NeuroImage 109 (2015) 438–448

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Language–motor interference reflected in MEG beta oscillations

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ARTICLE INFO

Article history:
Accepted 29 December 2014
Available online 8 January 2015

Keywords:
Embodied cognition
MEG
Beta oscillations
Action verbs
Interference
Imageability

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.

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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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http://dx.doi.org/10.1016/j.neuroimage.2014.12.077
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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

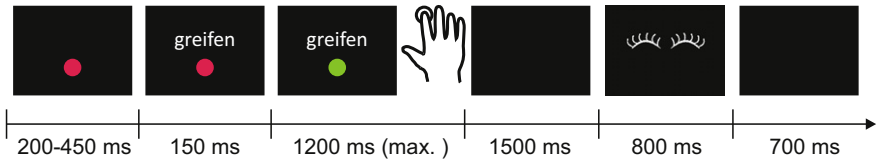

Fig. 1. Experimental procedure. The red cue was followed by a hand, foot, or abstract verb. The cue turning green was the Go signal. Subjects had to respond using their right hand for concrete (i.e., hand and foot) verbs. The eye pictogram determined the time window for eye blinks.

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

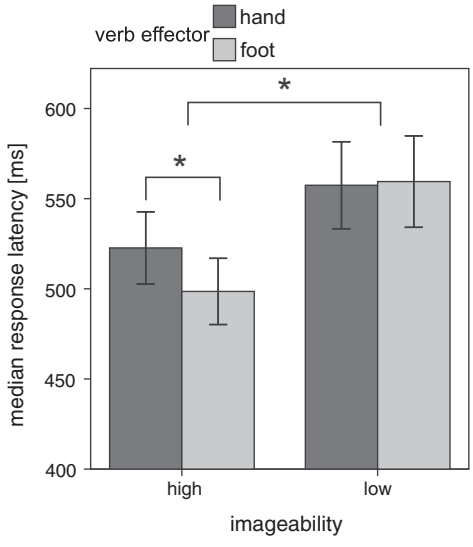

Fig. 2. Behavioural results. Response latencies are in reference to the Go signal 150 ms after verb onset. Error bars indicate standard error of the mean. * = $p < 0.05$.

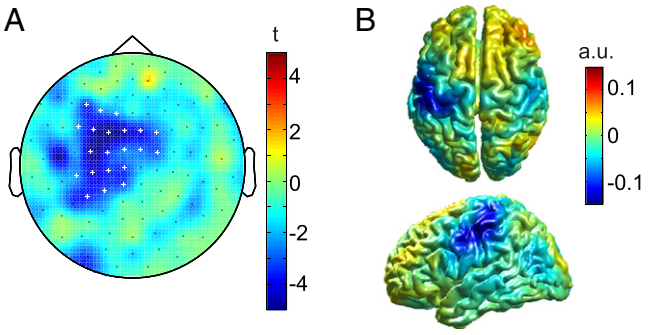

Fig. 3. Results from the localizer task. A: Statistically defined channel selection derived from the contrast −1 to −0.75 vs. −0.5 to −0.25 s before button press. Frequency is averaged for 15–25 Hz. Blue colours indicate stronger beta suppression in the later time window. B: Source reconstruction of 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

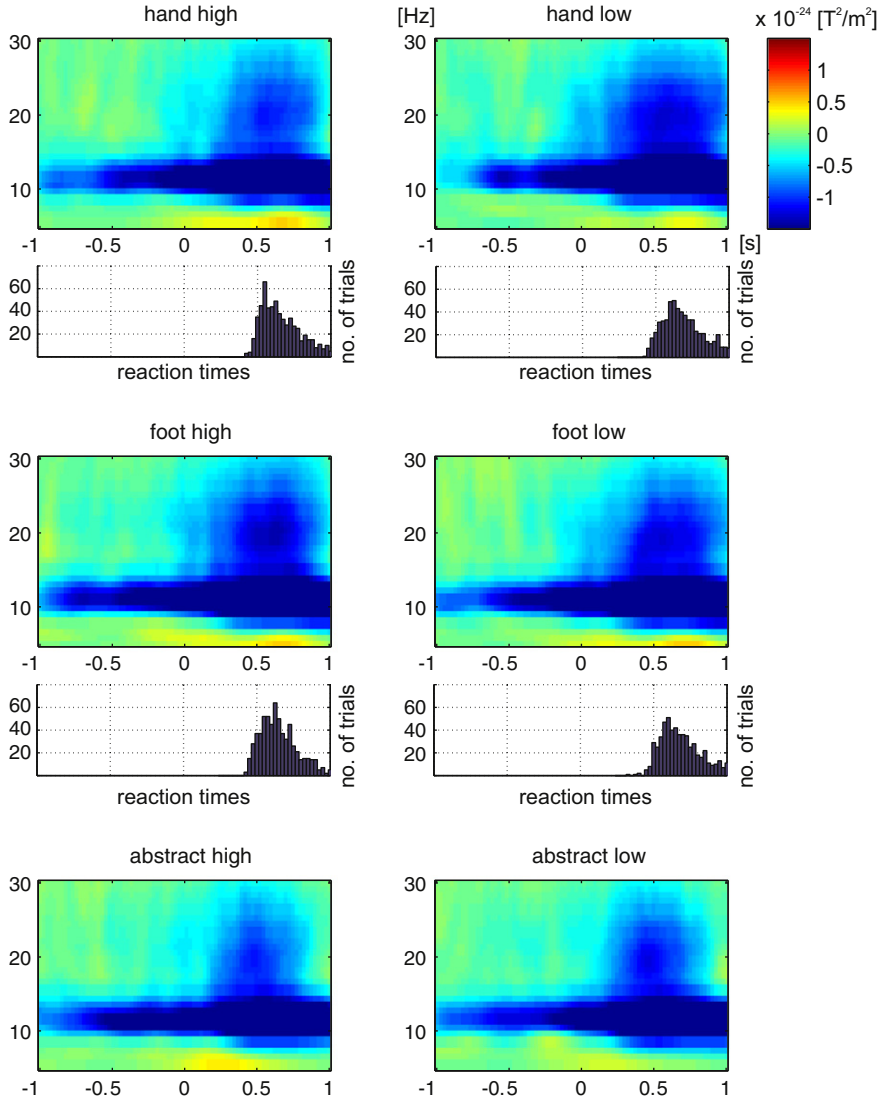

Fig. 4. Stimulus-locked analysis: time–frequency representations in the selected channels derived from the localizer task, for all six subconditions (hand, foot, abstract; high, low imageability). Time point 0 is word onset. The panels for the concrete verbs include distributions of single trial reaction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

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.

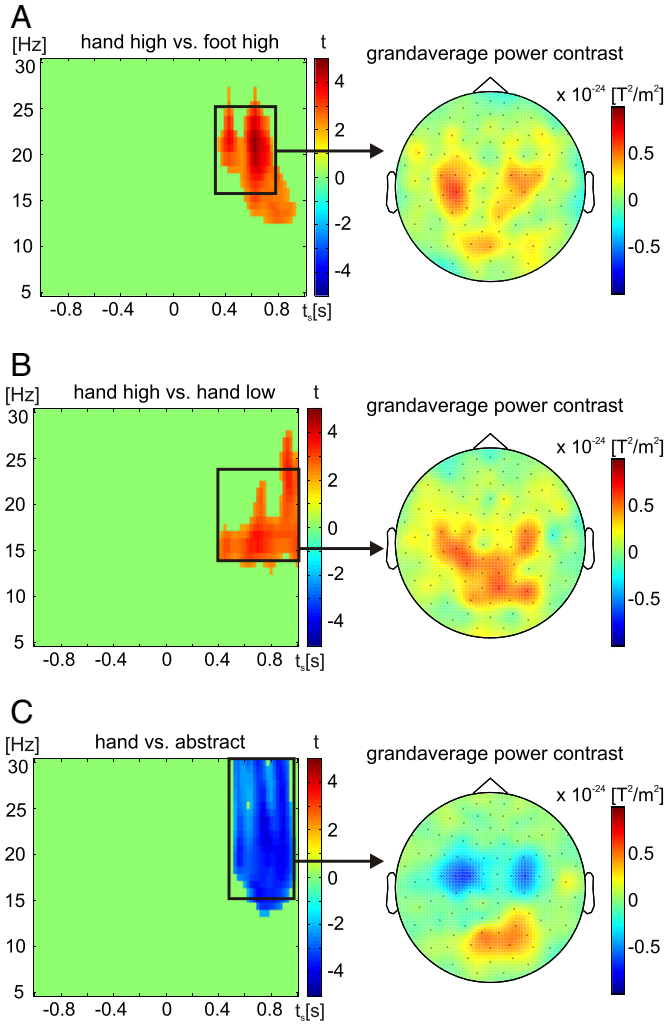

Fig. 5. Stimulus-locked analysis: statistical results from the spectral power analysis. Non-significant time–frequency tiles are masked. The roughly corresponding topographical representations of the significant clusters in the grandaverages are also shown. A: Contrast hand high vs. foot high. B: Contrast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

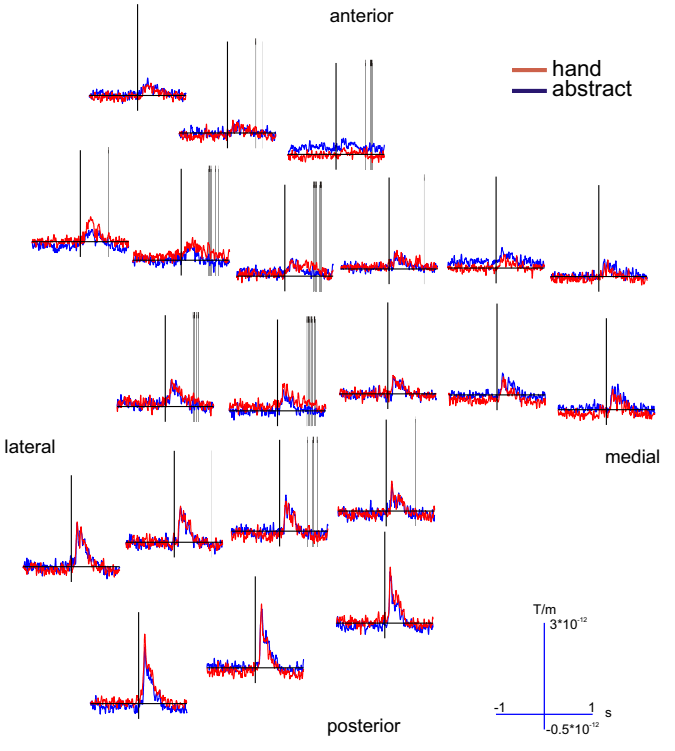

Fig. 6. Stimulus-locked analysis: statistical results from event-related fields, pooled contrast hand vs. abstract verbs. Each channel in the channel selection was analysed separately. Please refer to Fig. 3 for the locations of the sensors with respect to the head. Significant clusters in time are indicated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

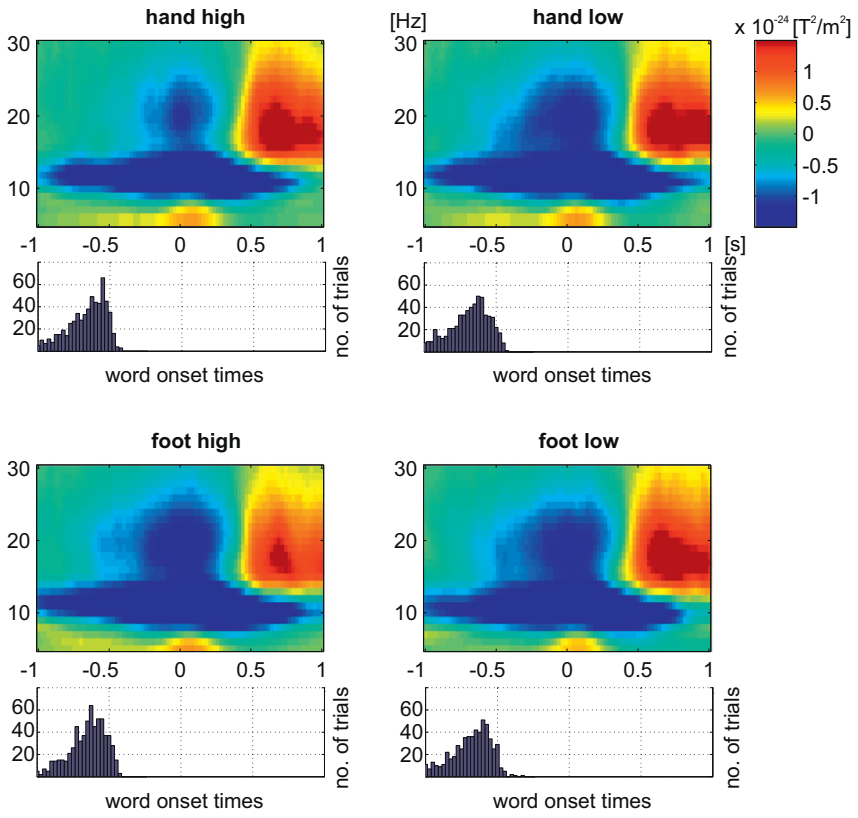

Fig. 7. Response-locked analysis: spectral power in the selected channels derived from the localizer task, for the four concrete subconditions. Time point 0 is the response. Panels include distributions of word onset times across all participants.

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.

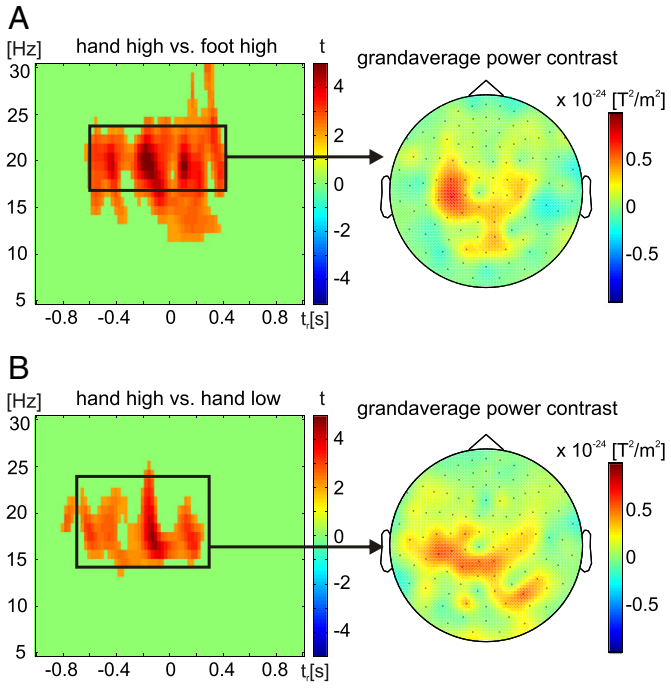

Fig. 8. Response-locked analysis: statistical results. Non-significant time–frequency tiles are masked. The roughly corresponding topographical representation of the significant clusters in the grandaverages are also shown. A: Contrast hand high vs. foot high. B: Contrast hand high vs. hand low.

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.

Acknowledgments

This work was supported by the Deutsche Forschungsgemeinschaft (SFB 991/1, B03). We thank Erika Rädisch for the acquisition of MRIs.

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.

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