of embodied cognition (Alemanno et al., 2012; Moreno et al., 2013; van Elk et al., 2010; Vukovic and Shtyrov, 2014) but focused on different aspects than the somatotopic contrast. For Study 2, it was important to use data from the same paradigm as Study 1, strictly controlled for movement and without linguistic context or overt semantic tasks. While the results from Study 1 show modulation of peak latencies around 200 ms after verb onset, with possible later effects non-detectable in an analysis of evoked responses, Study 2 was aimed to detect these ongoing yet transient effects in the time-frequency domain.

A novel aspect with respect to previous studies was the use of a localiser task to find sensors of interest to be used in the analysis of the verb processing task. To this end, corticomuscular coherence (CMC) between MEG sensors and signals from muscle activity in each limb was calculated. As a further control, the stimulus sets were also split for high and low imageability, and this contrast inspected in the MEG analysis. Together with the latency of power modulations this is informative about a lexical-semantic or post-semantic, imagery-based nature of effects.

7.1 Methods

The identical data recordings from the same 15 participants as for Study 1 were used. Thus, the verb reading task was the same silent reading paradigm with interleaved lexical decision trials calling for saccades as responses. In addition to the verb paradigm, another control task was employed to localise hand and foot motor cortex. Here, continuous isometric contractions at 50% of maximal force of bilateral arms followed by bilateral feet was used to compute CMC at 15-25 Hz. Like for Study 1, raw data from the 204 planar gradiometers of the MEG were used, but processed completely independently for the time-frequency analysis of Study 2, including the preprocessing, artefact rejection and all subsequent analysis steps. The MEG sensor selection derived from the CMC pattern for hands and feet was then used to directly compare hand vs. abstract and foot vs. abstract verbs, respectively. The measure of interest was the oscillatory response to verb reading in the beta and alpha frequency band. For statistical assessment, the relevant contrasts were restricted to the CMC sensor selection in each hemisphere, and tests performed separately for the beta and the alpha frequency band. A permutation-based non-parametric clustering approach was used, effectively correcting for multiple comparisons (Maris and Oostenveld, 2007). From the first-level contrasts t-values were derived subjectwise, and for the second-level group analyses were permuted 1000 times against a dummy distribution of zeros. This resulted in time-frequency clusters that were taken to be significant at $p = 0.05$ when the observed test statistic exceeded the threshold defined by the randomisation distribution. Separate analyses for the imageability contrast were performed in the same way.

7.2 Results

Behavioural results were the same as for Study 1, with mean performance rates of 89.4 ± 6.2% confirming the subjects' attention. The right and left hand localiser task resulted in a selection of eight frontolateral sensor pairs for the hand motor area in the respective contralateral hemisphere. The right and left foot localiser task showed effects in centro-medial sensors, with six sensor pairs for each task. Since due to their medial localisation four out of the six sensor pairs were part of both clusters, all eight sensor pairs were pooled for the subsequent analysis of the verb reading task.

For the left-hemispheric hand motor area, beta power suppression between 20-24 Hz was stronger for hand verbs than for abstract verbs in a time window around 200 ms after word onset. No differences could be found in the right hemisphere. For the foot vs. abstract contrast, differences were observed in three right centrolateral channel pairs between 15-20 Hz also at around 200 ms. In the alpha band, the hand vs. abstract contrast yielded a significant effect between 10-12 Hz with a latency of 375 ms after verb onset, again in the left hemisphere sensors. No effects were found when contrasting hand with abstract verbs in the foot area and vice versa, further corroborating the somatotopy of effects. Moreover, no effects of imageability were observed.

7.3 Discussion

Study 2 aimed to describe the neuro-oscillatory correlates of single action verb reading and its somatotopy. The results show that silently reading hand and foot verbs without a semantic task is sufficient to elicit specific neuronal responses. These activations were expressed as a differentially increased beta and alpha power suppression compared with abstract verbs. This indicates that motor cortex activation, reflected in a power suppression and desynchronisation, is more pronounced for action verbs than for abstract verbs. Moreover, effects were found in effector-specific MEG channel selections, suggesting not only language processing in the motor system in general, but somatotopical and specific effects in these motor-related frequency bands. Importantly, the latency of significant effects of about 200 ms for the beta band and 375 ms for the alpha band suggests that motor cortex recruitment is a part of the lexical-semantic access stage and not associated with later imagery processes. This is corroborated by the lack of effects for imageability. Complimentary to Study 1, where effects where found for a peak around 200 ms in the evoked responses, the analysis of neuronal oscillations also permits insight into the duration of effects. Here, the beta band effects lasted around 50 ms and the alpha effect about 200 ms. This further strengthens the notion that motor system activation is one of the steps in the access to word meaning and not part of longer-lasting post-lexical processing.

Effects for the hand verb contrast were left-lateralised. This could be a correlate of the general language dominance of the left hemisphere. Moreover, all subjects were right-handed and the stimulus set consisted of both uni- and bimanual action verbs. Previous results are inconsistent regarding the lateralisation of embodied language processing (Hauk and Pulvermüller, 2011; Kemmerer and Gonzalez-Castillo, 2010).

Like for Study 1 with ECDs, the functional localisation of the foot motor area by CMC proved more difficult than for the hand motor area. One important reason for this may be the cortical architecture. MEG is most sensitive to tangential current flow in neuronal patches, which is strongest in the parallel apical dendrites along the walls of cortical sulci. Moreover, the gradiometers used to analyse MEG data can detect activity better the closer it is to the cortical surface. The foot motor cortex, however, encompasses the very superior portion of the primary motor cortex but also curves into the medial surfaces within the longitudinal fissure, where cell orientation is less optimal for MEG and also further away from the sensors, compared to the hand area. Therefore, the less robust results for the foot verb contrast than for the hand verb contrast are likely due to anatomical and measurement parameter reasons.

The abstract verbs also showed beta power suppression (relative to baseline), albeit much weaker than the action verb conditions. Weak motor cortex activations in response to abstract language have frequently been described in the embodied language processing literature (Boulenger et al., 2009; Rüschemeyer et al., 2007), and may in fact play an important role in explaining how abstract concepts can develop if sensorimotor grounding is a universal principle (Barsalou, 2008; Lakoff and Johnson, 1999).

Interestingly, the precise frequency of significant beta band effects was different for hand and foot verbs, with higher frequencies (20-24 Hz) for hand than for foot verbs (16-20 Hz). This could be explained by properties of primary motor cortex organisation with different intrinsic frequency bands in different portions (Pfurtscheller et al., 1997). Effects of embodied language processing in the alpha frequency band were only found in the hand verb contrast. It is unclear whether this alpha effect reflects more somatosensory simulation in line with its predominant spatial origin (Hari et al., 1997). Other studies on embodied language processing found effects of alpha and claimed that they were part of the sensorimotor simulation in word understanding (Alemanno et al., 2012; Moreno et al., 2013). The results of Study 2 and others (van Elk et al., 2010; Vukovic and Shtyrov, 2014) indicate that the beta frequency band may be the more important or more direct correlate of embodied language processing.

7.4 Conclusion

Study 2 showed that across participants, a differential modulation of beta and alpha oscillations in somatotopical motor cortices was observed depending on the linguistic material silently processed. A suppression of beta and alpha power, known from motor execution and imagery behaviour, was also seen for hand verbs in the hand motor area and for foot verbs in the motor area, significantly stronger than for abstract verbs. These results did not depend on deep semantic conscious processing of the verbs and moreover, effects started around 200 ms in the beta band. This is strongly arguing in favour of a role for early and automatic motor cortex activation during language processing. Power suppression in the beta and alpha band is thought to index neuronal activation in the motor system, and in this sense, Study 2 provides corroborating evidence for the results from Study 1. However, its interpretation can go a step further from pure activation in a certain area. A precise matching of neuronal activity during separate tasks could only be achieved using single cell recordings, like shown for mirror neurons in monkey area F5 (Di Pellegrino et al., 1992). However, since beta and alpha oscillations are well-described functional correlates of motor processes, it can be assumed that the motor cortex activation during language processing is not only originating in the same area as motor processing, but that it draws on the same functional loops and mechanisms.

8 Study 3

Study 3 (Appendix 3) investigated the interaction of action-related language processing with overt motor behaviour. The rationale behind this is that simultaneous recruitment of the same effector-specific motor cortical areas by verb processing and action execution should lead to modulations of behaviour and neurophysiological measures. Therefore, this effector-matching condition is compared to a control condition in which verb and action processing also occur simultaneously, but do not share features such as the effector. Study 3 again used the hand, foot, and abstract verbs, and the task required button presses using the right index finger in response to hand and foot verbs. Thus, the matching-effector condition was the hand verb condition. The expected effect of the overlapping verb and action processing is inhibitory (compare Mirabella et al., 2012; Sato et al., 2008), leading to interference expressed in longer reaction times and modulations in motor-related cortical beta oscillations.

Language-motor interactions can be expressed by word or sentence processing modulating motor behaviour kinematics or reaction times (Bergen et al., 2010; Buccino et al., 2005; Dalla Volta et al., 2009; Glenberg and Kaschak, 2002; Nazir et al., 2008), or by actions influencing linguistic processing (Liepelt et al., 2012; Shebani and Pulvermüller, 2013). Depending on the combination of language stimuli and task and stimulus timing, both facilitating and interfering effects have been described. Study 3 is based on a behavioural study using a smaller set of Italian hand, foot, and abstract verbs (Sato et al., 2008). Here, subjects performed a semantic decision by pressing a button after a short delay between word onset and response cue. This resulted in prolonged reaction times for hand as compared with foot verbs, a pattern that was also expected to emerge in Study 3 with the same paradigm and the larger set of German verbs. Again, imageability was also included in the analysis mainly as a control variable. Study 2 revealed the beta frequency band to be most interesting in embodied language research, and beta power suppression is observed to be evident during motor preparation. Thus, the beta band is where effects were expected on the neurophysiological level for Study 3. Importantly, the results from Study 2 are not directly transferable to Study 3 because the task is fundamentally different. More specifically, the pattern of beta power suppression at 200-250 ms after word onset for the action verbs was not expected to be the same in the presence of the motor behaviour task and its accompanying strong beta power modulation. Due to the speeded reaction time task with a certain variance in the latency between word onset and response, both a stimulus-locked (word onset) and a response-locked (button press) analysis were performed to be able to focus on effects with different temporal relations to word processing and response preparation, respectively.

8.1 Methods

Stimuli in Study 3 also consisted of hand, foot, and abstract verbs, and the verb category sets were additionally split at the median of imageability ratings, thus creating six conditions. Nineteen healthy subjects were measured with MEG while performing a semantic judgement task on single verbs. Responses were given using the right hand index finger. The task required subjects to press the response button if the verb was concrete (comprising the sets of hand and foot verbs), and to suppress responding for abstract verbs. A cue acting as a Go signal appeared 150 ms after word onset, which was directly adapted from Sato et al. (2008) and was shown in pilot runs for Study 3 to decrease average reaction times and increase differences between conditions. The forced speed component of the task is presumed to be important to give rise to interference effects by maximizing the temporal overlap of language and motor processing.

Reaction time differences were assessed using repeated measures ANOVA, and significant effects defined which conditions to compare in the oscillatory responses. MEG analyses were performed on sensor level but in a set of sensors derived from a functional localizer task which consisted of self-paced button presses. For the localizer task, source analysis with DICS (dynamic imaging of coherent sources, Gross et al., 2001) was used to determine the cortical origin of beta oscillatory modulations in the motor preparation period. This sensor selection entered all analyses of the different contrasts in the verbal task.

Separate stimulus-locked and response-locked approaches allowed a focus on different aspects of the hypothesis: With averaging for stimulus onset, possible stimulus-driven effects can be detected, while the exact moment of the response execution is temporally jittered by reaction time differences. The reverse is true for the response-locked analysis. Here, a similar pattern of response preparation and execution can be assumed across trials, while the exact moment of word onset is jittered. Both analyses, however, are suited to investigate the overlap of language and motor processing and differences between conditions. Statistical assessment was, like for Study 2, performed using the non-parametric randomisation based clustering approach (Maris and Oostenveld, 2007). For the localiser task, this meant contrasting two equal-length time windows in the motor preparation period averaged for 15-25 Hz. The significant channel cluster defined the motor channel selection to be used in the verb task analysis. There, time-frequency signals were averaged across this motor channel selection, while time points (1 s before and after the word or response) and frequencies (5-30 Hz) were not averaged. This allowed an unbiased assessment of effects across time and in all frequencies. In addition to the data driven approach of contrasting the conditions with reaction time effects, a comparison of hand and abstract verbs in the stimulus-locked analysis was also determined a priori to allow tentative comparisons with the previous studies. EMG signals from the first dorsal interosseus (FDI) muscle were also collected and compared between conditions to control for different movement force or timing characteristics that might confound oscillatory effects.

8.2 Results

Behavioural results showed an unexpected interaction with verb imageability: The interference effect was only found for high imageability verbs, with reaction times for hand verbs slower than for foot verbs. For the low imageability subgroups, no differences were seen. Moreover, imageability also yielded a significant main effect, with faster reactions to high imageability verbs.

Thus, the conditions of interest to compare in the MEG analysis were most importantly the contrast high imageability hand vs. high imageability foot verbs. Moreover, imageability was directly contrasted for hand verbs, and the stimulus-locked analysis also allowed a comparison between hand and abstract verbs. The localizer task revealed significant beta power suppression during motor preparation in a set of left central sensors. Source localisation of the grandaverage effect pointed to a pericentral origin of this effect, comprising pre- and primary motor as well as somatosensory hand areas.

For the main contrast of interest, beta power suppression was weaker for high imageability hand compared with high imageability foot verbs and focused around 20 Hz. In the stimulus-locked analysis this effect lasted from 350 ms to 750 ms after word onset, while in the response-locked analysis it started 625 ms before the response and ended 425 ms after the response. Directly comparing high and low imageability for the hand verbs showed smaller beta suppression for the high imageability condition, again both in the stimulus-locked (starting at 400 ms after word onset until the end of the analysis window at 1000 ms) and response-locked analysis (800 ms before to 250 ms after the response). The exploratory contrast between hand and abstract verbs in the stimulus-locked analysis showed stronger beta suppression for hand than abstract verbs starting around 400 ms after verb onset. No power differences were seen in alpha or other frequency bands. Visual inspection of power topographies suggested that both alpha and beta activity were modulated in posterior channels as well as in a separate centrolateral cluster, but only for the beta band differential effects in the experimental conditions were found. Importantly, no differences between any hand and foot verb conditions were observed in the EMG signals.

8.3 Discussion

Study 3 found the expected interaction between language and motor processing to depend on an inherent semantic feature of the verbs, namely imageability. The interference effect was reflected neurophysiologically in reduced beta power suppression for high imageability hand compared with high imageability foot verbs in a time window of concurrent verb processing and motor preparation.

The interaction with imageability indicates that processing in motor cortical areas is stronger for high imageability verbs, implying that high imageability is indirectly associated with action features of the verbs. This was directly assessed in a follow up rating questionnaire. Here, imageability correlated with the verbs' *motor prototypicality* which was defined as *the extent to which the verb implies one typical action rather than several different ones.* Moreover, the *amount of hand movement* in the action described by each verb correlated with hand verb imageability and the *amount of leg movement* with foot verb imageability.

The finding of reduced beta power suppression for the hand verbs with high imageability is in line with reports of reduced cortical excitability in a language-motor interference paradigm contrasting hand and abstract verbs (Boulenger et al., 2008). The relevant factor may be the incompatibility with action schemata activated by the verbs and the action plans for the response (Buccino et al., 2005). In this sense, the experimental operationalisation of verbs referring to different effectors is only one way to create this incompatibility, but similar effects can be observed within the same effector for verbs compatible vs. incompatible with the direction of movement for the response (Liepelt et al., 2012). The chained activation of action schemata and their degree of overlap with the executed action can account for the facilitatory and interfering effects found in different studies with different stimulus material and stimulus timing (Chersi et al., 2010). Crucially, the interaction of language and motor processing shows that the two processes indeed recruit the same or closely associated functional mechanisms. The conditions under which this interaction arises show that it is specific and not epiphenomenal.

In contrast to Studies 1 and 2 which did not require deep semantic processing of the verbs, Study 3 used a concrete/abstract decision paradigm. Previous behavioural studies showed that a superficial lexical decision task is not sufficient to provoke language-motor interference (Sato et al., 2008). This is in line with the more subtle effects seen during silent reading paradigms and also with the fact that low-imageability verbs seem to lead to a motor cortical activation that is not strong enough to interact with motor behaviour.

8.4 Conclusion

Studies 1 and 2 investigated action verb processing in isolation and with as little task demands as possible, and showed motor cortex contributions even in this minimal setting. Study 3 provoked exactly what studies 1 and 2 strictly avoided: an overlap of verb with overt motor processing. Indeed, the behavioural interference effect correlated with modulations in beta power. This suggests that language-motor interference results from both verbal processing and motor preparation recruit the same functional loops in the motor cortex. This double recruitment may transiently decrease cortical excitability through inhibitory loops, creating the behavioural slowing and reduced beta suppression.

The influence of imageability as an inherent semantic verb property is particularly interesting in light of the current line of embodied cognition research which stresses situational and context factors. The results of Study 3 show that information about the action schemata of verbs seems lexicalized in the sense that their activation differentially weighs processing in multimodal brain regions.

9 General Discussion

This thesis investigated the motor-cortical contributions to action verb processing. The results offer conclusions about the different aspects predicted by embodied cognition: The spatial pattern of verb processing and its relation to individual functional neurophysiology (Study 1), the oscillatory mechanism underlying both movement and verb processing in the motor system (Study 2), and the dynamics of these processes when they directly interact (Study 3). Embodied cognition hypotheses are supported by the results of each study.

The fitting of individual motor dipole sources in Study 1 allowed a level of investigating individual functionality that has not been achieved by previous studies on embodied language processing. This transcends beyond findings that verb processing recruits brain areas in locations where they are expected to be based on motor system anatomy, or partly overlap locations found in action execution. Study 1 showed that the neuronal sources reflecting real hand and foot movements are also preferentially active when processing verbs describing actions with the matching effector. A different kind of functional specificity was used in Studies 2 and 3. They capitalised on the functional role of neuronal oscillations in the alpha and beta frequency bands that are seen as one of the core common mechanisms of dynamic neuronal communication in the sensorimotor system. By showing that verb processing specifically recruits these oscillatory frequency bands, this thesis demonstrates that language processing is not only located in specific locations in the motor cortex, but presumably relies on the same functional circuits. Neuronal oscillations arise from an interaction of excitation and inhibition in neuronal populations from within the same cortical patch and between different cortical patches and even cortical layers (Buzsáki, 2007). Thus, it is possible that verb processing uses the same functional loops as motor processing, producing the same synchronisation patterns and oscillatory output. This is corroborated by the findings from Study 3, in which motor preparatory modulations in the beta frequency band were associated with behavioural interference when hand verbs were processed in parallel with a hand action. Importantly, all three studies support the hypothesis that motor cortex recruitment is a functional mechanism in language understanding by showing that the latency of effects is within the time frame of early semantic access, around 200 ms after word onset.

Thus, this thesis shows strong evidence for motor cortex contributions to action verb processing using novel analysis methods in embodied cognition research. However, there are some differences between the results and interpretations from each study.

While in Study 1, left hemisphere involvement in language conditions started earlier for all conditions but no difference for verb conditions was found, Study 2 revealed effects for the hand vs. abstract verbs contrast only in the left hemisphere. Note that lateralisation could not be assessed for the foot vs. abstract verb contrast because the localiser task results overlapped in the medial sensors to the extent that pooling them was most feasible. The difference in lateralisation effects provides another example of how evoked and oscillatory analyses are complementary. Study 1 and 2 differ not only regarding the kind of analyses used, but also regarding the spatial resolution and the contrasts between conditions. Thus, no firm conclusions about the body specificity hypothesis can be drawn.

Study 2 and 3 provide oscillatory effects in the beta band that at first glance may seem challenging to reconcile. Study 2 shows that action verbs are accompanied by more pronounced beta power suppression than abstract verbs, indicating embodied language processing. In Study 3, the condition associated with the strongest influence of embodied processing (as also expressed in the behavioural reaction time results) is the one with weaker beta power suppression than the other action verb conditions. This implies that embodied language processing does not simply and under all circumstances increase beta power suppression. Rather, it shows how strongly neurophysiological effects depend on the precise situation under which they are recorded. In this case, apart from the contrast of interest, the drastically different task setting is presumably the reason leading to the flexible effects of embodiment. This is precisely what is hypothesized for sensorimotor contributions to semantic processing, for which functional mechanisms cannot be expected to be activated uniformly, but in the fashion and to the extent relevant for the specific situation. The three studies in this thesis offer insight both into single word processing in isolation, focusing on more automatic processes, and in direct interaction with motor behaviour. For both types of task setting, motor system involvement was found.

Overall, results from this thesis confirm that MEG and the complementary analyses it offers are particularly valuable tools to investigate language processing in the human brain and to gain insight into the hypotheses of embodied cognitions.

10 Outlook

This thesis provides comprehensive evidence for functionally relevant motor cortical contributions to German action verb processing. New open questions directly arise from these results, to be investigated in the future.

The good temporal as well as spatial resolution of MEG and developing methods in the analysis of functional connectivity can foster more complex analyses of language processing regarding multimodal interaction of brain regions in the motor and sensory system. For instance, primary and premotor cortex may not be the only parts of the motor system involved in processing action knowledge, but visual motion areas in the occipito-parietal cortex, biological motion areas in the superior temporal sulcus, and parietal areas involved in processing tool use may all interact for verbs whose meaning comprises these different features. Moreover, other sensory modalities may be involved, too: Verbs can also derive an important part of their meaning and their neuronal simulation from the somatosensory, visual or auditory domains. For example, the verb *to clap* may strongly activate the primary motor, somatosensory and auditory cortex, enhancing activity in and task-related functional connectivity between these regions, while verbs like *to hammer* are simulated in these same brain regions with the addition of the parietal tool-use-related areas. It is a challenge to find verbal stimulus material of sufficient sample size that is well-characterised on these different meaning components. Nevertheless, evidence for functional interactions of multimodal regions during access to semantic memory would provide compelling evidence for the embodied cognition's claim that all the neuronal assemblies used to execute an action are active to simulate its meaning.

Apart from these action-related meaning components that can be investigated, this thesis also indicates that recruitment of sensorimotor brain areas during verb processing is to some extent flexible. This directly follows from the interaction with verb imageability in Study 3, implying that this variable can influence the relative relevance of the motor meaning component. Thus, future studies should investigate the details about flexible motor recruitment and semantic meaning components such as motor content or action prototypicality. An important step in this line of research is also developing paradigms in which double dissociations can be observed. This would further support the functionality of language-motor interaction and decrease their dependency on language material. For instance, this can be achieved by combining both hand and foot responses and investigating their interaction with hand and foot verb processing, respectively.

Another aspect to be investigated in future studies is the contribution of neuronal oscillations in the gamma frequency range to the pattern found in this thesis for the alpha and beta band. While gamma oscillations have been predominantly investigated in the visual system (e.g. Hoogenboom et al., 2006), they were also described to show burst-like activity shortly after a movement. In both domains, gamma oscillations are thought to index rather local neuronal communication, compared to the more long-range effects of slower frequencies. They also have characteristic patterns of coupling with lower frequencies, especially alpha, and also theta in the memory system (Colgin, 2015). For language processing, successful modelling of gamma activity has recently been achieved (van Ackeren et al., 2014), possibly leading to the availability of optimised analysis parameters for this approach. Thus, gamma oscillations should also be investigated in future studies of embodied language processing.

Further insight into the role of motor system contributions may be gained from brain stimulation studies. Here, the selective up- or down-regulation of motor cortical areas can be assessed regarding its consequences on language processing, for instance in language-motor interaction tasks like shown in Study 3. Advances in brain stimulation techniques even allow a specific entrainment of neuronal oscillations in a certain frequency band (Helfrich et al., 2014). This may be used to further investigate the functional role of alpha and beta oscillations in action language processing.

Generally, the methods successfully used in this thesis, combined with new analysis tools such as functional connectivity, can be used in experiments with novel language tasks to broaden the understanding of the mechanisms behind embodied language processing.

11 References

Adam, H. and Galinsky, A. D. (2012). Enclothed cognition. *J Exp Soc Psycho*, 48(4):918–925.

Alemanno, F., Houdayer, E., Cursi, M., Velikova, S., Tettamanti, M., Comi, G., Cappa, S., and Leocani, L. (2012). Action-related semantic content and negation polarity modulate motor areas during sentence reading: An event-related desynchronization study. *Brain Res*, 1484:39–49.

Andrews, M., Frank, S., and Vigliocco, G. (2014). Reconciling embodied and distributional accounts of meaning in language. *Top Cogn Sci*, 6(3):359–370.

Aravena, P., Delevoye-Turrell, Y., Deprez, V., Cheylus, A., Paulignan, Y., Frak, V., and Nazir, T. (2012). Grip force reveals the context sensitivity of language-induced motor activity during “action words” processing: evidence from sentential negation. *PloS One*, 7(12):e50287.

Arbib, M. A., Gasser, B., and Barrès, V. (2014). Language is handy but is it embodied? *Neuropsychologia*, 55:57–70.

Aziz-Zadeh, L. and Damasio, A. (2008). Embodied semantics for actions: findings from functional brain imaging. *J Physiol Paris*, 102(1-3):35–39.

Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., and Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Curr Biol*, 16(18):1818–1823.

Bak, T. H. and Hodges, J. R. (2004). The effects of motor neurone disease on language: further evidence. *Brain Lang*, 89(2):354–361.

Bak, T. H., O’Donovan, D. G., Xuereb, J. H., Boniface, S., and Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease-dementia-aphasia syndrome. *Brain*, 124(Pt 1):103–120.

Barrett, L. (2011). *Beyond the brain: How body and environment shape animal and human minds.* Princeton Univ Press, New Jersey.

Barrós-Loscertales, A., González, J., Pulvermüller, F., Ventura-Campos, N., Bustamante, J. C., Costumero, V., Parcet, M. A., and Ávila, C. (2012). Reading salt activates gustatory brain regions: fMRI evidence for semantic grounding in a novel sensory modality. *Cereb Cortex*, 22(11):2554–2563.

Barsalou, L. W. (1992). Frames, concepts, and conceptual fields. In Lehrer A. and Kittay E. F., editor, *Frames, Fields, and Contrasts.* Lawrence Erlbaum Associates Publishers, Hillsdale NJ.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behav Brain Sci*, 22(4):577–609; discussion 610–60.

Barsalou, L. W. (2008). Grounded cognition. *Annu Rev Psychol*, 59:617–645.

Barsalou, L. W. (2010). Grounded cognition: Past, present, and future. *Top Cogni Sci*, 2(4):716–724.

Barsalou, L. W., Kyle Simmons, W., Barbey, A. K., and Wilson, C. D. (2003). Grounding conceptual knowledge in modality-specific systems. *Trends Cogni Sci*, 7(2):84–91.

Bastiaansen, M. and Hagoort, P. (2006). Oscillatory neuronal dynamics during language comprehension. *Prog Brain Res*, 159:179–196.

Bedny, M. and Caramazza, A. (2011). Perception, action, and word meanings in the human brain: the case from action verbs. *Ann N Y Acad Sci*, 1224:81–95.

Bellebaum, C., Tettamanti, M., Marchetta, E., Della Rosa, P., Rizzo, G., Daum, I., and Cappa, S. F. (2013). Neural representations of unfamiliar objects are modulated by sensorimotor experience. *Cortex*, 49(4):1110–1125.

Bergen, B., Lau, T.-T. C., Narayan, S., Stojanovic, D., and Wheeler, K. (2010). Body part representations in verbal semantics. *Mem Cognit*, 38(7):969–981.

Berger, H. (1929). Über das Elektrenkephalogramm des Menschen. *Archiv für Psychiatrie und Nervenkrankheiten*, 87(1):527–570.

Bernstein, L. E. and Liebenthal, E. (2014). Neural pathways for visual speech perception. *Front Neurosci*, 8:386.

Biermann-Ruben, K., Miller, A., Franzkowiak, S., Finis, J., Pollok, B., Wach, C., Südmeyer, M., Jonas, M., Thomalla, G., Müller-Vahl, K., Münchau, A., and Schnitzler, A. (2012). Increased sensory feedback in Tourette syndrome. *NeuroImage*, 63(1):119–125.

Biermann-Ruben, K., Salmelin, R., and Schnitzler, A. (2005). Right rolandic activation during speech perception in stutterers: a MEG study. *NeuroImage*, 25(3):793–801.

Boulenger, V., Hauk, O., and Pulvermüller, F. (2009). Grasping ideas with the motor system: Semantic somatotopy in idiom comprehension. *Cereb Cortex*, 19(8):1905–1914.

Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M., and Nazir, T. A. (2006). Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *J Cogn Neurosci*, 18(10):1607–1615.

Boulenger, V., Shtyrov, Y., and Pulvermüller, F. (2012). When do you grasp the idea? MEG evidence for instantaneous idiom understanding. *NeuroImage*, 59(4):3502–3513.

Boulenger, V., Silber, B. Y., Roy, A. C., Paulignan, Y., Jeannerod, M., and Nazir, T. A. (2008). Subliminal display of action words interferes with motor planning: a combined EEG and kinematic study. *J Physiol Paris*, 102(1-3):130–136.

Brinkman, L., Stolk, A., Dijkerman, H. C., Lange, F. P. d., and Toni, I. (2014). Distinct roles for alpha- and beta-band oscillations during mental simulation of goal-directed actions. *J Neurosci*, 34(44):14783–14792.

Broca, P. (1861). Remarques sur le siège de la faculté du langage articulé, suivies d'une observation d'aphémie (perte de la parole). *Bulletins de la Société d'anatomie (Paris)*, (6):330–357.

Broca, P. (1865). Sur le siège de la faculté du langage articulé. *Bulletin de la Société d'anthropologie*, (6):337–393.

Brooks, R. A. (1991). Intelligence without reason. In *Computers and Thought, IJCAI-91*, pages 569–595. Morgan Kaufmann.

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., and Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Brain Res Cogn Brain Res*, 24(3):355–363.

Buzsáki, G. (2007). The structure of consciousness. *Nature*, 446(7133):267.

Caramazza, A., Hillis, A. E., Rapp, B. C., and Romani, C. (1990). The multiple semantics hypothesis: Multiple confusions? *Cogn Neuropsychol*, 7(3):161–189.

Carota, F., Moseley, R., and Pulvermüller, F. (2012). Body-part-specific representations of semantic noun categories. *J Cogn Neurosci*, 24(6):1492–1509.

Carreiras, M., Armstrong, B. C., Perea, M., and Frost, R. (2014). The what, when, where, and how of visual word recognition. *Trends Cogn Sci*, 18(2):90–98.

Casasanto, D. (2011). Different bodies, different minds: The body specificity of language and thought. *Curr Dir Psychol Sc*, 20(6):378–383.

Chang, E. F., Raygor, K. P., and Berger, M. S. (2015). Contemporary model of language organization: an overview for neurosurgeons. *J Neurosurg*, 122(2):250–261.

Chemero, A. (2003). An outline of a theory of affordances. *Ecol Psychol*, 15(2):181–195.

Chemero, A. (2009). *Radical embodied cognitive science*. MIT Press, Cambridge, MA.

Chersi, F., Thill, S., Ziemke, T., and Borghi, A. M. (2010). Sentence processing: linking language to motor chains. *Front Neurorobot*, 4:4.

Cheyne, D., Kristeva, R., and Deecke, L. (1991). Homuncular organization of human motor cortex as indicated by neuromagnetic recordings. *Neurosci Lett*, 122(1):17–20.

Cheyne, D. and Weinberg, H. (1989). Neuromagnetic fields accompanying unilateral finger movements: pre-movement and movement-evoked fields. *Exp Brain Res*, 78(3):604–612.

Chomsky, N. (2002). *Syntactic structures*. Mouton de Gruyter, Berlin and New York, 2nd edition.

Cohen, L., Lehéricy, S., Chochon, F., Lemer, C., Rivaus, S., and Dehaene, S. (2002). Language-specific tuning of visual cortex? functional properties of the visual word form area. *Brain*, 125(Pt 5):1054–1069.

Colgin, L. L. (2015). Theta–gamma coupling in the entorhinal–hippocampal system. *Curr Opin Neurobiol*, 31:45–50.

Comrie, B. (1976). *Aspect: An introduction to the study of verbal aspect and related problems*. Cambridge textbooks in linguistics. Cambridge University Press, Cambridge and New York.

Connine, C. M., Mullennix, J., Shernoff, E., and Yelen, J. (1990). Word familiarity and frequency in visual and auditory word recognition. *J Exp Psychol Learn Mem Cogn*, 16(6):1084–1096.

Dalla Volta, R., Gianelli, C., Campione, G. C., and Gentilucci, M. (2009). Action word understanding and overt motor behavior. *Ex Brain Res*, 196(3):403–412.

Daniele, A., Giustolisi, L., Silveri, M. C., Colosimo, C., and Gainotti, G. (1994). Evidence for a possible neuroanatomical basis for lexical processing of nouns and verbs. *Neuropsychologia*, 32(11):1325–1341.

de Lange, F. P., Jensen, O., Bauer, M., and Toni, I. (2008). Interactions between posterior gamma and frontal alpha/beta oscillations during imagined actions. *Front Human Neurosci*, 2:7.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., and Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Exp Brain Res*, 91(1):176–180.

Dick, A. S., Bernal, B., and Tremblay, P. (2014). The language connectome: new pathways, new concepts. *Neuroscientist*, 20(5):453–467.

Diefenbach, C., Rieger, M., Massen, C., and Prinz, W. (2013). Action-sentence compatibility: the role of action effects and timing. *Front Psychol*, 4:272.

Dronkers, N. F., Plaisant, O., Iba-Zizen, M. T., and Cabanis, E. A. (2007). Paul broca's historic cases: high resolution MR imaging of the brains of leborgne and lelong. *Brain*, 130(5):1432–1441.

Eerland, A., Guadalupe, T. M., and Zwaan, R. A. (2011). Leaning to the left makes the Eiffel Tower seem smaller: Posture-modulated estimation. *Psychol Sci*, 22(12):1511–1514.

Endo, H., Kato, Y., Kizuka, T., Masuda, T., and Takeda, T. (2004). Bilateral cerebral activity for unilateral foot movement revealed by whole-head magnetoencephalography. *Somatosens Mot Res*, 21(1):33–43.

Engel, A. K. and Fries, P. (2010). Beta-band oscillations–signalling the status quo? *Curr Opinion Neurobiol*, 20(2):156–165.

Fadiga, L., Fogassi, L., Pavesi, G., and Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *J Neurophysiol*, 73(6):2608–2611.

Fargier, R., Paulignan, Y., Boulenger, V., Monaghan, P., Reboul, A., and Nazir, T. A. (2012). Learning to associate novel words with motor actions: language-induced motor activity following short training. *Cortex*, 48(7):888–899.

Fernandino, L., Conant, L. L., Binder, J. R., Blindauer, K., Hiner, B., Spangler, K., and Desai, R. H. (2012). Parkinson's disease disrupts both automatic and controlled processing of action verbs. *Brain Lang*, 127(1):65–74.

Fodor, J. A. (1983). *The modularity of mind: An essay on faculty psychology.* A Bradford book. MIT Press, Cambridge, MA.

Fodor, J. A. and Pylyshyn, Z. W. (1988). Connectionism and cognitive architecture: a critical analysis. *Cognition*, 28(1-2):3–71.

Fontolan, L., Morillon, B., Liegeois-Chauvel, C., and Giraud, A.-L. (2014). The contribution of frequency-specific activity to hierarchical information processing in the human auditory cortex. *Nat Commun*, 5:4694.

Friederici, A. D. and Gierhan, S. M. E. (2013). The language network. *Curr Opin Neurobiol*, 23(2):250–254.

Gallese, V. (2008). Mirror neurons and the social nature of language: the neural exploitation hypothesis. *Soc Neurosci*, 3(3-4):317–333.

Gallese, V. and Lakoff, G. (2005). The brain's concepts: the role of the sensory-motor system in conceptual knowledge. *Cogn Neuropsychol*, 22(3):455–479.

Geschwind, N. (1970). The organization of language and the brain. *Science*, 170(3961):940–944.

Gibson, J. J. (1979). *The ecological approach to visual perception.* Houghton Mifflin, Boston.

Giraud, A.-L. and Poeppel, D. (2012). Cortical oscillations and speech processing: emerging computational principles and operations. *Nat Neurosci*, 15(4):511–517.

Glenberg, A. M. and Kaschak, M. P. (2002). Grounding language in action. *Psychon Bull Rev*, 9(3):558–565.

Glover, S., Rosenbaum, D. A., Graham, J., and Dixon, P. (2004). Grasping the meaning of words. *Exp Brain Res*, 154(1):103–108.

González, J., Barros-Loscertales, A., Pulvermüller, F., Meseguer, V., Sanjuán, A., Belloch, V., and Avila, C. (2006). Reading cinnamon activates olfactory brain regions. *NeuroImage*, 32(2):906–912.

Gross, J., Kujala, J., Hamalainen, M., Timmermann, L., Schnitzler, A., and Salmelin, R. (2001). Dynamic imaging of coherent sources: Studying neural interactions in the human brain. *Proc Natl Acad Sci U S A*, 98(2):694–699.

Grossman, M., Anderson, C., Khan, A., Avants, B., Elman, L., and McCluskey, L. (2008). Impaired action knowledge in amyotrophic lateral sclerosis. *Neurology*, 71(18):1396–1401.

Hall, S. D., Barnes, G. R., Furlong, P. L., Seri, S., and Hillebrand, A. (2010). Neuronal network pharmacodynamics of GABAergic modulation in the human cortex determined using pharmaco-magnetoencephalography. *Hum Brain Mapp*, 31(4):581–594.

Hämäläinen, M., Hari, R., Ilmoniemi, R. J., Knuutila, J., and Lounasmaa, O. V. (1993). Magnetoencephalography – theory, instrumentation, and applications to noninvasive studies of the working human brain. *Rev Mod Phys*, 65:413–497.

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., and Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc Natl Acad Sci U S A*, 95(25):15061–15065.

Hari, R. and Salmelin, R. (2012). Magnetoencephalography: From SQUIDs to neuroscience. *NeuroImage*, 61(2):386–396.

Hari, R., Salmelin, R., Mäkelä, J. P., Salenius, S., and Helle, M. (1997). Magnetoencephalographic cortical rhythms. *Int J Psychophysiol*, 26(1-3):51–62.

Hauk, O., Johnsrude, I., and Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41(2):301–307.

Hauk, O. and Pulvermüller, F. (2011). The lateralization of motor cortex activation to action-words. *Front Hum Neurosci*, 5:149.

Hebb, D. O. (1949). *The Organization of Behavior: A Neuropsychological Theory*. Wiley, New York.

Held, R. and Hein, A. (1963). Movement-produced stimulation in the development of visually guided behavior. *J Comp Physiol Psychol*, 56(5):872–876.

Helenius, P., Salmelin, R., Service, E., and Connolly, J. F. (1998). Distinct time courses of word and context comprehension in the left temporal cortex. *Brain*, 121 (Pt 6):1133–1142.

Helfrich, R. F., Knepper, H., Nolte, G., Strüber, D., Rach, S., Herrmann, C. S., Schneider, T. R., and Engel, A. K. (2014). Selective modulation of interhemispheric functional connectivity by HD-tACS shapes perception. *PLoS Biol*, 12(12):e1002031.

Herrera, E., Rodríguez-Ferreiro, J., and Cuetos, F. (2012). The effect of motion content in action naming by Parkinson's disease patients. *Cortex*, 48(7):900–904.

Hoogenboom, N., Schoffelen, J.-M., Oostenveld, R., Parkes, L. M., and Fries, P. (2006). Localizing human visual gamma-band activity in frequency, time and space. *NeuroImage*, 29(3):764–773.

Hurley, S. L. (1998). *Consciousness in action.* Harvard University Press, Cambridge, MA.

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *NeuroImage*, 14(1):103–109.

Jensen, O., Goel, P., Kopell, N., Pohja, M., Hari, R., and Ermentrout, B. (2005). On the human sensorimotor-cortex beta rhythm: sources and modeling. *NeuroImage*, 26(2):347–355.

Jirak, D., Menz, M. M., Buccino, G., Borghi, A. M., and Binkofski, F. (2010). Grasping language–a short story on embodiment. *Conscious Cogn*, 19(3):711–720.

Kemmerer, D., Castillo, J. G., Talavage, T., Patterson, S., and Wiley, C. (2008). Neuroanatomical distribution of five semantic components of verbs: evidence from fMRI. *Brain Lang*, 107(1):16–43.

Kemmerer, D. and Gonzalez-Castillo, J. (2010). The Two-Level Theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system. *Brain Lang*, 112(1):54–76.

Kiefer, M., Sim, E.-J., Herrnberger, B., Grothe, J., and Hoenig, K. (2008). The sound of concepts: four markers for a link between auditory and conceptual brain systems. *J Neurosci*, 28(47):12224–12230.

Klatzky, R. L., Pellegrino, J. W., McCloskey, B. P., and Doherty, S. (1989). Can you squeeze a tomato? The role of motor representations in semantic sensibility judgments. *J Mem Lang*, 28(1):56–77.

Koelewijn, T., van Schie, Hein T, Bekkering, H., Oostenveld, R., and Jensen, O. (2008). Motor-cortical beta oscillations are modulated by correctness of observed action. *NeuroImage*, 40(2):767–775.

Kousta, S.-T., Vigliocco, G., Vinson, D. P., Andrews, M., and Del Campo, E. (2011). The representation of abstract words: why emotion matters. *J Exp Psychol Gen*, 140(1):14–34.

Kristeva-Feige, R., Walter, H., Lütkenhöner, B., Hampson, S., Ross, B., Knorr, U., Steinmetz, H., and Cheyne, D. (1994). A neuromagnetic study of the functional organization of the sensorimotor cortex. *Eur J Neurosci*, 6(4):632–639.

Kutas, M. and Hillyard, S. A. (1984). Brain potentials during reading reflect word expectancy and semantic association. *Nature*, 307(5947):161–163.

Lakoff, G. and Johnson, M. (1999). *Philosophy in the flesh: The embodied mind and its challenge to Western thought.* Basic Books, New York.

Levelt, W. J., Praamstra, P., Meyer, A. S., Helenius, P., and Salmelin, R. (1998). An MEG study of picture naming. *J Cogn Neurosci*, 10(5):553–567.

Levin, B. (1993). *English Verb Classes and Alternations: A Preliminary Investigation.* University of Chicago Press, Chicago, IL.

Lewis, A. G., Wang, L., and Bastiaansen, M. (2015). Fast oscillatory dynamics during language comprehension: Unification versus maintenance and prediction? *Brain Lang*, page available online 7 February 2015.

Liepelt, R., Dolk, T., and Prinz, W. (2012). Bidirectional semantic interference between action and speech. *Psychol Res*, 76(4):446–455.

Maris, E. and Oostenveld, R. (2007). Nonparametric statistical testing of eeg- and meg-data. *J Neurosci Methods*, 164(1):177–190.

Maris, M. and te Boekhorst, R. (1996). Exploiting physical constraints: Heap formation through behavioural error in a group of robots. In *Proceedings IEEE/RSJ International Conference on Intelligent*, volume on Intelligent Robots and Systems (IROS).

Meier, J. D., Aflalo, T. N., Kastner, S., and Graziano, M. S. A. (2008). Complex organization of human primary motor cortex: A high-resolution fMRI study. *J Neurophysiol*, 100(4):1800–1812.

Meugnot, A., Almecija, Y., and Toussaint, L. (2014). The embodied nature of motor imagery processes highlighted by short-term limb immobilization. *Exp Psychol.*, 61(3):180–186.

Mirabella, G., Iaconelli, S., Spadacenta, S., Federico, P., and Gallese, V. (2012). Processing of hand-related verbs specifically affects the planning and execution of arm reaching movements. *PloS One*, 7(4):e35403.

Moreno, I., Vega, M. d., and León, I. (2013). Understanding action language modulates oscillatory mu and beta rhythms in the same way as observing actions. *Brain Cogn*, 82(3):236–242.

Moseley, R., Carota, F., Hauk, O., Mohr, B., and Pulvermüller, F. (2012). A role for the motor system in binding abstract emotional meaning. *Cereb Cortex*, 22(7):1634–1647.

Moseley, R. L., Pulvermüller, F., and Shtyrov, Y. (2013). Sensorimotor semantics on the spot: brain activity dissociates between conceptual categories within 150 ms. *Sci Rep*, 3.

Muthukumaraswamy, S., Myers, J., Wilson, S., Nutt, D., Lingford-Hughes, A., Singh, K., and Hamandi, K. (2013). The effects of elevated endogenous GABA levels on movement-related network oscillations. *NeuroImage*, 66:36–41.

Nazir, T. A., Boulenger, V., Roy, A., Silber, B., Jeannerod, M., and Paulignan, Y. (2008). Language-induced motor perturbations during the execution of a reaching movement. *Q J Exp Psychol (Hove)*, 61(6):933–943.

Orgs, G., Dombrowski, J.-H., Heil, M., and Jansen-Osmann, P. (2008). Expertise in dance modulates alphabeta event-related desynchronization during action observation. *Eur J Neurosci*, 27(12):3380–3384.

Papeo, L., Corradi-Dell'Acqua, C., and Rumiati, R. I. (2011). "She" is not like "I": the tie between language and action is in our imagination. *J Cogn Neurosci*, 23(12):3939–3948.

Paulus, M., Lindemann, O., and Bekkering, H. (2009). Motor simulation in verbal knowledge acquisition. *Q J Exp Psychol (Hove)*, 62(12):2298–2305.

Penfield, Wilder; Rasmussen, T. (1950). The cerebral cortex of man: A clinical study of localization of function. *Journal of the American Medical Association*, 144(16):1412.

Perniss, P. and Vigliocco, G. (2014). The bridge of iconicity: from a world of experience to the experience of language. *Philos Trans R Soc Lond B Biol Sci*, 369(1651):20130300.

Pfurtscheller, G., Brunner, C., Schlögl, A., and Lopes da Silva, F. H. (2006). Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage*, 31(1):153–159.

Pfurtscheller, G. and Lopes da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin Neurophysiol*, 110(11):1842–1857.

Pfurtscheller, G., Neuper, C., Andrew, C., and Edlinger, G. (1997). Foot and hand area mu rhythms. *Int J Psychophysiol.*, 26(1-3):121–135.

Postle, N., McMahon, K. L., Ashton, R., Meredith, M., and de Zubicaray, G. I. (2008). Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. *NeuroImage*, 43(3):634–644.

Pulvermüller, F. (2013). Semantic embodiment, disembodiment or misembodiment? in search of meaning in modules and neuron circuits. *Brain Lang*, 127(1):86–103.

Pulvermüller, F. and Fadiga, L. (2010). Active perception: sensorimotor circuits as a cortical basis for language. *Nat Rev Neurosci*, 11(5):351–360.

Pulvermüller, F. and Garagnani, M. (2014). From sensorimotor learning to memory cells in prefrontal and temporal association cortex: a neurocomputational study of disembodiment. *Cortex*, 57:1–21.

Pulvermüller, F., Garagnani, M., and Wennekers, T. (2014). Thinking in circuits: toward neurobiological explanation in cognitive neuroscience. *Biol Cybern*, 108(5):573–593.

Pulvermüller, F., Härle, M., and Hummel, F. (2001). Walking or talking? behavioral and neurophysiological correlates of action verb processing. *Brain Lang*, 78(2):143–168.

Pulvermüller, F., Hauk, O., Nikulin, V. V., and Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *Eur J Neurosci*, 21(3):793–797.

Rabovsky, M., Sommer, W., and Abdel Rahman, R. (2012). The time course of semantic richness effects in visual word recognition. *Front Hum Neurosci*, 6:11.

Repetto, C., Colombo, B., Cipresso, P., and Riva, G. (2013). The effects of rTMS over the primary motor cortex: the link between action and language. *Neuropsychologia*, 51(1):8–13.

Rüschemeyer, S.-A., Brass, M., and Friederici, A. D. (2007). Comprehending prehending: neural correlates of processing verbs with motor stems. *J Cogn Neurosci*, 19(5):855–865.

Salmelin, R., Hämäläinen, M., Kajola, M., and Hari, R. (1995). Functional segregation of movement-related rhythmic activity in the human brain. *NeuroImage*, 2(4):237–243.

Salmelin, R., Schnitzler, A., Schmitz, F., and Freund, H. J. (2000). Single word reading in developmental stutterers and fluent speakers. *Brain*, 123 (Pt 6):1184–1202.

Sato, M., Mengarelli, M., Riggio, L., Gallese, V., and Buccino, G. (2008). Task related modulation of the motor system during language processing. *Brain Lang*, 105(2):83–90.

Schnitzler, A., Salenius, S., Salmelin, R., Jousmäki, V., and Hari, R. (1997). Involvement of primary motor cortex in motor imagery: a neuromagnetic study. *NeuroImage*, 6(3):201–208.

Schott, G. D. (1993). Penfield's homunculus: a note on cerebral cartography. *J Neurol Neurosurg Psychiatry*, 56(4):329–333.

Schuil, K. D. I., Smits, M., and Zwaan, R. A. (2013). Sentential context modulates the involvement of the motor cortex in action language processing: an FMRI study. *Front Human Neurosci*, 7:100.

Shebani, Z. and Pulvermüller, F. (2013). Moving the hands and feet specifically impairs working memory for arm- and leg-related action words. *Cortex*, 49(1):222–231.

Shtyrov, Y., Hauk, O., and Pulvermüller, F. (2004). Distributed neuronal networks for encoding category-specific semantic information: the mismatch negativity to action words. *Eur J Neurosci*, 19(4):1083–1092.

Smith, L. B. (2005). Action alters shape categories. *Cogn Sci*, 29(4):665–679.

Smolka, E., Preller, K. H., and Eulitz, C. (2014). 'verstehen' ('understand') primes 'stehen' ('stand'): Morphological structure overrides semantic compositionality in the lexical representation of german complex verbs. *J Mem Lang*, 72:16–36.

Strafella, A. P. and Paus, T. (2000). Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. *Neuroreport*, 11(10):2289–2292.

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., Fazio, F., Rizzolatti, G., Cappa, S. F., and Perani, D. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *J Cogn Neurosci*, 17(2):273–281.

Thelen, E., Schöner, G., Scheier, C., and Smith, L. B. (2001). The dynamics of embodiment: a field theory of infant perseverative reaching. *Behav Brain Sci*, 24(1):1–34; discussion 34–86.

Tomasino, B., Weiss, P. H., and Fink, G. R. (2010). To move or not to move: imperatives modulate action-related verb processing in the motor system. *Neuroscience*, 169(1):246–258.

Tucker, M. and Ellis, R. (2004). Action priming by briefly presented objects. *Acta Psychol*, 116(2):185–203.

Turing, A. M. (1950). Computing machinery and intelligence. *Mind*, 59(236):433–460.

Turken, A. U. and Dronkers, N. F. (2011). The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Front Syst Neurosci.*, 5:1.

Turvey, M. (1992). Affordances and prospective control: An outline of the ontology. *Ecol Psychol*, 4(3):173–187.

Ursino, M., Cuppini, C., and Magosso, E. (2010). A computational model of the lexical-semantic system based on a grounded cognition approach. *Front Psychol*, 1:221.

van Ackeren, M. J., Schneider, T. R., Müsch, K., and Rueschemeyer, S.-A. (2014). Oscillatory neuronal activity reflects lexical-semantic feature integration within and across sensory modalities in distributed cortical networks. *J Neurosci*, 34(43):14318–14323.

van Dam, W. O., Rueschemeyer, S. A., and Bekkering, H. (2010). How specifically are action verbs represented in the neural motor system: an fMRI study. *NeuroImage*, 53(4):1318–1325.

van Dijk, H., Nieuwenhuis, I. L., and Jensen, O. (2010). Left temporal alpha band activity increases during working memory retention of pitches. *Eur J Neurosci*, 31(9):1701–1707.

van Elk, M., van Schie, H T, Zwaan, R. A., and Bekkering, H. (2010). The functional role of motor activation in language processing: motor cortical oscillations support lexical-semantic retrieval. *NeuroImage*, 50(2):665–677.

Varela, F. J., Thompson, E., and Rosch, E. (1991). *The embodied mind: Cognitive science and human experience*. MIT Press, Cambridge, MA.

Vartiainen, J., Parviainen, T., and Salmelin, R. (2009). Spatiotemporal convergence of semantic processing in reading and speech perception. *J Neurosci*, 29(29):9271–9280.

Vega, M. d., Moreno, V., and Castillo, D. (2013). The comprehension of action-related sentences may cause interference rather than facilitation on matching actions. *Psychol Res*, 77(1):20–30.

Vukovic, N. and Shtyrov, Y. (2014). Cortical motor systems are involved in second-language comprehension: Evidence from rapid mu-rhythm desynchronisation. *NeuroImage*, 102:695–703.

Wang, L., Jensen, O., van den Brink, D., Weder, N., Schoffelen, J.-M., Magyari, L., Hagoort, P., and Bastiaansen, M. (2012). Beta oscillations relate to the N400m during language comprehension. *Hum Brain Mapp*, 33(12):2898–2912.

Weisberg, J., van Turennout, M., and Martin, A. (2007). A neural system for learning about object function. *Cereb Cortex*, 17(3):513–521.

Weiss, S. and Mueller, H. M. (2012). Too many betas do not spoil the broth: The role of beta brain oscillations in language processing. *Front Psychol*, 3:201.

Wellsby, M. and Pexman, P. M. (2014). The influence of bodily experience on children's language processing. *Top Cogn Sci*, 6(3):425–441.

Wernicke, C. (1874). *Der aphasische Symptomencomplex: eine psychologische Studie auf anatomischer Basis*. Cohn & Weigert, Breslau.

Willems, R. M., Hagoort, P., and Casasanto, D. (2010). Body-specific representations of action verbs: neural evidence from right- and left-handers. *Psychol Sci*, 21(1):67–74.

Wilson, A. D. and Golonka, S. (2013). Embodied cognition is not what you think it is. *Front Psychol*, 4:58.

Woodhead, Z. V. J., Barnes, G. R., Penny, W., Moran, R., Teki, S., Price, C. J., and Leff, A. P. (2014). Reading front to back: MEG evidence for early feedback effects during word recognition. *Cereb Cortex*, 24(3):817–825.

Yamawaki, N., Stanford, I., Hall, S., and Woodhall, G. (2008). Pharmacologically induced and stimulus evoked rhythmic neuronal oscillatory activity in the primary motor cortex in vitro. *Neuroscience*, 151(2):386–395.

Zwaan, R. A. (2014). Embodiment and language comprehension: reframing the discussion. *Trends Cogn Sci*, 18(5):229–234.

12 Erklärung

Hiermit erkläre ich, dass ich die vorgelegte Dissertation eigenständig und ohne unerlaubte Hilfe angefertigt habe. Die Dissertation wurde in der vorliegenden oder in ähnlicher Form noch bei keiner anderen Institution eingereicht. Ich habe bisher keine erfolglosen Promotionsversuche unternommen.

Düsseldorf, den

Anne Klepp

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14 Appendix

This work is based on

Publication 1 (Appendix 1)

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Appendix 1

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Neuromagnetic hand and foot motor sources recruited during action verb processing

Anne Klepp[a,*], Hannah Weissler[a], Valentina Niccolai[a], Anselm Terhalle[b], Hans Geisler[b], Alfons Schnitzler[a], Katja Biermann-Ruben[a]

[a] *Institute of Clinical Neuroscience and Medical Psychology, Medical Faculty, Heinrich Heine University, Universitätsstr. 1, 40225 Düsseldorf, Germany*
[b] *Department of Romance Languages and Literatures, Heinrich Heine University, Universitätsstr. 1, 40225 Düsseldorf, Germany*

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ABSTRACT

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

1. Introduction

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

Evidence for sensorimotor involvement in action-related language processing stems from behavioural, neuroimaging, electrophysiological, neuropsychological and brain stimulation studies. For instance, verbs referring to actions performed with the mouth (*to lick*), the hands (*to pick*) or the feet (*to kick*) were shown to elicit blood-oxygenation-level-dependent (BOLD) activity in cortical areas also involved in executing actions with the mouth, hands, and feet (Hauk & Pulvermüller, 2004). Similar results of somatotopy in bilateral or left-lateralized premotor and primary motor areas have been reported using functional magnetic resonance imaging (fMRI) both for single action verbs (Rüschemeyer, Brass, & Friederici, 2007; Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008; Willems, Toni, Hagoort, & Casasanto, 2010b; Hauk & Pulvermüller, 2011) and phrases or sentences (Tettamanti et al., 2005; Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Boulenger, Hauk, & Pulvermüller, 2009). Language processing was shown to occur in cortical regions representing action execution (Hauk & Pulvermüller, 2004, 2011; Boulenger et al., 2009) or observation (Aziz-Zadeh et al., 2006), despite some concerns about the precise location and functional overlap of motor and language functions (Postle, McMahon, Ashton, Meredith, & Zubicaray, 2008).

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

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* Corresponding author. Address: Anne Klepp, Institut für Klinische Neurowissenschaften und Medizinische Psychologie, Heinrich-Heine-Universität, Universitätsstr. 1, 23.02.03.41, 40225 Düsseldorf, Germany.
E-mail address: anne.klepp@uni-duesseldorf.de (A. Klepp).

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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.

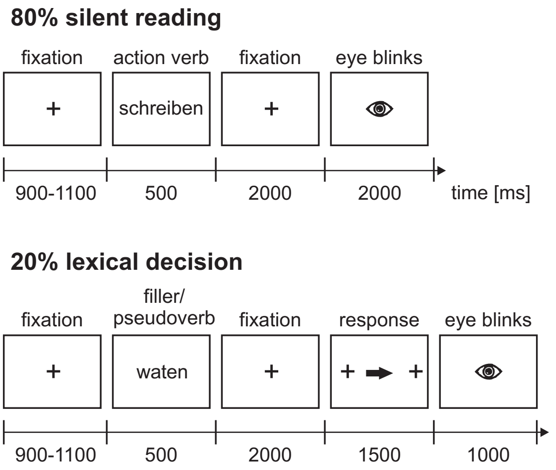

Fig. 1. Experimental procedure for the language paradigm. Until the response prompt stimulus, presentation times were identical for silent reading and lexical decision trials.

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 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.

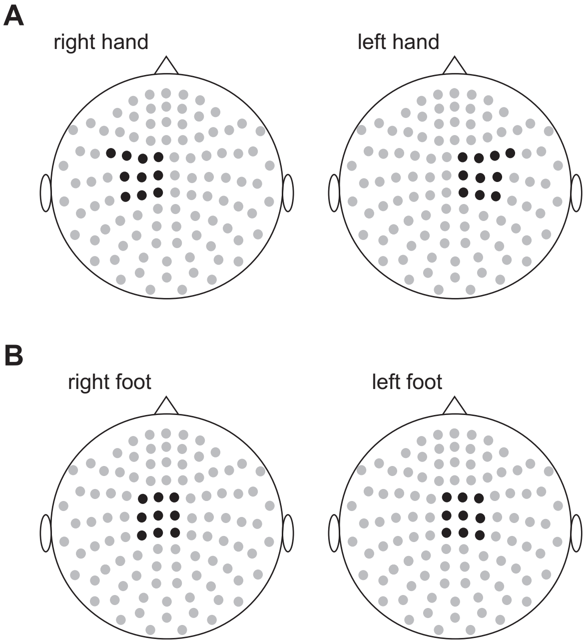

Fig. 2. MEG channel selection for dipole fitting of MF and MEF. Selected channels are indicated by a black dot, other channels are shown in grey. Each dot represents one pair of orthogonal gradiometer sensors, i.e., 102 channel locations are depicted for the 204 gradiometers. (A) Hand movements (B) foot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

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

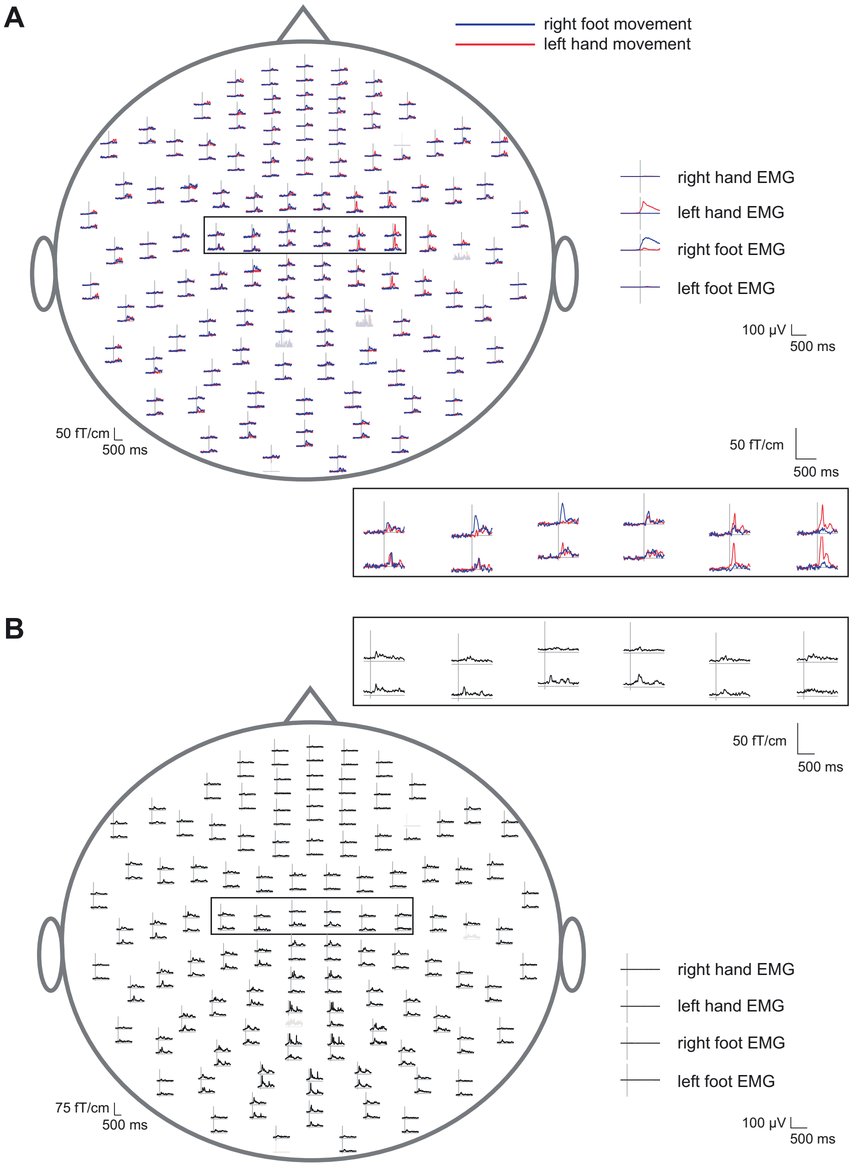

Fig. 3. Grandaverage root mean square evoked responses during the movement task and the verb paradigm in the 204 planar gradiometers. Top view, left is left, anterior is up. Bad channels are semi-transparently masked. (A) Movement task. An enlarged selection of sensorimotor channels is shown separately 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 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.

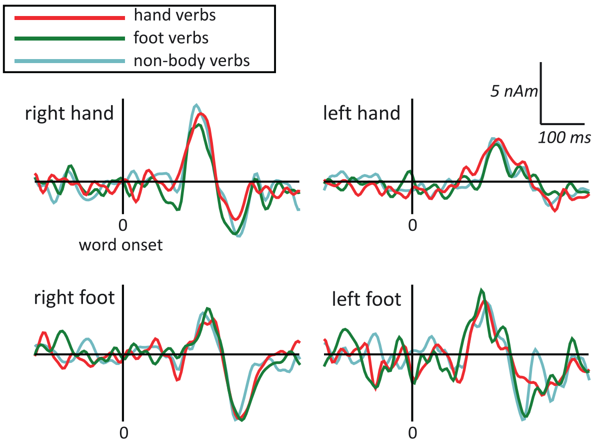

Fig. 4. Grandaverage time course of MF dipole activation during the verb processing paradigm for the three conditions (hand, foot, non-body verbs). Data from all subjects for which MF could be fitted for the respective effector are included. Baseline correction was applied from −200 ms until word onset.

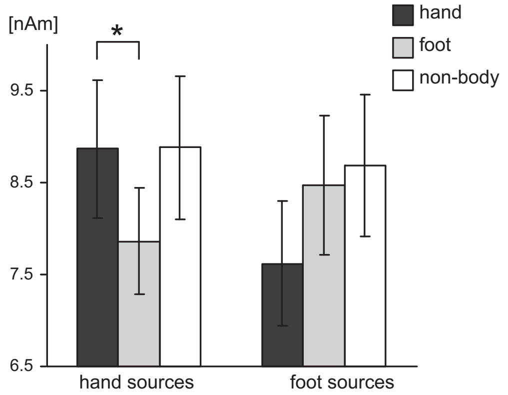

Fig. 5. Mean peak amplitudes for MF hand and foot sources in the three verb conditions, averaged across hemispheres. Error bars show SEM. * = $p < .05$

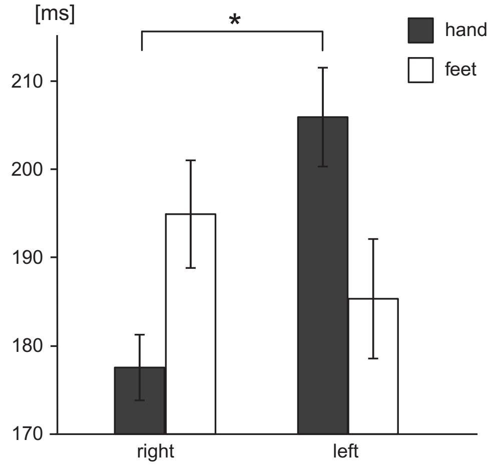

Fig. 6. Peak latencies for hand and foot MF sources, averaged across the three verb conditions. Note that right limb sources correspond to left hemispheric ECDs and vice versa. * = $p < .008$ (according to Bonferroni correction).

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

Acknowledgments

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Appendix A. stimulus characteristics

Table 1.

Table 1
Stimuli in each of the three experimental conditions.

Condition	German	English	Frequency	Familiarity	Imageability	Letters
H	angeln	to fish	3.37	3.50	15	6
H	basteln	to tinker	3.67	3.60	13	7
H	binden	to tie	3.47	3.50	12	6
H	boxen	to box	3.40	3.47	12	5
H	buddeln	to dig	3.07	3.40	16	7
H	falten	to fold	3.50	3.73	15	6
H	fassen	to grab	3.57	3.43	11	6
H	feilen	to file	3.17	3.47	14	6
H	flechten	to plait	3.00	3.50	16	8
H	fuchteln	to wave	2.76	3.10	18	8
H	greifen	to grasp	3.90	3.90	10	7
H	häkeln	to crochet	2.97	3.33	19	6
H	kehren	to sweep	3.13	3.40	12	6
H	klatschen	to clap	3.77	3.77	13	9
H	kneifen	to pinch	3.47	3.57	16	7
H	kneten	to knead	3.47	3.70	17	6
H	knoten	to knot	3.23	3.57	19	6
H	melken	to milk	3.20	3.37	16	6
H	nähen	to sew	3.47	3.70	15	5
H	paddeln	to paddle	3.10	3.60	16	7
H	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

(*continued on next page*)

Table 1 (*continued*)

Condition	German	English	Frequency	Familiarity	Imageability	Letters
F	kicken	to kick	2.97	3.33	14	6
F	knien	to kneel	3.40	3.72	16	5
F	latschen	to traipse	2.80	3.13	18	8
F	laufen	to run	4.00	3.90	8	6
F	radeln	to cycle	3.57	3.70	15	6
F	rasen	to rush	3.50	3.24	13	5
F	rennen	to run	3.90	4.00	12	6
F	scharren	to scrabble	2.40	2.93	16	8
F	schleichen	to creep	3.53	3.57	14	10
F	schlendern	to saunter	3.13	3.23	14	10
F	schlittern	to slither	2.73	3.27	16	10
F	schlurfen	to scuffle	2.80	3.20	17	9
F	schreiten	to stride	2.90	2.87	14	9
F	skaten	to skate	2.97	3.47	17	6
F	springen	to jump	3.97	3.90	11	8
F	sprinten	to sprint	3.30	3.60	16	8
F	spurten	to spurt	2.67	2.97	17	7
F	stampfen	to stomp	3.10	3.30	15	8
F	stapfen	to trudge	2.93	3.00	16	7
F	stehen	to stand	3.93	3.90	6	6
F	steigen	to climb	3.60	3.33	8	7
F	steppen	to tap-dance	2.47	2.73	17	7
F	stolpern	to stumble	3.60	3.67	14	8
F	strampeln	to struggle	3.07	3.40	16	9
F	stürmen	to storm	3.23	2.93	12	7
F	tänzeln	to prance	2.83	3.03	17	7
F	torkeln	to stagger	2.70	3.43	17	7
F	trampeln	to trample	3.17	3.47	16	8
F	treten	to kick	3.87	3.77	9	6
F	trotten	to trot	2.47	2.87	16	7
F	wandern	to hike	3.73	3.90	12	7
F	watscheln	to waddle	2.47	2.87	17	9
F	wippen	to seesaw	3	3.23	16	6
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**

References

Aravena, P., Delevoye-Turrell, Y., Deprez, V., Cheylus, A., Paulignan, Y., Frak, V., et al. (2012). Grip force reveals the context sensitivity of language-induced motor activity during "action words" processing: Evidence from sentential negation. *PLoS One, 7*, e50287.

Aziz-Zadeh, L., & Damasio, A. (2008). Embodied semantics for actions: Findings from functional brain imaging. *Journal of Physiology Paris, 102*, 35–39.

Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology, 16*, 1818–1823.

Bak, T. H., O'Donovan, D. G., Xuereb, J. H., Boniface, S., & Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease-dementia-aphasia syndrome. *Brain, 124*, 103–120.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review Psychology, 59*, 617–645.

Barsalou, L. W., Santos, A., Simmons, W. K., & Wilson, C. D. (2008). Language and simulation in conceptual processing. In M. d. Vega, A. Glenberg, & A. Graesser (Eds.), *Symbols and embodiment debates on meaning and cognition* (pp. 245–284). Oxford University Press.

Biemann, C., Heyer, G., Quasthoff, U., & Richter, M. (2007). The Leipzig Corpora Collection – Monolingual corpora of standard size. In *Proceedings of corpus linguistics 2007*. Birmingham, UK.

Biermann-Ruben, K., Miller, A., Franzkowiak, S., Finis, J., Pollok, B., Wach, C., et al. (2012). Increased sensory feedback in Tourette syndrome. *Neuroimage, 63*, 119–125.

Binder, J. R., Westbury, C. F., McKiernan, K. A., Possing, E. T., & Medler, D. A. (2005). Distinct brain systems for processing concrete and abstract concepts. *Journal of Cognitive Neuroscience, 17*, 905–917.

Boulenger, V., Hauk, O., & Pulvermüller, F. (2009). Grasping ideas with the motor system: Semantic somatotopy in idiom comprehension. *Cerebral Cortex, 19*, 1905–1914.

Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M., & Nazir, T. A. (2006). Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *Journal of Cognitive Neuroscience, 18*, 1607–1615.

Boulenger, V., Shtyrov, Y., & Pulvermüller, F. (2012). When do you grasp the idea? MEG evidence for instantaneous idiom understanding. *Neuroimage, 59*, 3502–3513.

Boulenger, V., Silber, B. Y., Roy, A. C., Paulignan, Y., Jeannerod, M., & Nazir, T. A. (2008). Subliminal display of action words interferes with motor planning: A combined EEG and kinematic study. *Journal of Physiology Paris, 102*, 130–136.

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Brain Research, Cognitive Brain Research, 24*, 355–363.

Carota, F., Moseley, R., & Pulvermüller, F. (2012). Body-part-specific representations of semantic noun categories. *Journal of Cognitive Neuroscience, 24*, 1492–1509.

Cheyne, D., & Weinberg, H. (1989). Neuromagnetic fields accompanying unilateral finger movements: Pre-movement and movement-evoked fields. *Experimental Brain Research, 78*, 604–612.

van Dam, W. O., Rüschemeyer, S. A., & Bekkering, H. (2010). How specifically are action verbs represented in the neural motor system: An fMRI study. *Neuroimage, 53*, 1318–1325.

Desai, R. H., Binder, J. R., Conant, L. L., & Seidenberg, M. S. (2010). Activation of sensory-motor areas in sentence comprehension. *Cerebral Cortex, 20*, 468–478.

D'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. J., et al. (1997). A functional MRI study of mental image generation. *Neuropsychologia, 35*, 725–730.

Ehrenstein, W. H., & Arnold-Schulz-Gahmen, B. E. (1997). Auge, Ohr, Hand und Fuß: Bestimmung des individuellen Lateralitätsprofils. Dortmund: Institut für Arbeitsforschung.

Endo, H., Kato, Y., Kizuka, T., Masuda, T., & Takeda, T. (2004). Bilateral cerebral activity for unilateral foot movement revealed by whole-head magnetoencephalography. *Somatosensory Motor Research, 21*, 33–43.

Fernandino, L., Conant, L. L., Binder, J. R., Blindauer, K., Hiner, B., Spangler, K., et al. (2012). Parkinson's disease disrupts both automatic and controlled processing of action verbs. *Brain and Language, 51*, 1510–1517.

Friederici, A. D., Opitz, B., & Cramon, D. Y. v. (2000). Segregating semantic and syntactic aspects of processing in the human brain: An fMRI investigation of different word types. *Cerebral Cortex, 10*, 698–705.

Gallese, V. (2008). Mirror neurons and the social nature of language: The neural exploitation hypothesis. *Society for Neuroscience, 3*, 317–333.

Gallese, V., & Lakoff, G. (2005). The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology, 22*, 455–479.

Glover, S., Rosenbaum, D. A., Graham, J., & Dixon, P. (2004). Grasping the meaning of words. *Experimental Brain Research, 154*, 103–108.

Hämäläinen, M., Hari, R., Ilmoniemi, R., Knuutila, J., & Lounasmaa, O. (1993). Magnetoencephalography – Theory, instrumentation, and applications to noninvasive studies of the working human brain. *Reviews of Modern Physics, 65*, 413–497.

Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron, 41*, 301–307.

Hauk, O., & Pulvermüller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping, 21*, 191–201.

Hauk, O., & Pulvermüller, F. (2011). The lateralization of motor cortex activation to action-words. *Frontiers in Human Neuroscience, 5*, 149.

Herrera, E., Rodríguez-Ferreiro, J., & Cuetos, F. (2012). The effect of motion content in action naming by Parkinson's disease patients. *Cortex, 48*, 900–904.

Kemmerer, D., Castillo, J. G., Talavage, T., Patterson, S., & Wiley, C. (2008). Neuroanatomical distribution of five semantic components of verbs: Evidence from fMRI. *Brain and Language, 107*, 16–43.

Kemmerer, D., & Gonzalez-Castillo, J. (2010). The Two-Level Theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system. *Brain and Language, 112*, 54–76.

Kemmerer, D., Miller, L., Macpherson, M. K., Huber, J., & Tranel, D. (2013). An investigation of semantic similarity judgments about action and non-action verbs in Parkinson's disease: Implications for the Embodied Cognition Framework. *Frontiers in Human Neuroscience, 7*, 146.

Kousta, S.-T., Vigliocco, G., Vinson, D. P., Andrews, M., & Del Campo, E. (2011). The representation of abstract words: Why emotion matters. *Journal of Experimental Psychology – General, 140*, 14–34.

Kristeva, R., Cheyne, D., & Deecke, L. (1991). Neuromagnetic fields accompanying unilateral and bilateral voluntary movements: Topography and analysis of cortical sources. *Electroencephalography and Clinical Neurophysiology, 81*, 284–298.

Kristeva-Feige, R., Walter, H., Lütkenhöner, B., Hampson, S., Ross, B., Knorr, U., et al. (1994). A neuromagnetic study of the functional organization of the sensorimotor cortex. *European Journal of Neuroscience, 6*, 632–639.

Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature, 379*, 649–652.

Moseley, R., Carota, F., Hauk, O., Mohr, B., & Pulvermüller, F. (2012). A role for the motor system in binding abstract emotional meaning. *Cerebral Cortex, 22*, 1634–1647.

Nazir, T. A., Boulenger, V., Roy, A., Silber, B., Jeannerod, M., & Paulignan, Y. (2008). Language-induced motor perturbations during the execution of a reaching movement. *Quarterly Journal of Experimental Psychology (Hove), 61*, 933–943.

Oishi, M., Kameyama, S., Fukuda, M., Tsuchiya, K., & Kondo, T. (2004). Cortical activation in area 3b related to finger movement: An MEG study. *Neuroreport, 15*, 57–62.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97–113.

Postle, N., Ashton, R., McFarland, K., & Zubicaray, G. I. d. (2013). No specific role for the manual motor system in processing the meanings of words related to the hand. *Frontiers in Human Neuroscience, 7*, 11.

Postle, N., McMahon, K. L., Ashton, R., Meredith, M., & Zubicaray, G. I. d. (2008). Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. *Neuroimage, 43*, 634–644.

Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience, 6*, 576–582.

Pulvermüller, F., Härle, M., & Hummel, F. (2000). Neurophysiological distinction of verb categories. *Neuroreport, 11*, 2789–2793.

Pulvermüller, F., Härle, M., & Hummel, F. (2001). Walking or talking? Behavioral and neurophysiological correlates of action verb processing. *Brain and Language, 78*, 143–168.

Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005a). Functional links between motor and language systems. *European Journal of Neuroscience, 21*, 793–797.

Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005b). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience, 17*, 884–892.

Repetto, C., Colombo, B., Cipresso, P., & Riva, G. (2013). The effects of rTMS over the primary motor cortex: The link between action and language. *Neuropsychologia, 51*, 8–13.

Rodríguez-Ferreiro, J., Gennari, S. P., Davies, R., & Cuetos, F. (2011). Neural correlates of abstract verb processing. *Journal of Cognitive Neuroscience, 23*, 106–118.

Rüschemeyer, S.-A., Brass, M., & Friederici, A. D. (2007). Comprehending prehending: Neural correlates of processing verbs with motor stems. *Journal of Cognitive Neuroscience, 19*, 855–865.

Rüschemeyer, S.-A., Lindemann, O., van Elk, M., & Bekkering, H. (2009). Embodied cognition: The interplay between automatic resonance and selection-for-action mechanisms. *European Journal of Social Psychology, 39*, 1180–1187.

Salmelin, R., Schnitzler, A., Schmitz, F., & Freund, H. J. (2000). Single word reading in developmental stutterers and fluent speakers. *Brain, 123*(Pt 6), 1184–1202.

Schuil, K. D. I., Smits, M., & Zwaan, R. A. (2013). Sentential context modulates the involvement of the motor cortex in action language processing: An fMRI study. *Frontiers in Human Neuroscience, 7*, 100.

Shebani, Z., & Pulvermüller, F. (2013). Moving the hands and feet specifically impairs working memory for arm- and leg-related action words. *Cortex, 49*, 222–231.

Shtyrov, Y., Hauk, O., & Pulvermüller, F. (2004). Distributed neuronal networks for encoding category-specific semantic information: The mismatch negativity to action words. *European Journal of Neuroscience, 19*, 1083–1092.

Simmons, W. K., Hamann, S. B., Harenski, C. L., Hu, X. P., & Barsalou, L. W. (2008). fMRI evidence for word association and situated simulation in conceptual processing. *Journal of Physiology Paris, 102*, 106–119.

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience, 17*, 273–281.

Tomasino, B., Weiss, P. H., & Fink, G. R. (2010). To move or not to move: Imperatives modulate action-related verb processing in the motor system. *Neuroscience, 169*, 246–258.

Uusitalo, M. A., & Ilmoniemi, R. J. (1997). Signal-space projection method for separating MEG or EEG into components. *Medical and Biological Engineering and Computing, 35*, 135–140.

Vigliocco, G., Kousta, S.-T., Della Rosa, P. A., Vinson, D. P., Tettamanti, M., Devlin, J. T., et al. (2013). The neural representation of abstract words: The role of emotion. *Cerebral Cortex*. epub ahead of print, http://dx.doi.org/10.1093/cercor/bht025.

Willems, R. M., Hagoort, P., & Casasanto, D. (2010a). Body-specific representations of action verbs: Neural evidence from right- and left-handers. *Psychological Science, 21*, 67–74.

Willems, R. M., Toni, I., Hagoort, P., & Casasanto, D. (2010b). Neural dissociations between action verb understanding and motor imagery. *Journal of Cognitive Neuroscience, 22*, 2387–2400.

Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: Motor resonance in language comprehension. *Journal of Experimental Psychology – General, 135*, 1–11.

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Appendix 2

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

Valentina Niccolai*, Anne Klepp, Hannah Weissler, Nienke Hoogenboom, Alfons Schnitzler, Katja Biermann-Ruben

Institute for Clinical Neuroscience and Medical Psychology, Medical Faculty, Heinrich Heine University, Düsseldorf, Germany

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.

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* Email: Valentina.Niccolai@hhu.de

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 pseudorandomly 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 magnetometers. 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 toolbox for MEG and EEG analyses [48]. Data from 204 gradiometers 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

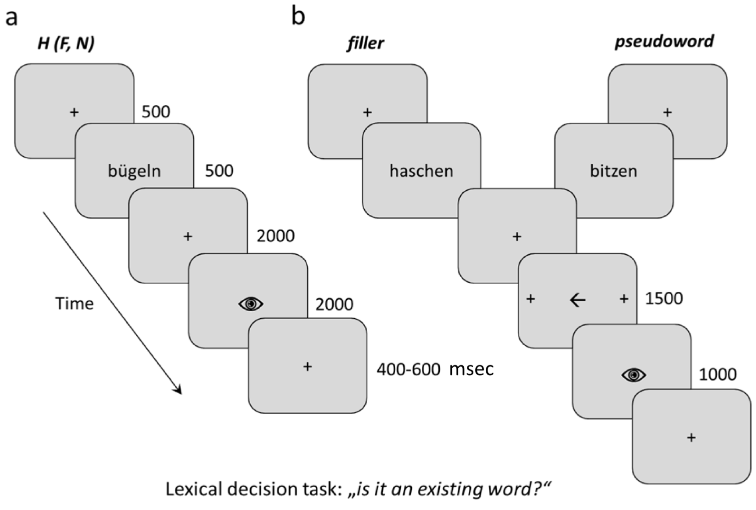

Figure 1. Experimental design. Trials which were not followed by a cue (a) were included in the analysis. The prompt to respond followed fillers and pseudowords (b).
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condition were further segmented into high and low imageable sub-conditions. Data 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

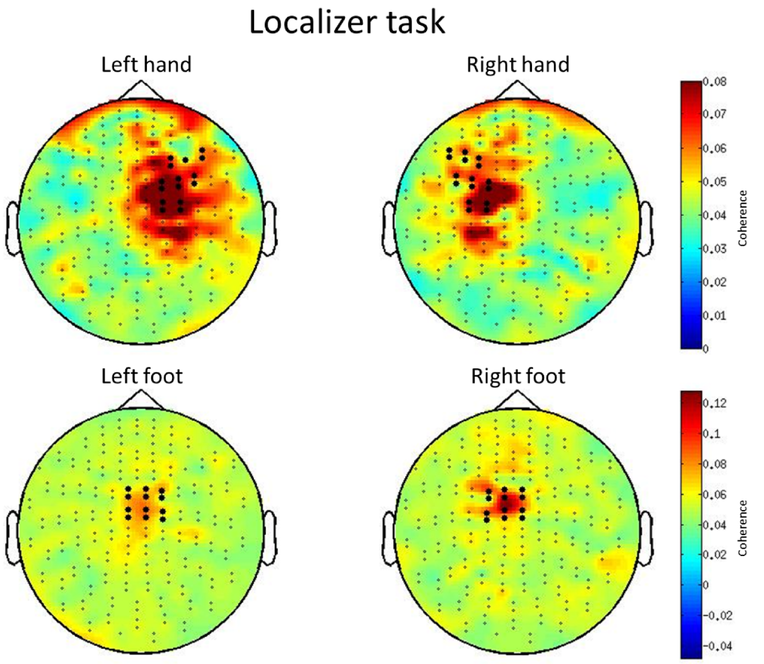

Figure 2. Grand-average of corticomuscular coherence in the beta (15–25 Hz) range related to hands (top) and to feet (bottom) isometric contraction across 15 subjects. Bold points represent gradiometer pairs selected for frequency analysis in the word paradigm.
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right 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

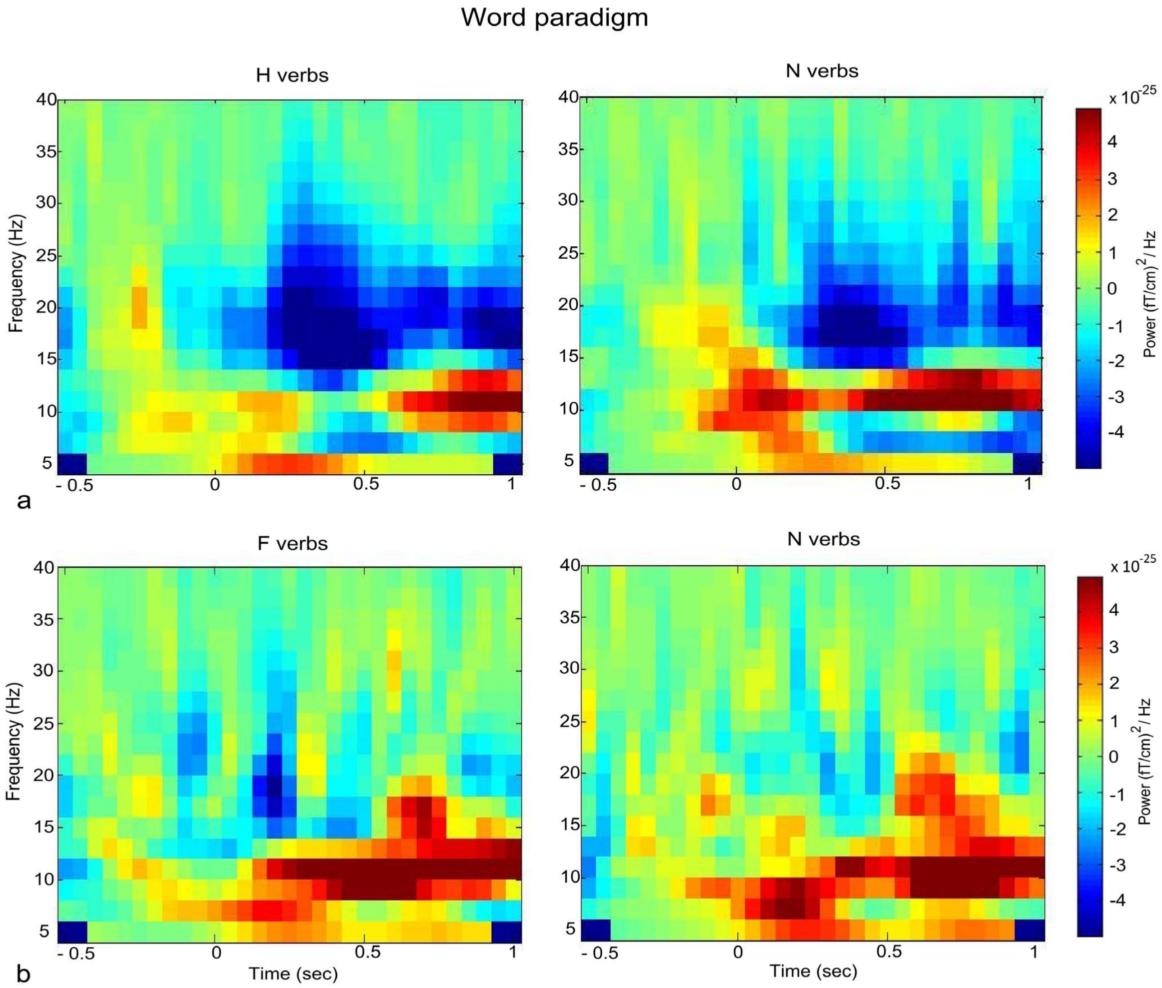

Figure 3. Grand-average of frequency spectra. a) Grand-average of the H (left) and the N (right) condition on the average of the left-hemispheric hand-related sensors selected with the localizer task. b) Grand-average of the F (left) and the N (right) condition on the average of three foot-related sensors 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.

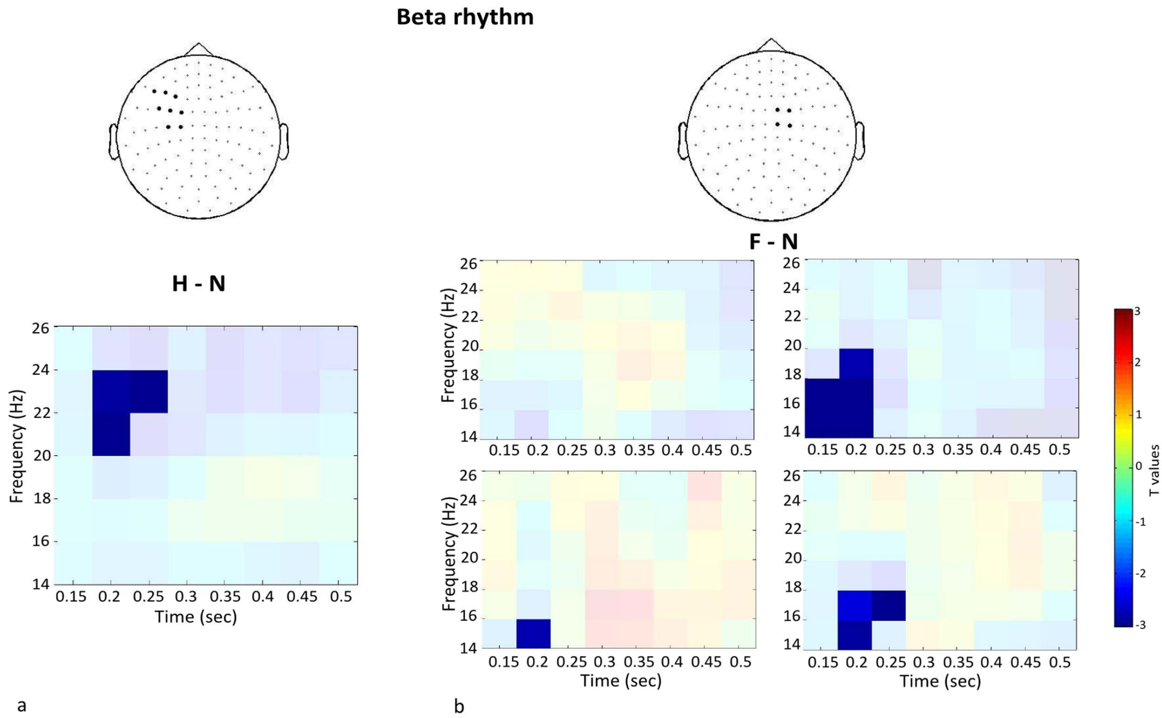

Figure 4. Statistical outcomes for the beta rhythm. a) T-values on a time-frequency map related to the H-N contrast, showing a significant cluster (saturated colours) on the average of the selected left-hemispheric hand-related sensors. b) Time-frequency maps of the F-N contrast showing a significant 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

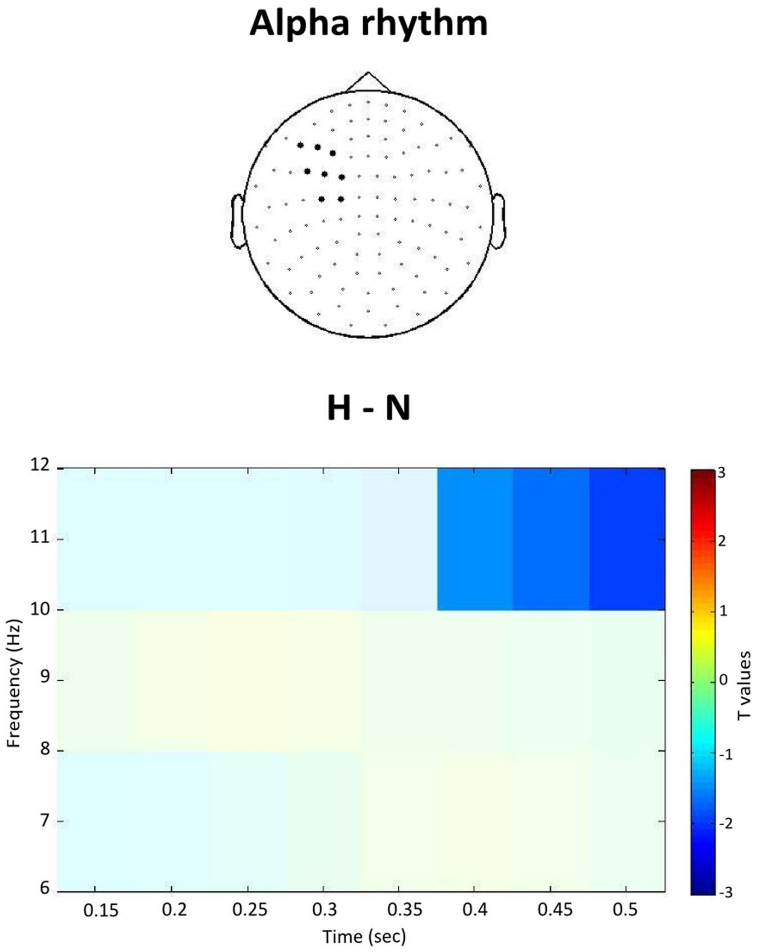

Figure 5. Statistical outcome for the alpha rhythm. T-values on a time-frequency map related to the H-N contrast, showing a significant cluster (saturated colours) on the average of the selected left-hemispheric hand-related sensors.
doi:10.1371/journal.pone.0108059.g005

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)

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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.

References

1. Fodor J (2001) The mind doesn't work that way. The scope and limits of computational psychology. Cambridge, Mass: MIT Press. 126 p.
2. Pylyshyn ZW ((1984)) Computation and cognition. Toward a foundation for cognitive science. Cambridge, Mass: MIT Pr. 292 p.
3. Barsalou LW (2008) Grounded cognition. Annu Rev Psychol 59: 617–645.
4. Lakoff G, Johnson M (1999) Philosophy in the flesh. The embodied mind and its challenge to western thought. New York, NY: Basic Books. 624 p.
5. Pulvermüller F (2005) Brain mechanisms linking language and action. Nat. Rev. Neurosci. 6 (7): 576–582.
6. Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci.2 (9): 661–670.
7. Hebb DO (1949) The organization of behavior. A neuropsycholog. theory. New York: Wiley. 335 p.
8. Pulvermüller F, Lutzenberger W, Preissl H (1999) Nouns and verbs in the intact brain: evidence from event-related potentials and high-frequency cortical responses. Cereb. Cortex 9 (5): 497–506.
9. Corballis MC (2009) Language as gesture. Hum Mov Sci 28 (5): 556–565.
10. Postle N, McMahon KL, Ashton R, Meredith M, Zubicaray GI de (2008) Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. Neuroimage 43 (3): 634–644.
11. Aziz-Zadeh L, Wilson SM, Rizzolatti G, Iacoboni M (2006) Congruent embodied representations for visually presented actions and linguistic phrases describing actions. Curr. Biol. 16 (18): 1818–1823.
12. Boulenger V, Hauk O, Pulvermüller F (2009) Grasping ideas with the motor system: semantic somatotopy in idiom comprehension. Cereb. Cortex 19 (8): 1905–1914.
13. Hauk O, Pulvermüller F (2004) Effects of word length and frequency on the human event-related potential. Clin Neurophysiol 115 (5): 1090–1103.
14. Kemmerer D, Castillo JG, Talavage T, Patterson S, Wiley C (2008) Neuroanatomical distribution of five semantic components of verbs: evidence from fMRI. Brain Lang 107 (1): 16–43.
15. Rüschemeyer S, Brass M, Friederici AD (2007) Comprehending prehending: neural correlates of processing verbs with motor stems. J Cogn Neurosci 19 (5): 855–865.
16. Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, et al. (2005) Listening to action-related sentences activates fronto-parietal motor circuits. J Cogn Neurosci 17 (2): 273–281.
17. Buccino G, Riggio L, Melli G, Binkofski F, Gallese V, et al. (2005) Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. Brain Res Cogn Brain Res 24 (3): 355–363.
18. Pulvermüller F, Hauk O, Nikulin VV, Ilmoniemi RJ (2005) Functional links between motor and language systems. Eur. J. Neurosci. 21 (3): 793–797.
19. Willems RM, Labruna L, D'Esposito M, Ivry R, Casasanto D (2011) A functional role for the motor system in language understanding: evidence from theta-burst transcranial magnetic stimulation. Psychol Sci 22 (7): 849–854.
20. Perrin F, Pernier J, Bertrand O, Echallier JF (1989) Spherical splines for scalp potential and current density mapping. Electroencephalogr Clin Neurophysiol 72 (2): 184–187.

21. Babiloni C, Babiloni F, Carducci F, Cincotti F, Cocozza G, et al. (2002) Human cortical electroencephalography (EEG) rhythms during the observation of simple aimless movements: a high-resolution EEG study. Neuroimage 17 (2): 559–572.
22. Hari R, Forss N, Avikainen S, Kirveskari E, Salenius S, et al. (1998) Activation of human primary motor cortex during action observation: a neuromagnetic study. Proc. Natl. Acad. Sci. U.S.A. 95 (25): 15061–15065.
23. Koelewijn T, van Schie HT, Bekkering H, Oostenveld R, Jensen O (2008) Motor-cortical beta oscillations are modulated by correctness of observed action. Neuroimage 40 (2): 767–775.
24. Burianová H, Marstaller L, Sowman P, Tesan G, Rich AN, et al. (2013) Multimodal functional imaging of motor imagery using a novel paradigm. Neuroimage 71: 50–58.
25. Lange FP de, Jensen O, Bauer M, Toni I (2008) Interactions between posterior gamma and frontal alpha/beta oscillations during imagined actions. Front Hum Neurosci 2: 7.
26. Nakagawa K, Aokage Y, Fukuri T, Kawahara Y, Hashizume A, et al. (2011) Neuromagnetic beta oscillation changes during motor imagery and motor execution of skilled movements. Neuroreport 22 (5): 217–222.
27. Pfurtscheller G, Brunner C, Schlögl A, Lopes da Silva FH (2006) Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. Neuroimage 31 (1): 153–159.
28. Schnitzler A, Salenius S, Salmelin R, Jousmäki V, Hari R (1997) Involvement of primary motor cortex in motor imagery: a neuromagnetic study. Neuroimage 6 (3): 201–208.
29. Canolty RT, Soltani M, Dalal SS, Edwards E, Dronkers NF, et al. (2007) Spatiotemporal dynamics of word processing in the human brain. Front Neurosci 1 (1): 185–196.
30. Moreno I, Vega M de, León I (2013) Understanding action language modulates oscillatory mu and beta rhythms in the same way as observing actions. Brain Cogn 82 (3): 236–242.
31. van Elk M, van Schie HT, Zwaan RA, Bekkering H (2010) The functional role of motor activation in language processing: motor cortical oscillations support lexical-semantic retrieval. Neuroimage 50 (2): 665–677.
32. Doyle LMF, Yarrow K, Brown P (2005) Lateralization of event-related beta desynchronization in the EEG during pre-cued reaction time tasks. Clin Neurophysiol 116 (8): 1879–1888.
33. Pfurtscheller G, Lopes da Silva FH (1999) Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin Neurophysiol 110 (11): 1842–1857.
34. Crone NE, Miglioretti DL, Gordon B, Sieracki JM, Wilson MT, et al. (1998) Functional mapping of human sensorimotor cortex with electrocorticographic spectral analysis. I. Alpha and beta event-related desynchronization. Brain 121 (Pt 12): 2271–2299.
35. Tecchio F, Zappasodi F, Porcaro C, Barbati G, Assenza G, et al. (2008) High-gamma band activity of primary hand cortical areas: a sensorimotor feedback efficiency index. Neuroimage 40 (1): 256–264.
36. Höller Y, Bergmann J, Kronbichler M, Crone JS, Schmid EV, et al. (2013) Real movement vs. motor imagery in healthy subjects. Int J Psychophysiol 87 (1): 35–41.
37. Pfurtscheller G, Neuper C, Krausz G (2000) Functional dissociation of lower and upper frequency mu rhythms in relation to voluntary limb movement. Clin Neurophysiol 111 (10): 1873–1879.
38. Fisher AE, Furlong PL, Seri S, Adjamian P, Witton C, et al. (2008) Interhemispheric differences of spectral power in expressive language: a MEG study with clinical applications. Int J Psychophysiol 68 (2): 111–122.
39. Alemanno F, Houdayer E, Cursi M, Velikova S, Tettamanti M, et al. (2012) Action-related semantic content and negation polarity modulate motor areas during sentence reading: an event-related desynchronization study. Brain Res. 1484: 39–49.
40. Ehrenstein WH, Arnold-Schulz-Gahmen BE (1997) Auge, Ohr, Hand und Fuß: Bestimmung des individuellen Lateralitätsprofils [Interaktiver Fragebogen]. Available: http://www.ifado.de/forschung_praxis/umsetzung/lateralitaetsfragebogen/fragebogen/index.php. Accessed 2011 Nov 30.
41. Mima T, Hallett M (1999) Corticomuscular coherence: a review. J Clin Neurophysiol 16 (6): 501–511.
42. Pulvermüller F, Härle M, Hummel F (2001) Walking or talking? Behavioral and neurophysiological correlates of action verb processing. Brain Lang 78 (2): 143–168.
43. Pulvermüller F, Shtyrov Y, Ilmoniemi R (2005) Brain signatures of meaning access in action word recognition. J Cogn Neurosci 17 (6): 884–892.
44. Shtyrov Y, Hauk O, Pulvermüller F (2004) Distributed neuronal networks for encoding category-specific semantic information: the mismatch negativity to action words. Eur. J. Neurosci. 19 (4): 1083–1092.
45. Meteyard L, Cuadrado SR, Bahrami B, Vigliocco G (2012) Coming of age: a review of embodiment and the neuroscience of semantics. Cortex 48 (7): 788–804.
46. Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9 (1): 97–113.
47. Biemann C, Heyer G, Quasthoff U, Richter M (2007) The Leipzig Corpora Collection – Monolingual corpora of standard size. Proceedings of Corpus Linguistics 2007. Available: http://www.birmingham.ac.uk/research/activity/corpus/publications/conference-archives/2007-birmingham.aspx. Accessed 2011 Sep 15.
48. Oostenveld R, Fries P, Maris E, Schoffelen J (2011) FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput Intell Neurosci 2011: 156869.
49. Jung TP, Makeig S, Humphries C, Lee TW, McKeown MJ, et al. (2000) Removing electroencephalographic artifacts by blind source separation. Psychophysiology 37 (2): 163–178.
50. Hoogenboom N, Schoffelen J, Oostenveld R, Fries P (2010) Visually induced gamma-band activity predicts speed of change detection in humans. Neuroimage 51 (3): 1162–1167.
51. Lange J, Halacz J, van Dijk H, Kahlbrock N, Schnitzler A (2012) Fluctuations of Prestimulus Oscillatory Power Predict Subjective Perception of Tactile Simultaneity. Cerebral Cortex 22 (11): 2564–2574.
52. May ES, Butz M, Kahlbrock N, Hoogenboom N, Brenner M, et al. (2012) Pre- and post-stimulus alpha activity shows differential modulation with spatial attention during the processing of pain. NeuroImage 62 (3): 1965–1974.
53. Maris E, Oostenveld R (2007) Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods 164 (1): 177–190.
54. Formaggio E, Storti SF, Avesani M, Cerini R, Milanese F, et al. (2008) EEG and FMRI coregistration to investigate the cortical oscillatory activities during finger movement. Brain Topogr 21 (2): 100–111.
55. Formaggio E, Storti SF, Cerini R, Fiaschi A, Manganotti P (2010) Brain oscillatory activity during motor imagery in EEG-fMRI coregistration. Magn Reson Imaging 28 (10): 1403–1412.
56. Singh KD, Barnes GR, Hillebrand A, Forde EME, Williams AL (2002) Task-related changes in cortical synchronization are spatially coincident with the hemodynamic response. Neuroimage 16 (1): 103–114.
57. Repetto C, Colombo B, Cipresso P, Riva G (2013) The effects of rTMS over the primary motor cortex: The link between action and language. Neuropsychologia 51 (1): 8–13.
58. Kemmerer D, Rudrauf D, Manzel K, Tranel D (2012) Behavioral patterns and lesion sites associated with impaired processing of lexical and conceptual knowledge of actions. Cortex 48 (7): 826–848.
59. Neininger B, Pulvermüller F (2003) Word-category specific deficits after lesions in the right hemisphere. Neuropsychologia 41 (1): 53–70.
60. Salmelin R, Schnitzler A, Schmitz F, Freund HJ (2000) Single word reading in developmental stutterers and fluent speakers. Brain 123 (Pt 6): 1184–1202.
61. Willems RM, Hagoort P, Casasanto D (2010) Body-specific representations of action verbs: neural evidence from right- and left-handers. Psychol Sci 21 (1): 67–74.
62. Knecht S, Dräger B, Deppe M, Bobe L, Lohmann H, et al. (2000) Handedness and hemispheric language dominance in healthy humans. Brain 123 Pt 12: 2512–2518.
63. Vingerhoets G, Alderweireldt A, Vandemaele P, Cai Q, van der Haegen L, et al. (2013) Praxis and language are linked: Evidence from co-lateralization in individuals with atypical language dominance. Cortex 49 (1): 172–183.
64. Hirata M, Kato A, Taniguchi M, Saitoh Y, Ninomiya H, et al. (2004) Determination of language dominance with synthetic aperture magnetometry: comparison with the Wada test. Neuroimage 23 (1): 46–53.
65. Barsalou LW (1999) Perceptual symbol systems. Behav Brain Sci 22 (4): 577–609; discussion 610–60.
66. Vigliocco G, Warren J, Siri S, Arciuli J, Scott S, et al. (2006) The role of semantics and grammatical class in the neural representation of words. Cereb. Cortex 16 (12): 1790–1796.
67. Sakreida K, Scorolli C, Menz MM, Heim S, Borghi AM, et al. (2013) Are abstract action words embodied? An fMRI investigation at the interface between language and motor cognition. Front Hum Neurosci 7: 125.
68. Boulenger V, Shtyrov Y, Pulvermüller F (2012) When do you grasp the idea? MEG evidence for instantaneous idiom understanding. Neuroimage 59 (4): 3502–3513.
69. Desai RH, Binder JR, Conant LL, Mano QR, Seidenberg MS (2011) The neural career of sensory-motor metaphors. J Cogn Neurosci 23 (9): 2376–2386.
70. Glenberg AM, Sato M, Cattaneo L (2008) Use-induced motor plasticity affects the processing of abstract and concrete language. Curr. Biol. 18 (7): R290–1.
71. Zubicaray G de, Arciuli J, McMahon K (2013) Putting an "end" to the motor cortex representations of action words. J Cogn Neurosci 25 (11): 1957–1974.
72. Pfurtscheller G, Neuper C, Andrew C, Edlinger G (1997) Foot and hand area mu rhythms. Int J Psychophysiol 26 (1–3): 121–135.
73. Gross J, Tass PA, Salenius S, Hari R, Freund HJ, et al. (2000) Cortico-muscular synchronization during isometric muscle contraction in humans as revealed by magnetoencephalography. J. Physiol. (Lond.) 527 Pt 3: 623–631.
74. Hari R, Salmelin R, Mäkelä JP, Salenius S, Helle M (1997) Magnetoencephalographic cortical rhythms. Int J Psychophysiol 26 (1–3): 51–62.
75. Grabner RH, Brunner C, Leeb R, Neuper C, Pfurtscheller G (2007) Event-related EEG theta and alpha band oscillatory responses during language translation. Brain Res. Bull. 72 (1): 57–65.

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Appendix 3

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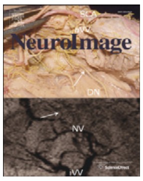

Language–motor interference reflected in MEG beta oscillations

Anne Klepp [a],*, Valentina Niccolai [a], Giovanni Buccino [b,c], Alfons Schnitzler [a], Katja Biermann-Ruben [a]

[a] *Institute of Clinical Neuroscience and Medical Psychology, Medical Faculty, Heinrich Heine University, Universitätsstr. 1, 40225 Düsseldorf, Germany*
[b] *Department of Medical and Surgical Science, University Magna Graecia, Catanzaro, Italy*
[c] *IRCCS Neuromed, Pozzilli, Is, Italy*

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ABSTRACT

The involvement of the brain's motor system in action-related language processing can lead to overt interference with simultaneous action execution. The aim of the current study was to find evidence for this behavioural interference effect and to investigate its neurophysiological correlates using oscillatory MEG analysis. Subjects performed a semantic decision task on single action verbs, describing actions executed with the hands or the feet, and abstract verbs. Right hand button press responses were given for concrete verbs only. Therefore, longer response latencies for hand compared to foot verbs should reflect interference. We found interference effects to depend on verb imageability: overall response latencies for hand verbs did not differ significantly from foot verbs. However, imageability interacted with effector: while response latencies to hand and foot verbs with low imageability were equally fast, those for highly imageable hand verbs were longer than for highly imageable foot verbs. The difference is reflected in motor-related MEG beta band power suppression, which was weaker for highly imageable hand verbs compared with highly imageable foot verbs. This provides a putative neuronal mechanism for language–motor interference where the involvement of cortical hand motor areas in hand verb processing interacts with the typical beta suppression seen before movements. We found that the facilitatory effect of higher imageability on action verb processing time is perturbed when verb and motor response relate to the same body part. Importantly, this effect is accompanied by neurophysiological effects in beta band oscillations. The attenuated power suppression around the time of movement, reflecting decreased cortical excitability, seems to result from motor simulation during action-related language processing. This is in line with embodied cognition theories.

Introduction

A major claim of embodied cognition theories (Barsalou, 2008; Pulvermüller, 2005) is that language processing and motor behaviour can interact with each other when the motor system is involved in the processing of action-related language such as action verbs or sentences. Evidence for language–motor interaction was found in a range of behavioural experiments (Bergen et al., 2010; Boulenger et al., 2006; Hirschfeld and Zwitserlood, 2012; Glenberg and Kaschak, 2002); as well as neurophysiological experiments (Buccino et al., 2005; Willems et al., 2011). Language processing can influence motor behaviour kinematics (Dalla Volta et al., 2009; Mirabella et al., 2012; Nazir et al., 2008) or reaction times (Liepelt et al., 2012; Buccino et al., 2005). Generally, the interaction between language and motor tasks can either produce interference or facilitation, depending on the respective task and situational factors such as stimulus timing or stimulus set (Paulus et al., 2009; Chersi et al., 2010; Diefenbach et al., 2013; de Vega et al., 2013). It can also be reversed, with action execution influencing verbal processing (Liepelt et al., 2012; Shebani and Pulvermüller, 2013). Sato et al. (2008) found an interference effect reflected in longer reaction times following semantic decisions on hand verbs than on foot verbs. No interference was observed when using a lexical decision rather than a semantic task (Sato et al., 2008).

The current study used a similar paradigm to investigate language–motor interference in a larger set of German action verbs. In addition to the replication of behavioural effects the focus of the current study was on identifying its neurophysiological correlates using MEG oscillations in the beta band (15–25 Hz). This frequency band of interest was chosen due to its relevance for the sensorimotor system and motor preparation processes (Pfurtscheller and Lopes da Silva, 1999; Engel and Fries, 2010). For instance, beta band oscillations are the predominant rhythm originating in the motor cortex with a typical pattern of suppression and rebound observed during movement (Pfurtscheller and Lopes da Silva, 1999; Hari et al., 1998). Beta suppression, or desynchronization, starts several hundred milliseconds before movement onset in self-paced or externally cued movements and becomes maximal around the time of movement execution. The suppression is then

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* Corresponding author at: Institut für Klinische Neurowissenschaften und Medizinische Psychologie, Heinrich-Heine-Universität, Universitätsstr. 1, 23.02.03.41, 40225 Düsseldorf, Germany.
E-mail address: anne.klepp@uni-duesseldorf.de (A. Klepp).

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followed by a distinct increase in beta power as a rebound of beta synchronization (Pfurtscheller and Lopes da Silva, 1999; Koelewijn et al., 2008; Leocani et al., 2001). Beta band modulations have also been described during movement observation (Moreno et al., 2013; Hari et al., 1998; Koelewijn et al., 2008) and motor imagery (Schnitzler et al., 1997; de Lange et al., 2008; Brinkman et al., 2014). A putative functional role for beta band effects originating in the sensorimotor cortex is also observed for action-related language processing (van Elk et al., 2010; Moreno et al., 2013; Vukovic and Shtyrov, 2014), while beta oscillations are also involved in language processing in the classical temporal and frontal language areas (Weiss and Mueller, 2012; Wang et al., 2012). Taken together, the role of beta oscillations in embodied language processing makes it a feasible candidate for a functional mechanism of language–motor interference. Similarly, alpha band (8–13 Hz) oscillations have been associated with action execution (Salmelin et al., 1995; Sebastiani et al., 2014), observation (Caetano et al., 2007; Avanzini et al., 2012), motor imagery (Pfurtscheller et al., 2006; de Lange et al., 2008), spoken language processing (Strauß et al., 2014), and action language processing (Alemanno et al., 2012; Fargier et al., 2012). Since alpha band oscillations may be more related to sensory than motor processing (Salmelin et al., 1995; Brinkman et al., 2014; Sebastiani et al., 2014; Coll et al., 2015), the focus in the current study is on the beta band, but alpha oscillations are also investigated.

We expected to find reaction time differences in semantic decisions on hand and foot action verbs depending on verb effector. Since responses were given using the hand, reaction times for hand verbs were hypothesized to be longer than for foot verbs in this paradigm adapted from Sato et al. (2008). The conditions with behavioural reaction time differences were compared using MEG oscillatory analyses. To control for a possible influence of the imageability of verbs, the level of imageability, which had previously been assessed in rating studies, was included in the analysis as a separate factor. In the presence of the speeded reaction time task we did not expect to see subtle oscillatory modulations in the alpha and beta band related to verbal processing in isolation (compare van Elk et al., 2010; Moreno et al., 2013; Niccolai et al., 2014). Rather, our design aimed at identifying the interaction of verb processing with the strong sensorimotor rhythms during response preparation and execution, mainly in the beta band. Nevertheless, separate stimulus-locked and response-locked analyses were performed to detect effects temporally related to the verb onset and the response, respectively. This served the purpose of investigating neuronal oscillations more directly associated with semantic verbal processing on the one hand, and differential modulations in the motor response preparation time-course on the other hand, which is where we expected language–motor interference to emerge. In the stimulus-locked analysis we also contrasted hand and abstract verbs to compare the current study to results of early differences between these types of stimuli from event related fields (Pulvermüller et al., 2001; Boulenger et al., 2012) and alpha/beta power modulations (van Elk et al., 2010; Moreno et al., 2013; Vukovic and Shtyrov, 2014; Niccolai et al., 2014). However, a direct comparison with previous results was impeded due to the motor task in the current study, as described above.

Material and methods

Participants

Twenty-four healthy subjects (11 female, mean age = 22.1 years, SD = 1.8) participated in the experiment. Written informed consent was acquired from all participants, who received financial reimbursement for their time. 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). Subjects had normal or corrected-to-normal vision and were native monolingual speakers of German. Formal education in linguistics, neurological or psychiatric disorder and use of medication were exclusion criteria. Moreover, subjects answered a questionnaire to ensure they were right-handed (Oldfield, 1971) and right-footed (Ehrenstein and Arnold-Schulz-Gahmen, 1997). Right-handedness was further assessed using a performance measure (HDT, Steingrüber, 2011) where hand dominance is defined by comparing right hand and left hand performance on three paper–pencil motor tasks. One participant was excluded because he showed no clear hand dominance. Another subject was excluded due to technical failure of the response recording device. High error rates also led to the exclusion of three subjects (with 19.64% missed responses, 45.24% and 27.38% false alarms, respectively). All analyses are reported for the final set of 19 subjects (9 female, mean age = 22.82 years, SD = 3.09). Mean error rates in this final set were 2.94% misses (SD = 2.28%) and 10.34% false alarms (SD = 6.51%).

Stimulus material

The verbal material consisted of 42 German bisyllabic hand action verbs (H), e.g. *greifen* (*to grasp*), 42 foot action verbs (F), e.g. *gehen* (*to walk*), and 42 abstract verbs (A), e.g. *raten* (*to guess*). These sets were the result of a multi-step rating and matching procedure (compare Klepp et al., 2014). While verb frequency was determined using a database (Leipzig Corpora Collection, LCC, Biemann et al., 2007, available at http://wortschatz.uni-leipzig.de), body part relatedness, verb familiarity and imageability were assessed in separate ratings (each n = 30). These verb variables were used to match conditions of 42 verbs per body part category as closely as possible. Note that in a previous study (Klepp et al., 2014) 48 verbs per condition were used, but for the current study we excluded six verbs from the "non-body" category which were nevertheless rated as "concrete" in pre-tests, and accordingly six verbs from the hand and foot set as well. Residual differences between stimulus sets were found in univariate ANOVAs for group means of imageability ($F(2;123) = 247.284$, $p < .001$), frequency ($F(2;123) = 9.215$, $p = .006$) and number of letters ($F(2;123) = 5.175$, $p = .007$), but not familiarity. These were due to the abstract verbs being less imageable, more frequent and shorter. No differences were found using paired t-tests to compare the main experimental conditions of hand and foot verbs (all $p > .283$). Furthermore, stimulus sets for each body part condition were divided into subsets with high and low imageability by a median split. The resulting subsets also did not differ between hand and foot verbs in any variable, as shown by paired t-tests (all $p > .277$). All stimuli are shown in Suppl. Table S1.

Procedure

Participants were comfortably seated in the magnetically shielded room to complete practice runs, after which MEG recording was started for the main experiment.

The experimental procedure is shown in Fig. 1. It was adapted from Sato et al. (2008) with some adjustments in the trial timing due to the MEG setting used in the current study. Presentation 14.9 software (Neurobehavioral Systems, Albany, California, USA) was used for stimulus presentation. Verbs were projected in white letters onto a black background. Participants were asked to fixate the centre of the screen throughout the experiment. Each trial started with the presentation of a red disc, jittered between 200 and 450 ms. Then the verb appeared while the red disc remained on the screen. After 150 ms the disc turned green, acting as a Go signal to indicate that participants were only now allowed to respond, as fast and as accurately as possible. Reaction times are reported in reference to the Go signal and not to the word onset. Participants were instructed to respond only if the verb was a concrete verb and to refrain from responding if an abstract verb had been shown. The concrete verb category was comprised of the hand and foot verbs, but this was not made transparent for the subjects. Manual responses were given using the right index finger on a button box. The trial was terminated either by the response or after 1200 ms if no response had been recorded. In the intertrial interval a black screen was presented

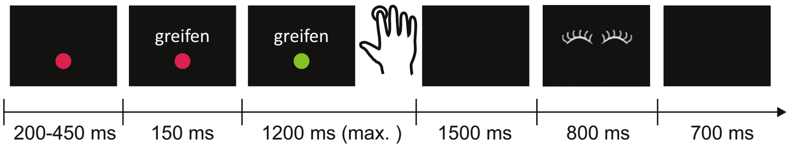

Fig. 1. Experimental procedure. The red cue was followed by a hand, foot, or abstract verb. The cue turning green was the Go signal. Subjects had to respond using their right hand for concrete (i.e., hand and foot) verbs. The eye pictogram determined the time window for eye blinks.

for 1500 ms, followed by the pictogram of closed eyes for 800 ms and a black screen for 700 ms. During the presentation of the eye pictogram eye blinks were permitted.

The experiment included four pseudorandomized blocks of 63 trials lasting about 5 min each and a short practice block with 12 trials (repeated if desired by the participant) at the beginning, containing different stimuli than those used in the main experiment. All verbs were shown once during blocks 1 and 2 and a second time during blocks 3 and 4, with randomized order of presentation in the two halves.

Subsequently, a localizer task was administered. Here, a black screen was shown while participants performed short self-paced button presses with the right index finger about every 4 s for a duration of 5 min.

Note that in the subjective semantic decision task moderately high error rates can be expected since there is no objective correct answer and stimulus categories are based on majority ratings. Therefore our error rate cut offs were set to 25% for the abstract verbs. This comparatively high cut off was chosen given the general property of a possible concrete reading for some verbs as well as due to the fact that responses were required in 67% of all trials, possibly increasing the false alarm probability. For the concrete verbs the error rate cut off was set to a more conservative 15%.

Neurophysiological data acquisition

Neuromagnetic brain activity was recorded continuously by a 306 channel Neuromag MEG system with 204 gradiometers and 102 magnetometers (Elekta Neuromag, Helsinki, Finland) located at University Hospital Düsseldorf. The sampling rate was 1000 Hz with an online bandpass filter of 0.03–330 Hz. All further analyses were performed offline.

Bipolar surface electromyogram (EMG) was recorded from the first dorsal interosseus (FDI) of the right hand. Two self-adhesive electrodes were placed on the skin approximately 1 cm apart. EMG signals captured the right index finger flexions executed in the verbal and the localizer task. EMG data were used to control for differences in movement force between conditions, which could also result in oscillatory beta modulation, thus confounding the expected semantic effect. In addition, vertical and horizontal electrooculogram (EOG) was recorded during MEG tasks for offline artifact rejection.

To determine the subjects' head position in the MEG machine, four head position indicator (HPI) coils were fixed to the scalp and their positions were digitized (Polhemus Isotrak, Colchester, Vermont, USA).

One to two weeks after the MEG session anatomical MRI images were acquired in a separate session with a 3 T Magnetom machine (Siemens, Erlangen, Germany). MRIs were aligned with the MEG coordinate system offline using the HPI coils and anatomical landmarks (nasion and preauricular points).

Data processing

Neurophysiological data from the 204 planar gradiometers were analysed using Fieldtrip (Oostenveld et al., 2011), an open source toolbox for Matlab (Mathworks, Natick, MA, USA). Data for correct trials in the interference experiment were epoched into segments from 2.2 s before until 2.8 s after word onset. Prior to the next step, data were visually inspected to identify broken channels (mean = 10.21, SD = 1.58). These were excluded from artifact rejection and preprocessing to be interpolated in the following step. A semiautomatic artifact rejection procedure was used to exclude data epochs contaminated by sensor jumps or head muscle artifacts. Line noise was filtered using bandstop filters with a width of 2 Hz centred at the line frequency of 50 Hz and its harmonics at 100 and 150 Hz. A lowpass filter at 260 Hz was used as well as a 2 Hz highpass filter. Data were demeaned and a padding of 10 s around each trial used for all preprocessing steps.

In the next step a nearest-neighbours approach was used to interpolate the signals of broken channels by the mean of their neighbouring channels according to the 3-dimensional layout. Vertical and horizontal gradiometer sensor types were processed separately. Principal component analysis (PCA) with 100 components was applied to identify components representing cardiac and eye movement artifacts. Component topographies and time-courses were inspected. For each subject, 1 or 2 components picking up cardiac signals (mean = 1.47, SD = 0.50) and eye blinks (mean = 1.05, SD = 0.22) were rejected. The backprojected data were then visually inspected and trials containing any additional artifacts removed. The number of trials per condition was on average 33.16 (SD = 0.77) and did not differ significantly between conditions (ANOVA, p = 0.676). Afterwards, data epochs were separated into the six subconditions (hand verbs, foot verbs, abstract verbs, and high and low imageability, respectively). Trials were cut to $t_s = -2$ to 1.5 s in the stimulus-locked and $t_r = -2.3$ to 1.5 s in the response-locked analysis. Note that for the purpose of disambiguation, t_s and t_r are used to denote the different timescales for the stimulus locked and response locked analyses, respectively. The two separate analyses were used to focus on distinct processing windows: in a stimulus-locked analysis, MEG signals were temporally aligned to the visual onset of the verb with the moment of the response jittered by reaction time differences between trials. In contrast, a response-locked analysis temporally aligns MEG signals to the response, while the information about the time point of word onset is jittered by reaction time differences. The same frequency analysis parameters were used for both analyses. While the same trials entered both analyses, their data points were not exactly identical due to the time axis shift.

Time–frequency representations (TFRs) for frequencies between 2 and 35 Hz with steps of 2 Hz were computed using a discrete Fourier transformation. This transformation was applied on an adaptive sliding time window with a width of 5 full cycles of the respective frequency f ($\Delta t = 5/f$) moving in steps of 25 ms. A single Hanning taper was used, resulting in a spectral smoothing of $1/\Delta t$. Vertical and horizontal planar gradiometers in the resulting time–frequency representations were combined to calculate the planar gradient. Stimulus-locked data were baseline corrected by subtracting the average power in the time window of $t_s = -1.5$ to -1 s before verb onset. Baseline correction for the response-locked data was performed analogously using the time window of $t_r = -2$ to -1.5 s before the response. This allowed an integer number of cycles at the centre frequency of interest (20 Hz) to fit into the baseline window, which was also before the onset of the red disk cue.

The same preprocessing and frequency analysis steps were applied to data in the functional localizer task, which was epoched into segments from 2 s before button press triggers to 1.6 s after. To illustrate the statistically defined channel selection (see section below) the cortical sources of the grandaveraged relative power differences were estimated using dynamic imaging of coherent sources (DICS), a beamforming approach in the frequency domain (Gross et al., 2001). The brain volume was discretized to a three dimensional grid with a 1 cm resolution. For each grid point a common spatial filter was constructed from the respective lead field and the cross-spectral density matrix at 15–25 Hz, pooled across the time windows of −1 to −0.75 s and −0.5 to −0.25 s. These times were also used for the statistical comparison and chosen a priori to contrast pre-movement activation without temporal overlap with the activation after movement onset due to the sliding window approach of frequency analysis. Since the centre frequency of analysis is 20 Hz, a window length of 250 ms can accommodate an integer multiple of its corresponding 50 ms cycles. The leadfield matrix was computed for a realistically shaped single-shell volume conduction model (Nolte, 2003) based on individual structural MRIs or, for three subjects for whom MRI measurements were not possible, based on standard brains. The spatial filters were then applied to the power of the Fourier-transformed data averaged in each time window. The subject-specific relative power differences were grandaveraged and visualized on the cortical surface of the Montreal Neurological Institute (MNI) brain.

Rectified EMG traces from the FDI muscles were extracted for each subcondition in the verbal task and lowpass filtered at 30 Hz.

Event-related fields (ERF) for the stimulus-locked verbal task were computed from the data split for each condition after PCA. To this end, a lowpass filter of 30 Hz was applied and the same baseline windows used as in the spectral analysis.

Statistical analysis

Median reaction times for each participant were entered into an analysis of variance (ANOVA) with the factors verb condition (hand, foot) and imageability (high, low). Significant effects were compared further by means of paired t-tests.

MEG data from the localizer task were used to define the subset of channels corresponding to processes of motor preparation for right index finger movements. The oscillatory beta power averaged for 15–25 Hz was statistically compared between a time window during motor preparation before the response trigger (−500 to −250 ms) and an earlier time window of the same length (−1000 to −750 ms). A two-step procedure was used, first assessing subject-specific contrasts and then using a non-parametric second level statistical procedure to identify significant clusters on group level. In the first step, we calculated pseudo-t-values for each subject for the trial-wise comparison of each sensor–time pair between the baseline and the motor preparation period, serving as a normalization of interindividual differences (compare Lange et al., 2011). All t-values were transformed to z-values using SPM2 resulting in sensor–time z-maps (e.g. van Dijk et al., 2010; Mazaheri et al., 2014) to account for varying trial numbers. In the next step these subject-specific z-maps were averaged across the two time windows, respectively. For group-level statistics, the consistency of z-maps across subjects was assessed. A non-parametric randomization approach was used, identifying spatially contiguous clusters of sensors (minimum of three neighbouring sensors) with significant changes and effectively correcting for multiple comparisons (Maris and Oostenveld, 2007). To this end, the sum of cluster t-values was used in the second-level statistics for a Monte Carlo procedure. By randomly permuting the data from the two time windows 5000 times a cluster level p-value can be obtained by identifying the proportion of elements in the randomization null distribution exceeding the observed maximum cluster level test statistic (compare de Lange et al., 2008; van Elk et al., 2010; Lange et al., 2011; May et al., 2012; Brinkman et al., 2014). Channels forming a significant cluster with a p-value below 0.05 were taken to be associated with motor preparatory processes and used for the verbal task analysis.

For the verbal task, MEG spectral power was compared between the experimental conditions of interest, defined by the behavioural results, using the non-parametric clustering approach described above. Therefore, the contrasts were between trials, as opposed to within the same trial in the localizer task. Here, the spatial information was averaged across the sensors derived from the localizer task while frequency (5 to 30 Hz) and time were not averaged. Hence, the subject-specific pseudo-t-values describe time–frequency pairs. The time window of interest was −1 to 1 s for both types of analyses, with time point 0 being the verb onset and the response, respectively. Hence, equal numbers of data points were used in both analyses. Cluster t-values of the contrasts were randomly permuted with 5000 repetitions. The resulting time–frequency clusters with cluster-level p-values below an alpha level of 0.05 are considered significant.

To assess statistical differences in ERFs, the same cluster-based randomization approach was used. Since the beta-frequency based sensor selection is not necessarily meaningful for evoked responses, the sensors in the selection were used for statistics but not averaged. Without frequency data clusters are formed in the time domain. The contrasts hand high vs. foot high as well as hand high vs. abstract high were assessed in the time window of $t_s = -1$ to 1 s in the stimulus-locked analysis.

Results

Behavioural

The ANOVA of median reaction times did not show a main effect of verb condition ($p = .173$), indicating that hand verbs were not generally responded to more slowly than foot verbs. However, a main effect of imageability was significant ($F(1;18) = 42.571$, $p < .001$) with high imageability verbs leading to faster reaction times than low imageability verbs. More importantly, the two factors interacted significantly ($F(1;18) = 5.496$, $p = .031$), see Fig. 2. For high imageability verbs, the expected reaction time interference effect was found: hand verbs were followed by longer reaction times than foot verbs ($t(18) = 2.687$, $p = .015$). No difference was seen for low imageability verbs ($p = .843$).

MEG spectral power and event-related fields

Localizer task

The resulting significant cluster is shown in Fig. 3 and this channel selection was used in the analyses of the verbal task. Source

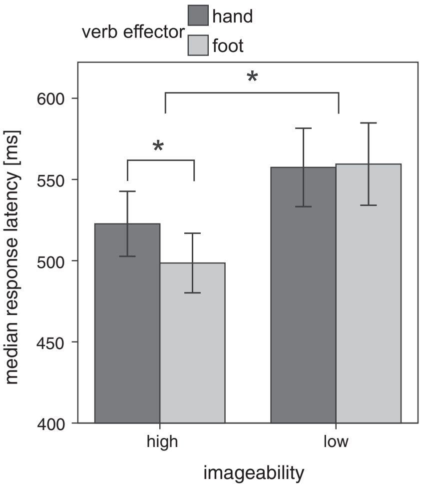

Fig. 2. Behavioural results. Response latencies are in reference to the Go signal 150 ms after verb onset. Error bars indicate standard error of the mean. * = $p < 0.05$.

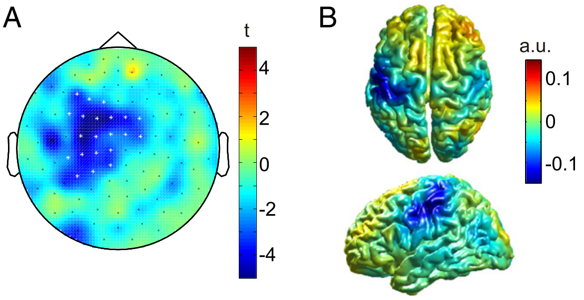

Fig. 3. Results from the localizer task. A: Statistically defined channel selection derived from the contrast −1 to −0.75 vs. −0.5 to −0.25 s before button press. Frequency is averaged for 15–25 Hz. Blue colours indicate stronger beta suppression in the later time window. B: Source reconstruction of grandaveraged power of the same contrast, projected onto the MNI template brain. View from the top (top row) and from the left (bottom row).

reconstruction of the grandaveraged power contrast is included for illustrative purposes and shows that in the localizer task, the significant channel selection was associated with beta power modulations in the pericentral region.

Semantic decision task

Since the behavioural effects were found in the comparison between high imageability hand and foot verbs, this was the main contrast of interest. Spectral power was thus compared between those subconditions (hand high and foot high). Moreover, exploratory comparisons were performed between hand high and hand low to investigate the imageability contrast, as well as between hand and abstract in the stimulus-locked analysis to compare results to the literature.

Stimulus-locked analysis. Time–frequency representations in the channels of interest for all conditions are shown in Fig. 4. Spectral power modulations in the beta frequency band are characterised by an early and sustained suppression that is maximal around the time of response execution. Note, however, that the mean response latency of between 650 and 700 ms after word onset is accompanied by substantial inter-trial differences as also depicted in Fig. 4. To exclude that differences seen in the motor preparation channels of interest were confounded by a spreading of activation from a location centred outside these channels, topographical representations of beta power were also inspected (see Suppl. Fig. S1 for the hand high, foot high and abstract high conditions). While there is beta suppression in posterior sensors with little power modulation across time, the left-lateralized central region

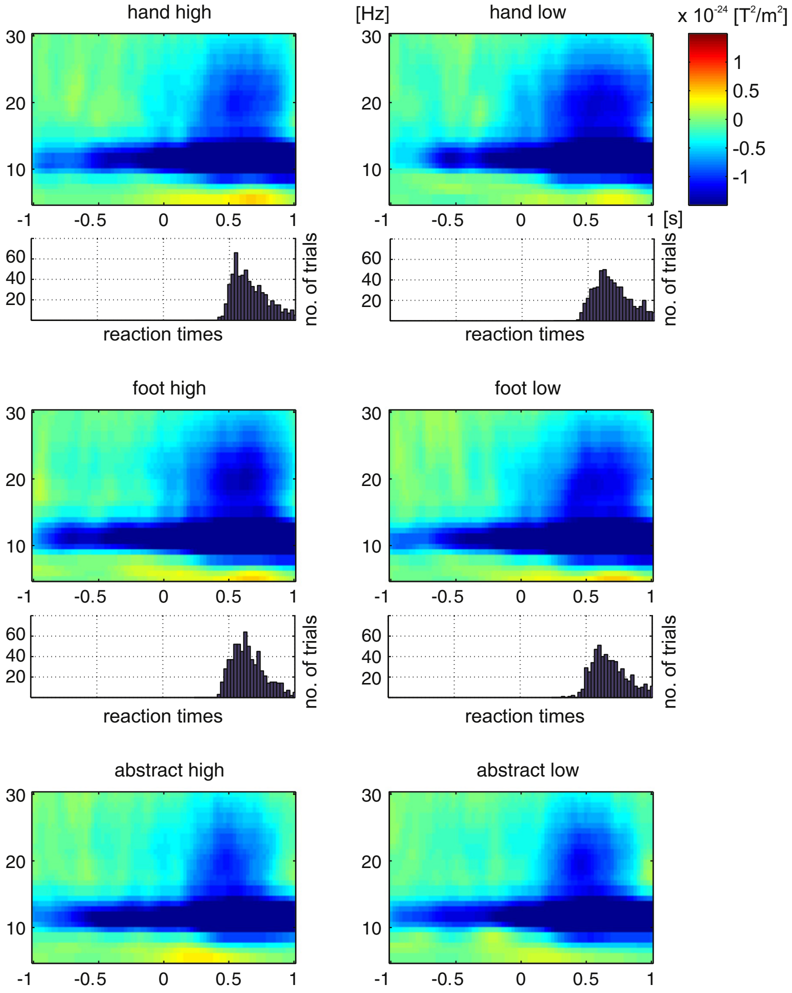

Fig. 4. Stimulus-locked analysis: time–frequency representations in the selected channels derived from the localizer task, for all six subconditions (hand, foot, abstract; high, low imageability). Time point 0 is word onset. The panels for the concrete verbs include distributions of single trial reaction times across all participants.

covered by the motor preparation channels evolves differentially in the experimental conditions. Alpha band power suppression is present in all conditions and starts earlier than beta effects. The topographical representations (compare also Suppl. Fig. S4) indicate that alpha suppression is stronger in posterior than central sensors until the time of the response in all conditions.

The statistical comparison between the hand high and foot high conditions in the sensorimotor channel selection resulted in a significant cluster at $t_s = 0.35$ to 0.75 s after word onset ($p = 0.010$), mainly focused around 20 Hz. The significant cluster is shown in Fig. 5A with its corresponding topographical spectral power representation. No clusters in other frequency bands were found. No differences in EMG amplitude were seen (compare Suppl. Fig. S5A).

The exploratory contrast hand high vs. hand low also resulted in significant differences in the beta band ($p = .010$, Fig. 5B). Beta suppression was attenuated for the hand high verbs, starting at $t_s = 0.4$ s after verb onset. Comparing hand vs. abstract verbs showed stronger beta suppression in the hand verbs across the beta frequency range ($p = .001$, Fig. 5C) and started at a similar time as the other contrasts, reaching into the response execution time window.

In ERFs (compare Suppl. Fig. S2), the contrast hand high vs. foot high did not reveal any differences in the sensor selection, which also captured part of the visual evoked field in all conditions. For the pooled comparison hand vs. abstract verbs, a few brief significant clusters were observed only in some channels, see Fig. 6. These included time windows before and around the mean reaction time, but the variability across sensors implies only transient and incoherent effects in ERFs.

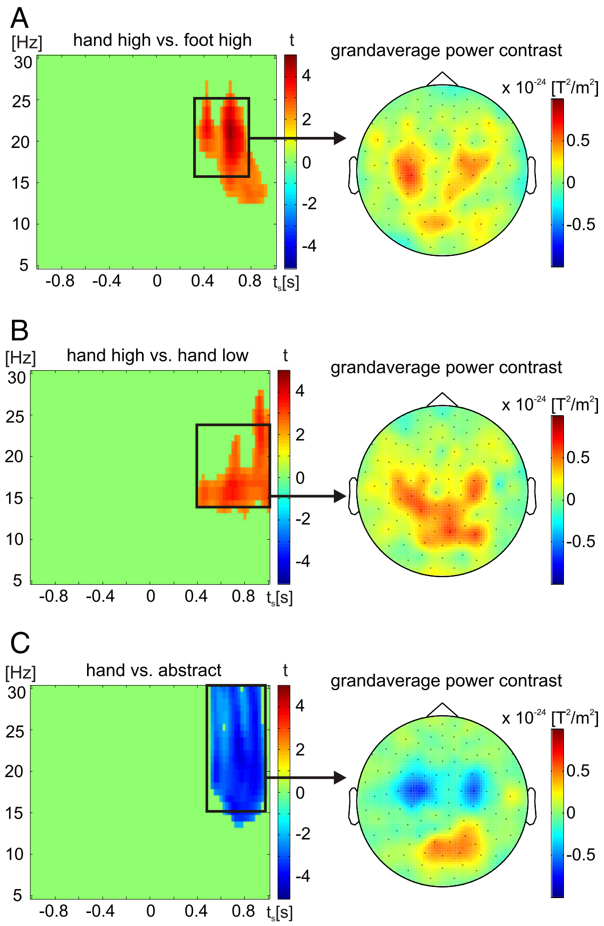

Fig. 5. Stimulus-locked analysis: statistical results from the spectral power analysis. Non-significant time–frequency tiles are masked. The roughly corresponding topographical representations of the significant clusters in the grandaverages are also shown. A: Contrast hand high vs. foot high. B: Contrast hand high vs. hand low. C: Contrast hand vs. abstract.

Response-locked analysis. Time–frequency representations in the channels of interest are shown in Fig. 7. The characteristic pattern of beta power suppression during movement preparation and execution, followed by a power increase as a post-movement rebound is visible. Note that for the abstract verbs a response-locked analysis is unfeasible since no response was given. Topographical representations (see Suppl. Fig. S3 for hand high and foot high conditions) show that there is differential beta power suppression modulation only in the sensors of interest.

Cluster statistics for the channel selection resulted in a significant cluster in the beta frequency between $t_r = -0.625$ and 0.425 s ($p = 0.005$). Like in the stimulus-locked analysis, the cluster was focused on a narrow frequency band around 20 Hz but also included lower beta frequencies. The statistical results are shown in Fig. 8A. No clusters in other frequency bands were found (see also Suppl. Fig. S4). No differences in EMG amplitude were seen (compare Suppl. Fig. S5B).

The exploratory contrast hand high vs. hand low also yielded a significant cluster in the beta band ($p = .001$, Fig. 8B) from $t_r = -0.8$ to 0.25 s, most pronounced for 15–20 Hz.

Discussion

The aim of the current study was to find neurophysiological evidence for the language–motor interference effect previously described in reaction time paradigms (Sato et al., 2008). Analogous to these experiments, our hypothesis was that longer response latencies would follow hand verbs than foot verbs. However, interference effects were only found for verbs with high but not low imageability.

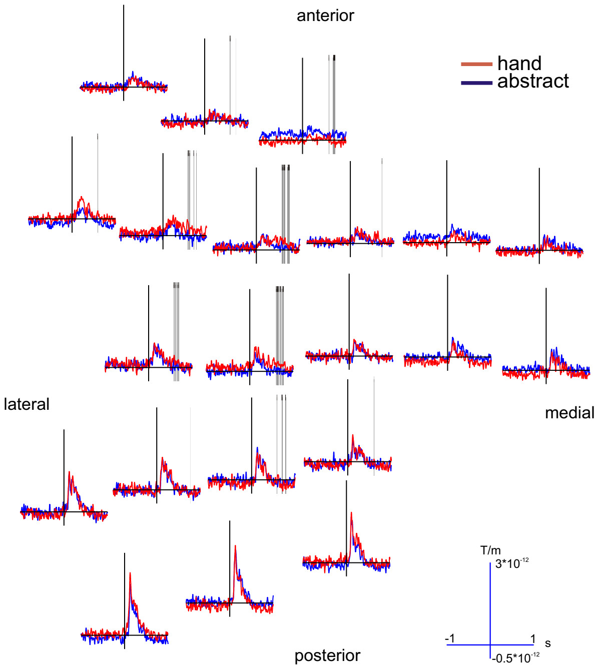

Fig. 6. Stimulus-locked analysis: statistical results from event-related fields, pooled contrast hand vs. abstract verbs. Each channel in the channel selection was analysed separately. Please refer to Fig. 3 for the locations of the sensors with respect to the head. Significant clusters in time are indicated by the shaded grey areas. Note that the short-lasting significant clusters emerge only in some channels, with a latency around 600 ms.

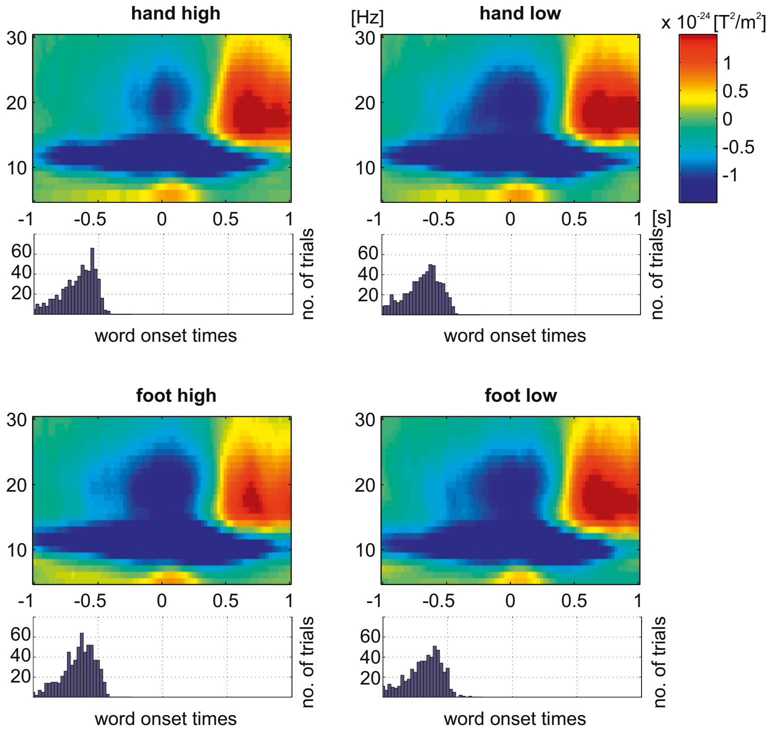

Fig. 7. Response-locked analysis: spectral power in the selected channels derived from the localizer task, for the four concrete subconditions. Time point 0 is the response. Panels include distributions of word onset times across all participants.

When comparing MEG beta power between high imageability hand and foot verbs, significant differences emerged in both the stimulus-locked and the response-locked analysis. These correspond to time windows during verbal processing and concurrent motor preparation as well as response execution. Beta suppression following the presentation of hand verbs was diminished compared to foot verbs. This indicates that the beta suppression during motor preparation is modulated by the semantic interference occurring when the verb's effector matches the response.

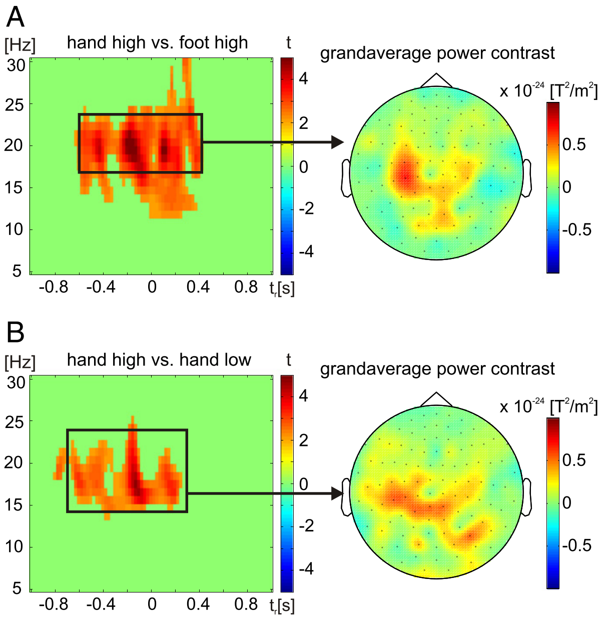

Fig. 8. Response-locked analysis: statistical results. Non-significant time–frequency tiles are masked. The roughly corresponding topographical representation of the significant clusters in the grandaverages are also shown. A: Contrast hand high vs. foot high. B: Contrast hand high vs. hand low.

In the following sections, we discuss the role of imageability for action-related language processing and the mechanisms of semantic interference separately.

The role of imageability

The reason to initially include imageability as an experimental factor was not an expected interaction with the interference effect based on the literature (Sato et al., 2008; Mirabella et al., 2012; Buccino et al., 2005). Rather, this factor was introduced to control for its facilitatory influence on reaction times (Giesbrecht et al., 2004; Newcombe et al., 2012) since our set of stimuli is characterised by a larger variability of imageability than reported in previous experiments (Mirabella et al., 2012).

In the light of embodied cognition theories it is conceivable that what leads to faster reaction times for high imageability verbs is in fact motor simulation. Imageability is a construct described in several theories of word processing and semantic knowledge, for instance Dual Coding Theory (Paivio, 1971). The imageability of a concept can index the strength, vividness, or speed with which an internal image can be generated during imagery. Moreover, it is a construct influencing the semantic stages of word recognition as seen for instance in event related potentials (West and Holcomb, 2000). Interestingly, in a priming task using nouns, imageability also increased fMRI activity in the inferior frontal/precentral gyrus (Giesbrecht et al., 2004). This indicates a potentially modulating influence of imageability on language processing in the motor system.

To exclude the possibility that item difficulty was underlying the interference interaction effect, we reran the reaction time analysis with the verb sets split for high and low familiarity instead of imageability. Higher word familiarity is also known to generally facilitate word recognition (Connine et al., 1990). In our sample, familiarity and imageability correlate significantly at $p = .01$ with $r = .83$. However, no interaction in the reaction time analysis was found for familiarity, indicating that item difficulty is not mediating the interference effect.

Taken together, it is conceivable that imageability effectively captures an inherent semantic property of action verbs that increases the relative importance of motor simulation for the understanding of their meaning, which is in line with embodied cognition theories (van Dam et al., 2010). For nouns, this seems to be the case with imageability and the construct "body object interaction" (Newcombe et al., 2012; Marino et al., 2013, for language–motor interference with hand-related nouns). To directly assess whether imageability correlates with more immediately motor-related semantic features, we post hoc performed a rating study with 22 participants. Indeed, imageability was shown to correlate with hand-action-relatedness in hand verbs ($r = .33$, $p = .03$) and with leg-action-relatedness in foot verbs ($r = .42$, $p < .01$). Moreover, the measure "motor prototypicality"—operationalised as how strongly a word suggests one prototypical action—correlated with imageability across the whole dataset ($r = .34$, $p < .01$) and for hand and foot verbs separately as well (hand verbs: $r = .32$, $p = .04$; foot verbs: $r = .41$, $p < .01$). This may indicate that verbs with a high imageability indeed evoke a stronger and clearer action simulation than low imageability verbs, which explains why imageability interacts with the interference effect. Directly contrasting the spectral power in hand verbs with high and low imageability, we found decreased beta suppression for high imageability verbs, in line with the behavioural interference effect.

MEG power modulations and semantic interference

Oscillatory power suppression in the alpha and beta frequency bands is thought to indicate neuronal activation (Pfurtscheller and Lopes da Silva, 1999; Engel and Fries, 2010). More specifically, beta band suppression—or desynchronization—has been shown to correlate with the blood oxygenation level dependent (BOLD) response in fMRI (Singh et al., 2002) as well as with an increase in single neuron firing rates in macaques (Panagiotaropoulos et al., 2013).

In the context of the current results, reduced beta suppression for highly imageable hand verbs seems to be a direct correlate of language–motor interference: the neuronal mechanism associated with motor preparation and execution is modulated differentially for hand and foot verbs, leading to altered behavioural responses. This is not a confound of reaction time differences since significant effects also emerge in the response-locked analysis.

Moreover, EMG traces were also inspected and no significant amplitude differences were found between the experimental conditions. This suggests that beta power differences are not associated with differences in downstream motor signals to the response muscles.

Regarding the time windows of beta oscillatory effects of interference, the stimulus-locked and response-locked analyses contribute complementary results, but both reveal differences during simultaneous verbal processing and an approaching response execution. In the stimulus-locked analysis, the latency (350 to 750 ms after word onset) of the significant effect between hand and foot verbs with high imageability corresponds to a processing window of concurrent semantic processing and motor preparation, while earlier clusters did not reach significance. This can be seen in the light of transient differences in early semantic processing in the motor system phase-locked to the word onset around 200 ms (Pulvermüller et al., 2001; Boulenger et al., 2012; Klepp et al., 2014) that are too subtle to be detected in the presence of a motor execution task. Nevertheless, the latency of the significant effects of around 400 ms is in the time window classically described for semantic processing (Kutas and Hillyard, 1984). The exploratory comparison of the imageability difference within hand verbs, showing that suppression was decreased in high imageability compared with low imageability verbs, also falls within this time range. This supports the interpretation that the high imageability hand verbs are affected by interference due to their stronger motor-relatedness, leading to more pronounced motor simulation.

In addition to this, stronger beta suppression for hand than abstract verbs in the stimulus-locked analysis was also found in the current study from around 400 ms onwards. Similarly, transient differences between hand and abstract verbs emerged in event-related fields with a latency of about 600 ms. These results may reflect the same processes as described before for alpha and beta in action-related versus abstract language processing in the absence of overt manual movement (van Elk et al., 2010; Alemanno et al., 2012; Moreno et al., 2013; Niccolai et al., 2014) where stronger power suppression is thought to indicate motor system activation by verb processing itself. Alternatively, since this is not directly transferable to situations with concurrent motor tasks as in the interference paradigm, differences may arise mainly from the difference in task demands in the Go vs. NoGo conditions where manual responses were given only in the hand verb conditions. Thus, both the spectral power and evoked effects concerning the comparison between hand and abstract verbs have to be interpreted with caution. Indeed, beta power suppression and rebound is also seen in the NoGo condition, illustrating how the expectation of an upcoming motor reaction is driving motor preparatory processes. This is in line with previous findings (Leocani et al., 2001). Also, alpha and beta power is suppressed in somatosensory regions already during the anticipation of a stimulus (van Ede et al., 2014). The transient beta suppression in the current NoGo condition is possibly exacerbated because the verbal task required responses in two thirds of all trials and responses were uniformly given using the right index finger. This allows the development of a task set which is defined by very early motor preparatory processes since they are advantageous to performance in most cases. Another indicator that this indeed took place is the high number of false alarms (>10%), possibly a result of failed response inhibition. For the occurrence of language–motor interference effects it is important that motor preparatory responses start early and consecutively with language processing, which was confirmed in all experimental conditions. This may also be the reason why no early differences emerged in the comparison of event-related fields within 350 ms following the verb onset, despite previous studies reporting (somatotopic) effects (Pulvermüller et al., 2001; Boulenger et al., 2012; Moseley et al., 2013; Klepp et al., 2014).

The presentation of the Go stimulus, ongoing motor preparation and response execution may all conceal any subtle differences in oscillatory and evoked responses. Still, it is conceivable that early processing of hand and foot action verbs in the current study did activate the motor system—presumably somatotopically—just as it does in the absence of movement tasks (Hauk et al., 2004; Tettamanti et al., 2005; Kemmerer et al., 2008; Niccolai et al., 2014), but that this is obliterated by the presence of motor preparatory processes.

Complementary to the stimulus-locked results, effects in the response-locked analysis begin earlier with respect to the motor preparation processes for the comparison between high imageability hand and foot verbs (−625 to 425 ms relative to the response). This is interesting because even though the significant cluster corresponds to a time window starting shortly after average verb onset, it appears not to be phase-locked to the verb onset due to the null finding in the stimulus-locked analysis, but rather related to early motor preparation characteristics. The significant effect is again focused mainly around 20 Hz. Generally, the interference effect in the response-locked analysis lasts longer than in the stimulus-locked analysis, from early motor preparation until the average response execution stage, but not reaching into the beta rebound period. This corroborates the notion that the interference effect we obtained is directly linked to motor cortical excitability changes as measured by beta oscillations. Like in the stimulus-locked analysis, differences between imageability levels within hand verbs are also found, again with weaker beta suppression in the high imageability hand verbs during motor preparation and execution. A comparison of hand and abstract verbs was not feasible in the response-locked analysis since no responses were given for abstract verbs.

All conditions also show a power decrease in the alpha frequency range (8–13 Hz). Despite a possible role for alpha oscillations in embodied language processing (van Elk et al., 2010; Fargier et al., 2012), no clusters in the alpha range were identified in the comparison between conditions nor were suggested by alpha power topographies. This indicates that oscillations in the beta band are the specific neurophysiological mechanism associated with language–motor interference.

While our results suggest that differential beta suppression patterns reflect the interaction of movements with verbal processing in reaction times, there are a few possible underlying neurophysiological processes. One mechanism that can reflect the prolonged reaction times for highly imageable hand verbs is competition for shared resources in the hand motor cortex that are accessed both by hand verb processing and by finger movement motor preparation (Sato et al., 2008). This is in line with reports of decreased cortical excitability in language–motor interaction paradigms measured by readiness potentials in EEG (Boulenger et al., 2008) and motor evoked potentials using transcranial magnetic stimulation (TMS, Buccino et al., 2005). These and the current oscillatory findings in beta power oscillations indicate that motor cortex excitability is specifically decreased by action language processing and reflects language–motor interference (see also Willems et al., 2011).

Interestingly, action observation seems to increase rather than decrease cortical excitability, even in muscle-specific areas (Fadiga et al., 1995; Strafella and Paus, 2000; Sundara et al., 2001). The crucial difference to verbal processing may be that action observation provides a specific instance of an action while action verbs and even sentences are underspecified (Nelissen et al., 2005; Buccino et al., 2005). In a computational model Chersi et al. (2010) describe chained activation of neurons involved in the motor acts of action sentences and verbs. Their relative overlap with the recruitment of action execution can produce both interference and facilitation effects, depending on timing. This indicates that in addition to competition for neuronal resources and a resulting decrease in cortical excitability, more fine-grained mechanisms underlie the different ways of how language processing and motor execution can interact. This model is important since language–motor interaction is not always expressed as interference between the two systems. Different tasks, stimulus sets and timing may lead to facilitation rather than interference effects (Pulvermüller et al., 2005; Boulenger et al., 2006; Zwaan and Taylor, 2006; Willems et al., 2011; de Vega et al., 2013).

Apart from task and timing, the more fine-grained issue is assumed to be the extent of overlap between neuronal assemblies accessed by verb processing and response execution (Chersi et al., 2010). The crucial factor is the (in)compatibility between the motor schemata accessed by verbal processing and motor preparation. Hand verbs typically define actions that involve several hand motor acts that are distinct from the motor act of pressing down the right index finger to execute a button press. These incompatible motor act programs are expected to inhibit each other, in line with the lateral inhibition that is seen in recurrent inhibitory feedback in the motor system (Windhorst, 1996; Buccino et al., 2005). This is also found with behavioural results showing that conceptually processing two actions that share an effector produces interference, with the amount of similarity between them presumably related to the amount of reciprocal inhibition (Bergen et al., 2010). Another behavioural study compared the processing of two opposed hand action verbs and their corresponding action executions (Liepelt et al., 2012). In this design, both conditions refer to the same effector, but interference was found whenever verbal processing and action execution were incompatible. This is in line with the current results and other interference experiments (Buccino et al., 2005; Mirabella et al., 2012) comparing verbal material related to different effectors. Here, the incompatibility between neuronal activations for a matching effector of verbal and action processing gives rise to interference effects.

Regarding the interpretation and generalizability of the current data it has to be taken into consideration that cortical sources of effects were not directly estimated from the verbal paradigm. The main reason for this is the small number of trials remaining in the experimental conditions to account for the interaction with imageability. It is an open question if the cortical source directly underlying language–motor interference is located in the primary or premotor cortex or perhaps in connected sensorimotor areas. Another limitation of the current study is that only manual responses and their interactions with hand verb processing were investigated. Future studies should apply the interference paradigm to foot responses, where reversed effects regarding reaction times and neurophysiological processes can be expected. Nevertheless, to our knowledge the current study is the first to report interference effects to depend on verb-inherent imageability. This challenges the current line in embodiment research stressing the role of context and task (Tomasino et al., 2010; Aravena et al., 2012; Schuil et al., 2013; Desai et al., 2013). Here, semantic properties of the verb material itself were also found to play a role. It will be of interest to further investigate the role of different semantic features such as imageability and motor prototypicality on embodied language processing. This may also lead to a more meaningful characterisation of verbal material than the mere categorisation according to effector, as also suggested by the basic versus subordinate distinction by van Dam et al. (2010) and by the investigations on semantic verb components (Kemmerer et al., 2008).

Conclusions

Taken together, our results imply that modulations in the beta frequency are associated with language–motor interference in the neurophysiological domain. In line with the slower manual responses following highly imageable hand verbs, beta power suppression was diminished following hand verbs compared with foot verbs. This provides evidence for and a characterisation of the functional role of the motor system for action language understanding within the framework of embodied cognition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2014.12.077.

References

Alemanno, F., Houdayer, E., Cursi, M., Velikova, S., Tettamanti, M., Comi, G., Cappa, S.F., Leocani, L., 2012. Action-related semantic content and negation polarity modulate motor areas during sentence reading: an event-related desynchronization study. Brain Res. 1484, 39–49.

Aravena, P., Delevoye-Turrell, Y., Deprez, V., Cheylus, A., Paulignan, Y., Frak, V., Nazir, T., 2012. Grip force reveals the context sensitivity of language-induced motor activity during action words processing: evidence from sentential negation. PLoS One 7, e50287.

Avanzini, P., Fabbri-Destro, M., Dalla Volta, R., Daprati, E., Rizzolatti, G., Cantalupo, G., 2012. The dynamics of sensorimotor cortical oscillations during the observation of hand movements: an EEG study. PLoS One 7, e37534.

Barsalou, L.W., 2008. Grounded cognition. Annu. Rev. Psychol. 59, 617–645.

Bergen, B., Lau, T.-T.C., Narayan, S., Stojanovic, D., Wheeler, K., 2010. Body part representations in verbal semantics. Mem. Cognit. 38, 969–981.

Biemann, C., Heyer, G., Quasthoff, U., M., R., 2007. The Leipzig Corpora Collection — monolingual corpora of standard size. Proceedings of Corpus Linguistics 2007.

Boulenger, V., Roy, A.C., Paulignan, Y., Deprez, V., Jeannerod, M., Nazir, T.A., 2006. Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. J. Cogn. Neurosci. 18, 1607–1615.

Boulenger, V., Silber, B.Y., Roy, A.C., Paulignan, Y., Jeannerod, M., Nazir, T.A., 2008. Subliminal display of action words interferes with motor planning: a combined EEG and kinematic study. J. Physiol. Paris 102, 130–136.

Boulenger, V., Shtyrov, Y., Pulvermüller, F., 2012. When do you grasp the idea? MEG evidence for instantaneous idiom understanding. NeuroImage 59, 3502–3513.

Brinkman, L., Stolk, A., Dijkerman, H.C., de Lange, F.P., Toni, I., 2014. Distinct roles for alpha- and beta-band oscillations during mental simulation of goal-directed actions. J. Neurosci. 34, 14783–14792.

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., Rizzolatti, G., 2005. Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. Brain Res. Cogn. Brain Res. 24, 355–363.

Caetano, G., Jousmäki, V., Hari, R., 2007. Actor's and observer's primary motor cortices stabilize similarly after seen or heard motor actions. Proc. Natl. Acad. Sci. U. S. A. 104, 9058–9062.

Chersi, F., Thill, S., Ziemke, T., Borghi, A.M., 2010. Sentence processing: linking language to motor chains. Front. Neurorobot. 4.

Coll, M.-P., Bird, G., Catmur, C., Press, C., 2015. Cross-modal repetition effects in the mu rhythm indicate tactile mirroring during action observation. Cortex 63, 121–131.

Connine, C.M., Mullennix, J., Shernoff, E., Yelen, J., 1990. Word familiarity and frequency in visual and auditory word recognition. J. Exp. Psychol. Learn. Mem. Cogn. 16, 1084–1096.

Dalla Volta, R., Gianelli, C., Campione, G.C., Gentilucci, M., 2009. Action word understanding and overt motor behavior. Exp. Brain Res. 196, 403–412.

de Lange, F.P., Jensen, O., Bauer, M., Toni, I., 2008. Interactions between posterior gamma and frontal alpha/beta oscillations during imagined actions. Front. Hum. Neurosci. 2, 7.

de Vega, M., Moreno, V., Castillo, D., 2013. The comprehension of action-related sentences may cause interference rather than facilitation on matching actions. Psychol. Res. 77, 20–30.

Desai, R.H., Conant, L.L., Binder, J.R., Park, H., Seidenberg, M.S., 2013. A piece of the action: modulation of sensory-motor regions by action idioms and metaphors. NeuroImage 83, 862–869.

Diefenbach, C., Rieger, M., Massen, C., Prinz, W., 2013. Action–sentence compatibility: the role of action effects and timing. Front. Psychol. 4, 272.

Ehrenstein, W.H., Arnold-Schulz-Gahmen, B.E., 1997. Auge, Ohr, Hand und Fuß: Bestimmung des individuellen Lateralitätsprofils. Institut für Arbeitsphysiologie, Dortmund.

Engel, A.K., Fries, P., 2010. Beta-band oscillations—signalling the status quo? Curr. Opin. Neurobiol. 20, 156–165.

Fadiga, L., Fogassi, L., Pavesi, G., Rizzolatti, G., 1995. Motor facilitation during action observation: a magnetic stimulation study. J. Neurophysiol. 73, 2608–2611.

Fargier, R., Paulignan, Y., Boulenger, V., Monaghan, P., Reboul, A., Nazir, T.A., 2012. Learning to associate novel words with motor actions: language-induced motor activity following short training. Cortex 48, 888–899.

Giesbrecht, B., Camblin, C.C., Swaab, T.Y., 2004. Separable effects of semantic priming and imageability on word processing in human cortex. Cereb. Cortex 14, 521–529.

Glenberg, A.M., Kaschak, M.P., 2002. Grounding language in action. Psychon. Bull. Rev. 9, 558–565.

Gross, J., Kujala, J., Hamalainen, M., Timmermann, L., Schnitzler, A., Salmelin, R., 2001. Dynamic imaging of coherent sources: studying neural interactions in the human brain. Proc. Natl. Acad. Sci. U. S. A. 98, 694–699.

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., Rizzolatti, G., 1998. Activation of human primary motor cortex during action observation: a neuromagnetic study. Proc. Natl. Acad. Sci. U. S. A. 95, 15061–15065.

Hauk, O., Johnsrude, I., Pulvermüller, F., 2004. Somatotopic representation of action words in human motor and premotor cortex. Neuron 41, 301–307.

Hirschfeld, G., Zwitserlood, P., 2012. Effector-specific motor activation modulates verb production. Neurosci. Lett. 523, 15–18.

Kemmerer, D., Castillo, J.G., Talavage, T., Patterson, S., Wiley, C., 2008. Neuroanatomical distribution of five semantic components of verbs: evidence from fMRI. Brain Lang. 107, 16–43.

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 Lang. 128, 41–52.

Koelewijn, T., van Schie, H.T., Bekkering, H., Oostenveld, R., Jensen, O., 2008. Motor-cortical beta oscillations are modulated by correctness of observed action. NeuroImage 40, 767–775.

Kutas, M., Hillyard, S.A., 1984. Brain potentials during reading reflect word expectancy and semantic association. Nature 307, 161–163.

Lange, J., Oostenveld, R., Fries, P., 2011. Perception of the touch-induced visual double-flash illusion correlates with changes of rhythmic neuronal activity in human visual and somatosensory areas. NeuroImage 54, 1395–1405.

Leocani, L., Toro, C., Zhuang, P., Gerloff, C., Hallett, M., 2001. Event-related desynchronization in reaction time paradigms: a comparison with event-related potentials and corticospinal excitability. Clin. Neurophysiol. 112, 923–930.

Liepelt, R., Dolk, T., Prinz, W., 2012. Bidirectional semantic interference between action and speech. Psychol. Res. 76, 446–455.

Marino, B.F., Gough, P.M., Gallese, V., Riggio, L., Buccino, G., 2013. How the motor system handles nouns: a behavioral study. Psychol. Res. 77, 64–73.

Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods 164, 177–190.

May, E.S., Butz, M., Kahlbrock, N., Hoogenboom, N., Brenner, M., Schnitzler, A., 2012. Pre- and post-stimulus alpha activity shows differential modulation with spatial attention during the processing of pain. NeuroImage 62, 1965–1974.

Mazaheri, A., van Schouwenburg, M.R., Dimitrijevic, A., Denys, D., Cools, R., Jensen, O., 2014. Region-specific modulations in oscillatory alpha activity serve to facilitate processing in the visual and auditory modalities. NeuroImage 87, 356–362.

Mirabella, G., Iaconelli, S., Spadacenta, S., Federico, P., Gallese, V., 2012. Processing of hand-related verbs specifically affects the planning and execution of arm reaching movements. PLoS One 7, e35403.

Moreno, I., de Vega, M., León, I., 2013. Understanding action language modulates oscillatory mu and beta rhythms in the same way as observing actions. Brain Cogn. 82, 236–242.

Moseley, R.L., Pulvermüller, F., Shtyrov, Y., 2013. Sensorimotor semantics on the spot: brain activity dissociates between conceptual categories within 150 ms. Sci. Rep. 3.

Nazir, T.A., Boulenger, V., Roy, A., Silber, B., Jeannerod, M., Paulignan, Y., 2008. Language-induced motor perturbations during the execution of a reaching movement. Q. J. Exp. Psychol. (Hove) 61, 933–943.

Nelissen, K., Luppino, G., Vanduffel, W., Rizzolatti, G., Orban, G.A., 2005. Observing others: multiple action representation in the frontal lobe. Science 310, 332–336.

Newcombe, P.I., Campbell, C., Siakaluk, P.D., Pexman, P.M., 2012. Effects of emotional and sensorimotor knowledge in semantic processing of concrete and abstract nouns. Front. Hum. Neurosci. 6, 275.

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, e108059.

Nolte, G., 2003. The magnetic lead field theorem in the quasi-static approximation and its use for magnetoencephalography forward calculation in realistic volume conductors. Phys. Med. Biol. 48, 3637–3652.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.

Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M., 2011. Fieldtrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput. Intell. Neurosci. 2011, 156869.

Paivio, A., 1971. Imagery and Verbal Processes. Holt, Rinehart and Winston, New York.

Panagiotaropoulos, T.I., Kapoor, V., Logothetis, N.K., 2013. Desynchronization and rebound of beta oscillations during conscious and unconscious local neuronal processing in the macaque lateral prefrontal cortex. Front. Psychol. 4, 603.

Paulus, M., Lindemann, O., Bekkering, H., 2009. Motor simulation in verbal knowledge acquisition. Q. J. Exp. Psychol. (Hove) 62, 2298–2305.

Pfurtscheller, G., Lopes da Silva, F.H., 1999. Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin. Neurophysiol. 110, 1842–1857.

Pfurtscheller, G., Brunner, C., Schlögl, A., Lopes da Silva, F.H., 2006. Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. NeuroImage 31, 153–159.

Pulvermüller, F., 2005. Brain mechanisms linking language and action. Nat. Rev. Neurosci. 6, 576–582.

Pulvermüller, F., Härle, M., Hummel, F., 2001. Walking or talking? Behavioral and neurophysiological correlates of action verb processing. Brain Lang. 78, 143–168.

Pulvermüller, F., Hauk, O., Nikulin, V.V., Ilmoniemi, R.J., 2005. Functional links between motor and language systems. Eur. J. Neurosci. 21, 793–797.

Salmelin, R., Hämäläinen, M., Kajola, M., Hari, R., 1995. Functional segregation of movement-related rhythmic activity in the human brain. NeuroImage 2, 237–243.

Sato, M., Mengarelli, M., Riggio, L., Gallese, V., Buccino, G., 2008. Task related modulation of the motor system during language processing. Brain Lang. 105, 83–90.

Schnitzler, A., Salenius, S., Salmelin, R., Jousmäki, V., Hari, R., 1997. Involvement of primary motor cortex in motor imagery: a neuromagnetic study. NeuroImage 6, 201–208.

Schuil, K.D., Smits, M., Zwaan, R.A., 2013. Sentential context modulates the involvement of the motor cortex in action language processing: an fMRI study. Front. Hum. Neurosci. 7, 100.

Sebastiani, V., de Pasquale, F., Costantini, M., Mantini, D., Pizzella, V., Romani, G.L., Della Penna, S., 2014. Being an agent or an observer: different spectral dynamics revealed by MEG. NeuroImage 102, 717–728.

Shebani, Z., Pulvermüller, F., 2013. Moving the hands and feet specifically impairs working memory for arm- and leg-related action words. Cortex 49, 222–231.

Singh, K., Barnes, G.R., Hillebrand, A., Forde, E.M., Williams, A.L., 2002. Task-related changes in cortical synchronization are spatially coincident with the hemodynamic response. NeuroImage 16, 103–114.

Steingrüber, H.-J., 2011. Hand-Dominanz-Test. Hogrefe, Göttingen.

Strafella, A.P., Paus, T., 2000. Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. Neuroreport 11, 2289–2292.

Strauß, A., Kotz, S.A., Scharinger, M., Obleser, J., 2014. Alpha and theta brain oscillations index dissociable processes in spoken word recognition. NeuroImage 97, 387–395.

Sundara, M., Namasivayam, A.K., Chen, R., 2001. Observation–execution matching system for speech: a magnetic stimulation study. Neuroreport 12, 1341–1344.

Tettamanti, M., Buccino, G., Saccuman, M.C., Gallese, V., Danna, M., Scifo, P., Fazio, F., Rizzolatti, G., Cappa, S.F., Perani, D., 2005. Listening to action-related sentences activates fronto-parietal motor circuits. J. Cogn. Neurosci. 17, 273–281.

Tomasino, B., Weiss, P.H., Fink, G.R., 2010. To move or not to move: imperatives modulate action-related verb processing in the motor system. Neuroscience 169, 246–258.

van Dam, W.O., Rueschemeyer, S.A., Bekkering, H., 2010. How specifically are action verbs represented in the neural motor system: an fMRI study. NeuroImage 53, 1318–1325.

van Dijk, H., Nieuwenhuis, I.L., Jensen, O., 2010. Left temporal alpha band activity increases during working memory retention of pitches. Eur. J. Neurosci. 31, 1701–1707.

van Ede, F., Szebényi, S., Maris, E., 2014. Attentional modulations of somatosensory alpha, beta and gamma oscillations dissociate between anticipation and stimulus processing. NeuroImage 97, 134–141.

van Elk, M., van Schie, H.T., Zwaan, R.A., Bekkering, H., 2010. The functional role of motor activation in language processing: motor cortical oscillations support lexical–semantic retrieval. NeuroImage 50, 665–677.

Vukovic, N., Shtyrov, Y., 2014. Cortical motor systems are involved in second-language comprehension: evidence from rapid mu-rhythm desynchronisation. NeuroImage 102, 695–703.

Wang, L., Jensen, O., van den Brink, D., Weder, N., Schoffelen, J.M., Magyari, L., Hagoort, P., Bastiaansen, M., 2012. Beta oscillations relate to the N400m during language comprehension. Hum. Brain Mapp. 33, 2898–2912.

Weiss, S., Mueller, H.M., 2012. Too many betas do not spoil the broth: the role of beta brain oscillations in language processing. Front. Psychol. 3, 201.

West, W.C., Holcomb, P.J., 2000. Imaginal, semantic, and surface-level processing of concrete and abstract words: an electrophysiological investigation. J. Cogn. Neurosci. 12, 1024–1037.

Willems, R.M., Labruna, L., D'Esposito, M., Ivry, R., Casasanto, D., 2011. A functional role for the motor system in language understanding: evidence from theta-burst transcranial magnetic stimulation. Psychol. Sci. 22, 849–854.

Windhorst, U., 1996. On the role of recurrent inhibitory feedback in motor control. Prog. Neurobiol. 49, 517–587.

Zwaan, R.A., Taylor, L.J., 2006. Seeing, acting, understanding: motor resonance in language comprehension. J. Exp. Psychol. Gen. 135, 1–11.

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