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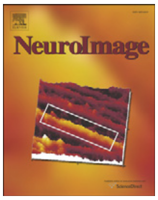

The functional role of motor activation in language processing: Motor cortical oscillations support lexical-semantic retrieval

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ABSTRACT

There is increasing experimental evidence that processing action-related language results in the automatic activation of associated regions of the motor and premotor cortex. However, the functional significance of motor activation in language processing is still under debate. In the present EEG study, we set out to investigate if language-induced motor activation primarily reflects the retrieval of lexical-semantic information or post-lexical motor imagery. The processing of action verbs was found accompanied by an early activation of motor-related brain areas, as reflected by a desynchronization in the mu- and beta-frequency bands which was localized to motor and premotor areas. A stronger motor activation was observed for verbs presented in an animal context (e.g. "The deer jumped over the stream") compared to a human context (e.g. "The athlete jumped over the fence") and motor resonance was directly modulated by the cloze probability of the noun–verb pairs. The onset of the motor effects preceded classical measures of semantic integration (i.e. the N400 component) and the strength of motor activation was found inversely related to the size of the N400 effect. These findings support the hypothesis that motor activation in language processing primarily supports the retrieval and integration of lexical-semantic information.

Introduction

Imagine yourself reading a story about your favorite football player, kicking the ball to make the winning goal with less then a minute left to play. Reading this story likely involves a great deal of vivid imagination, ranging from imagining the color of the player's shirt to representing his leg's kicking movements. During the last decade, a growing number of studies have indeed supported the suggestion that language understanding involves the activation of relevant visual and motor representations (for a review, see Fischer and Zwaan, 2008). Now suppose that you are reading Richard Adams' *Watership Down*, describing a rabbit that is kicking his feet to warn the rest of his group. An intriguing question is what kind of motor representations would support the understanding of the latter scenario. After all, the rabbit's kicking behavior is different from our own, specifically with respect to the motor programs involved. Thus, an interesting question is to what extent there is motor activation during the understanding of non-human actions relative to human actions (see also Buccino et al., 2004).

Studies on the representation of action-related verbs consistently show that reading verbs like "pick", "kick" or "lick" results in the activation of effector-specific regions of primary motor and premotor cortex, comparable to the activation observed when subjects move the effector most strongly associated with these verbs (i.e. the hand, foot or tongue; Aziz-Zadeh et al., 2006; Boulenger et al., 2009; Hauk et al., 2004; Pulvermuller, 2005). Further support for the notion that motor activation during language processing can be quite specific has been provided at a behavioral level as well. For example, subjects were faster in judging the sensibility of a sentence, when the response direction was congruent with the implied direction of the event described in the sentence (e.g. faster responding by making a movement towards the body when reading "he opens the drawer"; Glenberg and Kaschak, 2002). Furthermore, motor activation during language comprehension was found to occur relative to the onset of the critical verb, as reflected in faster responses when the rotation direction of manual responses and the implied direction by the sentences were congruent (Zwaan and Taylor, 2006).

Typically, the activation of motor-related brain areas in response to action-related verbs presented in isolation occurs very fast, within the first hundreds of milliseconds after a word is presented (Hauk et al., 2008; Pulvermuller et al., 2001). On the basis of these findings, it has been suggested that motor activation during language processing is a relatively automatic process, reflecting the spreading of activation through neuronal assemblies representing the word's meaning (Pulvermuller, 1999). In contrast, recent studies indicate that motor activation during the processing of action verbs is strongly modulated by linguistic context (Taylor et al., 2008; Tettamanti et al., 2008) and

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one's personal expertise (Beilock et al., 2008; Willems et al., 2009). For example, at a behavioral level, motor activation was found to be associated with words that disambiguate specific elements of the action rather than with the processing of the action verb itself (Taylor et al., 2008). When reading a sentence like, “He examined the pie through the microwave and turned the timer. The cooking time needed to be longer”, subjects were found to respond faster by making a clockwise rotation only for the disambiguating adverb “longer” but not for reading the verb “turned”, which was ambiguous with respect to the rotation direction. Furthermore, in a recent fMRI study motor-related brain areas were found to be less strongly activated when subjects listened to negative (e.g. “now I don't push the button”) compared to affirmative action sentences (e.g. “now I push the button”; Tettamanti et al., 2008).

In addition, motor activation during language processing is found to be related to one's personal expertise. For instance, in left- and right-handers the activation of premotor areas during the reading of action verbs appeared to be lateralized with respect to the handedness of the subject (i.e. stronger left-hemispheric activation for right-handers and vice versa for left-handers; Willems et al., 2009). Furthermore, a stronger activation of premotor cortex was observed when expert hockey players compared to novices were reading action sentences describing hockey events, likely reflecting the retrieval of learned motor programs (Beilock et al., 2008). In contrast, novices showed a stronger activation of the primary sensory-motor cortex during the processing of hockey-related language, suggesting that without the relevant action experience language understanding occurs at a lower level in the motor system. In sum, several studies suggest that motor activation in language comprehension can be quite specific, automatic and linked with the onset of the verb, whereas other studies suggest that motor activation may reflect higher aspects of the sentence's meaning and is strongly dependent on linguistic context and one's expertise.

Accordingly, the functional significance of motor activation during language processing is still under debate (for a discussion, see Mahon and Caramazza, 2008). That is, at present it is unclear whether motor activation primarily reflects the automatic activation of lexical-semantic features (e.g. Pulvermuller, 2005) or post-lexical motor imagery (e.g. Toni et al., 2008). In the present study, we aimed to distinguish between these two hypotheses. To obtain better insight in the functional role of motor activation during language processing, we selected action verbs that could be used to refer to actions of both humans and animals and presented these verbs in an animal or in a human context. For example, subjects read a sentence like “The athlete jumps over the hurdle” and subjects' EEG responses were recorded relative to the onset of the verb. In a similar fashion, subjects would read a sentence like “The deer jumps over the fence” and accordingly the critical verbs occurred equally often in both human and animal contexts.

The verbs presented in both an animal and a human context comprised the same words, but the kinematics implied by the verb were different. That is, the way in which most animals move is fundamentally different from the way in which humans move (e.g. the way in which a fish swims differs dramatically from the way in which a woman swims). In addition, because animals have only limited action capabilities compared to humans the range of verbs that can follow a noun is smaller for an animal context compared to a human context (e.g. a fish can swim or eat, whereas a human can perform an endless range of different actions). Thus, by presenting verbs in an animal compared to a human context we manipulated both the (1) action familiarity described by the verb and (2) the cloze probability of the noun–verb pair. This manipulation directly allowed us to disentangle the two possible hypotheses regarding the relation between language and motor activation. That is, motor activation in language processing could reflect primarily (1) motor imagery, related to the kinematics involved in the referential situation described by the sentence or (2) the implicit retrieval of lexical-semantic information. If motor activation in association with the verb primarily reflects motor imagery, we should expect stronger motor activation for verbs in a human context because human actions are easier to imagine than animal actions (see also below). In contrast, if motor activation reflects lexical-semantic retrieval, we should expect stronger motor activation for verbs in an animal context because the preceding noun limits the range of verbs that could possibly follow and thus facilitates the retrieval of motor-related information.

Motor imagery is here defined as the covert re-enactment of an action (Barsalou, 1999). Imagery is often considered a reflective process that has a retrospective function, such as retrieving information that was implicitly learned via perception (Pinker, 1984), confirming initial perceptual guesses during motor imagery (de Lange et al., 2005) or for post-lexical visualization (van Schie et al., 2005). Several studies indicate that one's expertise influences the amount of activation of motor-related brain areas during motor imagery tasks, with increased activation during imagery of actions that are well established in one's motor repertoire (Fourkas et al., 2008; Sacco et al., 2006; Wei and Luo, in press). Furthermore, many studies on action observation have shown that the motor system is more strongly activated for the observation of familiar compared to unfamiliar actions (Buccino et al., 2004; Calvo-Merino et al., 2005, 2006; van Elk et al., 2008b). For instance, Buccino et al. (2004) found that the observation of an action performed by a conspecific (e.g. observing a man biting a potato) resulted in a stronger activation of motor-related brain areas than the observation of an action performed by an animal with a different body (e.g. observing a dog biting a potato).

In sum, studies on motor imagery and action observation indicate that the motor system is more strongly activated for imagining or observing familiar compared to unfamiliar actions. Most animals' bodies and the way in which they perform certain actions differ in fundamental ways from humans' bodies and their action repertoire. Accordingly, motor imagery of human actions should be much easier than motor imagery of animal actions. Therefore, if motor activation in language processing primarily reflects *motor imagery*, we should expect a stronger motor activation for verbs presented in a human compared to an animal context.

Alternatively, if motor activation in language processing primarily reflects the *retrieval of lexical-semantic information*, we should expect stronger motor activation for animal compared to human sentences. That is, because animals have limited action capabilities as compared to humans, the cloze probability of animal noun–verb pairs is higher than the cloze probability of human noun–verb pairs, which should lead to a stronger prediction and facilitated retrieval of the action semantic information associated with the verb when presented in an animal compared to a human context. The hypothesis that motor activation supports lexical-semantic integration goes well with the notion that *motor resonance* reflects an implicit and automatic process used for prediction. For instance, reading the word “cup” results in predictions about the actions that are required for using the cup (Rueschemeyer et al., in press) and reading a verb like *grasp* may serve as an implicit cue to prepare the language user for likely actions (Barsalou, 2009). Furthermore, readers use both linguistic and extra-linguistic information to anticipate phonemes, words, syntactic constructs and discourse referents (Van Berkum et al., 2005). Thus, a core function of implicit motor activation during language processing could be prediction (called “presonance” by Zwaan and Kaschak, 2009). Furthermore, the hypothesis that motor activation reflects lexical-semantic processing rather than specific motor imagery goes well with the notion that motor representations cued by verbs must be underspecified enough to accommodate new incoming information. For instance, when reading the sentence “The scientist grabs…” motor activation in association with the word “grabs” would need to allow for varying sentence endings referring to different movement kinematics as in the case of “The scientist grabs his beer” or “The scientist grabs his notebook” (Taylor et al., 2008).

In addition to determining the sensitivity of language-induced motor activation to lexical-semantic or motor imagery constraints, the present study also tried to elucidate the time course of motor activation during language processing. If motor activation reflects the retrieval of lexical-semantic features, we should expect early effects in the motor system (i.e. concurring with or preceding classical measures of semantic retrieval, such as the N400 component; see also Pulvermuller, 2005; van Schie et al., 2005). Alternatively, if motor activation reflects post-lexical motor imagery, we should expect later effects in the motor system (i.e. >500 ms after word onset; cf. Papeo et al., 2009; van Schie et al., 2005).

Due to its high temporal resolution, EEG provides an excellent opportunity to capture the time course of the semantic and visuo-motor processes accompanying the onset of the action verb. Semantic processing has typically been associated with the N400 component in the ERP, a negative deflection found maximal over central sites approximately 400 ms after word onset (Kutas and Hillyard, 1984). The activation of motor areas is reflected in the EEG as a desynchronization (i.e. a decrease in power) in both the mu- and beta-frequency bands (Hari, 2006). For example, action execution, action observation and motor imagery are associated with decreases in power in the mu- and beta-frequency bands over central and parietal motor areas (Caetano et al., 2007; de Lange et al., 2008; Koelewijn et al., 2008; van Elk et al., 2008b). Interestingly, in the language domain hardly any studies have focused on mu- and beta-desynchronization as a functional measure of motor activation (for review of the functional significance of brain oscillations during language processing, see Bastiaansen and Hagoort, 2006). Given the robust findings of mu- and beta-suppression in the motor domain, we expected that motor-related activation during the processing of action verbs should become apparent in mu- and beta-desynchronization as well.

In sum, the present study aimed to identify whether motor activation in language processing primarily reflects *motor imagery*, which is defined as the reflective process of re-enacting familiar motor experiences (Barsalou, 2009) or *lexical-semantic integration*, which consists of the implicit and automatic activation of motor information used for prediction (i.e. presonance; Zwaan and Kaschak, 2009). If motor activation reflects *motor imagery*, we should expect (1) a stronger motor activation for verbs presented in a human context and (2) a relatively slow activation of motor-related brain areas (i.e. following classical measures of semantic integration, such as the N400; cf. van Schie et al., 2005). Alternatively, if motor activation reflects *lexical-semantic integration*, we should expect (1) a stronger motor activation for verbs presented in an animal context and (2) a relatively fast activation of motor-related brain areas (i.e. within the first hundreds of milliseconds after verb onset; cf. Pulvermuller et al., 2001).

Methods

Subjects

In total 28 subjects were tested, but data from 4 subjects were discarded due to excessive eye blinking or muscle artifacts, leaving 24 participants (4 males, mean age = 21.1 years) in the final analysis. All participants were right-handed and had Dutch as their mother tongue. The study was approved by the local ethics committee and all participants gave informed consent prior to the experiment, in accordance with the declaration of Helsinki.

Stimulus materials

Animal and human noun–verb pairs

A total of 68 verbs were used to create 136 sentences describing either a human action or an animal action (for example stimuli, see Table 1; the whole stimulus list is available as online supporting material). Each verb was presented twice, once in a human context and once in an animal context. For example, the verb "jump" was presented in a human context in the sentence "The athlete jumps over the hurdle" and in an animal context in the sentence "The deer jumps over the fence". Care was taken that the number of repeated nouns preceding the action verb was comparable for both human and animal noun–verb pairs. In addition, care was taken that the noun–verb pair always described a concrete action. By presenting verbs in a human compared to an animal context, the possibility for motor imagery of the kinematics implied by the sentence was directly manipulated. That is, the actions described by animal sentences are more unfamiliar than human sentences because in most cases different effectors and different movements are involved (e.g. the way a deer jumps is highly dissimilar from the way an athlete jumps).

Table 1
Example of stimulus materials. Critical verbs and words are marked in bold.

Human context		
Dutch	De vrouw **zwemt** in het water.	
English	The woman **is swimming** in the water.	
Dutch	De atleet **springt** over de horde.	
English	The athlete **jumps** over the hurdle.	
Animal context		
Dutch	De eend **zwemt** in de vijver.	
English	The duck **is swimming** in the pond.	
Dutch	Het hert **springt** over het hek.	
English	The deer **jumps** over the fence.	
Filler sentences		
		Related word
Dutch	De koetsier zorgt voor de paarden	**postkoets**
English	The coachmen is taking care of the horses	**post chaise**
		Unrelated word
Dutch	De acteur staat op het toneel	**postkoets**
English	The actor is standing at the stage	**post chaise**

Cloze probability of the noun–verb pairs

The construction of animal and human noun–verb pairs implicitly involved the manipulation of the cloze probability of the items. In other words, stronger semantic associations exist between animals and subsequently presented verbs (e.g. the fish—is swimming) than between humans and subsequently presented verbs (e.g. the woman—is swimming). To determine the cloze probability of the items, a cloze probability pre-test was conducted. Twenty-four subjects were presented with the first identifier and noun for each sentence and were asked to generate five different verbs that could continue the sentence. They were encouraged to write down the verbs that first came to their minds. Next, for each noun–verb pair used in the present study the cloze probability was calculated by taking the percentage of subjects that generated this specific verb in response to the noun. Overall, all sentences had a low cloze probability (mean overlap between responses = 11.8%, SD = 21.5), reflecting that the mere presentation of a noun poses only limited restrictions on the possible verbs that could follow. Importantly, noun–verb pairs for human sentences had a lower cloze probability (mean overlap between responses = 7.8%, SD = 18.2) than noun–verb pairs for animal sentences (mean = 15.8%, SD = 23.8), $t(134) = -2.2$, $p < .05$.

On the basis of the pre-test, it turned out that more than half of all items had a cloze probability of zero, indicating that none of the participants came up with the verb that was used in the experiment. To enable a more refined differentiation of the cloze probability of the items an additional measure was required. Therefore, for each noun–verb pair, the log of the number of hits using Google was calculated. The log cloze probability obtained in the cloze probability test and the log number of Google hits were found to be correlated, for both human items, $r = .425$, $p < .05$, and for animal items, $r = .374$, $p < .05$, indicating that both scales measured the same construct. Accordingly, both measures were combined in a cloze probability scale, by taking the average of (1) the log cloze probability obtained in the cloze probability test and (2) the log of the number of Google hits. On the basis of this scale, both human and animal noun–verb pairs could be split into items with a low cloze probability and items with a high cloze probability for subsequent analysis. As a consequence, in a subsequent analysis, the verbs were analyzed using a 2×2 design with the factors Context (Animal vs. Human) and Cloze Probability (High vs. Low), leaving 34 items per category.

Filler sentences

In addition to the human and the animal action sentences, 68 filler sentences were created (see Table 1). For half of all filler sentences a related noun was constructed, resulting in 34 related sentence-word pairs. By assigning the nouns to the remaining filler sentences, 34 additional unrelated sentence-word pairs were constructed (see Table 1). The ERP response to unrelated compared to related words could be used as a standard N400 effect to compare with the effects in response to the critical action verbs.

Procedure

The experiment was controlled using Presentation software (version 11.0.03, Neurobehavioral Systems, Albany, USA). During the experiment, participants were seated in a sound- and electrically shielded room. Words were presented in white on a black background in a font-size of 24, resulting in a visual angle of approximately 2 visual degrees. The sentences were randomly presented and appeared word by word on a screen in front of the subject. Word duration was 300 ms and each word was preceded by a 300-ms blank screen. Sentence final words were indicated with a period. In the target trials (human context and animal context), each sentence was followed by a blank screen for 3 s and next an asterisk indicated that the next sentence would be presented within 3 s. In the filler trials, each sentence was followed by a 1000-ms blank screen after which a related or unrelated word appeared (see Table 1). The word remained on the screen until the subject responded by indicating whether the word was related to the preceding sentence or not by pressing the left or the right button of a button box. After the subject responded, the screen went blank for 3 s and an asterisk indicated that the next trial would start in 3 s.

Participants were instructed to sit still in a comfortable position and to avoid blinking when the words were presented on the screen. The experiment started with 10 practice trials which contained different sentences than used during the main part of the experiment. Participants were instructed to carefully read all the sentences that were presented because sometimes they had to indicate whether a subsequently presented word was related to the preceding sentence or not. The experiment was run in two separate blocks of 98 trials and in between blocks the participants rested. In total the experiment took about 50 min.

Recording

The electroencephalogram (EEG) was recorded using 60 active electrodes that were placed in an actiCAP (BrainProducts, Munich, Germany). Electrode positions were based on the M-10 Equidistant 61-Channel-Arrangement, with an inter-electrode distance of 37 ± 3 mm (given a head circumference of 58 cm). All electrodes were referenced to the left mastoid online and re-referenced offline to the linked mastoids. The impedance of the electrodes was kept below 10 kΩ. EEG and EOG signals were amplified using two 32-channel BrainAmp DC EEG amplifiers. The signal was sampled at 500 Hz and filtered online with an 80-Hz high cutoff filter and a 10-s time constant.

Analysis

Analyses were conducted using Vision Analyzer (Brainproducts, Munich, Germany) and FieldTrip open source software (http://www.ru.nl/neuroimaging/fieldtrip/). The EEG data were segmented from −500 to 1200 ms relative to the onset of the critical verb. Trials with amplifier or movement artifacts were excluded from analysis on the basis of a semi-automated visual inspection procedure on the raw data.

For the ERP analysis, a baseline correction was applied from −100 ms to the onset of the critical verb. Event-related potentials (ERPs) were calculated relative to the onset of the verb by averaging all trial segments for each condition and subject separately. In addition, ERPs were calculated for related and unrelated words that were presented after the filler trials. In this way, a standard N400 effect could be identified, with which the effects to the critical verbs could be compared. To test for significant differences between both conditions a cluster-randomization procedure was applied, which identifies consistent changes between conditions in time-electrode clusters when applied to ERPs (for rationale of the cluster-randomization test, see below). The cluster-level randomization procedure controls effectively for the multiple comparisons problem in the statistical analysis of ERPs.

For the time-frequency analysis, the time-frequency representation (TFR) was computed for every trial by convolving a Morlet wavelet with the signal with a width of 7 cycles. Averaged TFRs were computed by averaging the power over single trials for every condition and subject separately. Differences between both conditions were tested for statistical significance by using a cluster-level randomization procedure to identify consistent changes between conditions in time-frequency electrode clusters when applied to TFRs.

The cluster-randomization procedure is used to control for multiple comparisons (Maris and Oostenveld, 2007). First, two-sided t-tests are computed and thresholded ($\alpha = 5\%$) for the difference between two conditions for individual channel–time pairs (ERP analysis) or for channel–time-frequency pairs (TFR analysis). Next, significant channel–time or channel–time-frequency pairs were clustered by identifying pairs showing the same direction of effect. To assess statistical significance of each cluster, a cluster-level test statistic was chosen by computing the sum of all t-statistics in the cluster. The significance of each cluster-level statistic was estimated by comparing the cluster statistic to its randomization distribution. The randomization distribution is the distribution of the test statistic under the null hypothesis that specifies the probability that conditions remain the same after permutation of these condition-specific averages. The randomization distribution was obtained by creating 1000 grand-average randomizations for relevant conditions by random permutation. Subsequently, the p-value was estimated as the proportion from the randomization null distribution in which the maximum cluster-level test statistic exceeded the observed cluster-level test statistic.

Main analysis focused on differences between verbs presented in a human context or in an animal context. For the ERP analysis, first a standard N400 effect was identified by comparing related and unrelated words presented after the filler items. Next, ERPs were compared between verbs presented in a human and in an animal context. For the TFR analysis, comparison of the power for verbs in a human and in an animal context revealed large differences in the mu- and beta-frequency bands (10–14 and 20–30 Hz, respectively) and cluster-randomization tests were applied to the power averaged over these frequency intervals. In subsequent analyses, it was investigated if the N400-amplitude and the mu- and beta-effects were modulated by the cloze probability of the noun–verb pairs. Verbs presented in filler sentences were not analyzed because the critical verbs were not matched between target and filler items. In contrast, for target sentences the critical verbs were perfectly matched between animal and human contexts. Accordingly, any difference between both conditions could be attributed solely to contextual differences, rather than to the presentation of different words.

Source analysis

To identify sources of oscillatory activity, a beam-forming approach was used (Dynamic Imaging of Coherent Sources; DICS). For source reconstruction, the data from all electrodes with respect to an average reference were used. The DICS technique uses adaptive spatial filters to localize power in the entire brain (Gross et al., 2005; Liljestrom et al., 2005). For all subjects, a standard multisphere forward model was used, based on the standard MNI/SPM brain (Montreal Neurological Institute (MNI), Montreal, Quebec, Canada; http://www.bic.mni.mcgill.ca/brainweb). The brain volume was discretized to a grid with a 1-cm resolution and using the cross-spectral density matrices and the forward model, spatial filters were constructed for each grid point. These filters were applied to the Fourier transformed data and the spatial distribution of power was estimated for each condition, separately for the mu- and beta-frequency bands. Grand average sources were calculated by averaging across subjects and different conditions were compared by calculating the relative difference in power for verbs presented in an animal compared to a human context.

Peak latency analysis

A peak correlation analysis was conducted to investigate relations between the N400 effect and the effects in the mu- and beta-frequency bands. For each individual subject, the peak latencies of the N400 component were identified per condition and correlated with the peak latencies of the power in the mu- and beta-frequency bands. Peak latencies were identified via an automated procedure. First, per subject and condition the derivative of the averaged signal was calculated across a cluster of electrodes that was found significant in the main analysis. On the basis of the zero-crossings of the derivative, the trough with the strongest local minimum could be selected in the interval from 160 to 600 ms after word onset. Visual inspection of the selected peaks confirmed the reliability of this automated procedure. Peak latencies of the N400 were identified on the individual ERPs, separately for verbs in a human and an animal context. Peak latencies of the mu-frequency band were identified on the basis of a cluster of electrodes that contributed to the mu-effect averaged over the mu-frequency band (10–14 Hz). Peak latencies of the beta-frequency band were identified on the basis of a cluster of electrodes that contributed to the beta-effect averaged over the beta-frequency band (20–30 Hz).

Results

Behavioral results

On average, subjects made incorrect responses to filler items in 5.7% of all trials and subject's average response latency was 1211 ms. Subjects were faster to respond to unrelated words (M = 1156 ms, SD = 294 ms) compared to related words (M = 1269 ms, SD = 339 ms), $t1(23) = 2.9$, $p < .01$. The item analysis showed the same direction of effect, with faster responses to unrelated (M = 1111 ms, SD = 94 ms) compared to related words (M = 1212 ms, SD = 106 ms), $t2(33) = 4.3$, $p < .001$. The faster responses to unrelated words likely reflect a general reaction time advantage for responses made by the dominant hand (Jacobson et al., 1986). That is, subjects always responded to unrelated filler words with their dominant hand (right hand button press) whereas related filler words were responded to with the non-dominant hand (left hand button press), thereby overshadowing any reaction time advantage of the congruency of the sentence and the noun.

ERP results

Standard N400 effect for filler items

A standard N400 effect was identified by comparing unrelated compared to related words that were presented as filler items. Unrelated compared to related filler words elicited a stronger N400 component from 310 to 612 ms after word onset, $p < .001$ (see left side of Fig. 1), and the difference between unrelated and related words was found broadly distributed with a maximum at central electrodes (see right side of Fig. 1).

N400 effect for verbs presented in a human context

For verbs presented in a human context, a stronger negative deflection compared to verbs presented in an animal context was found significant from 250 to 380 ms after verb onset, $p < .05$ (see left side of Fig. 2). The timing of this N400 effect partially overlaps with the standard N400 effect to filler items and is within the range of N400s reported previously (cf. van Berkum et al., 2003; van den Brink et al., 2006). Furthermore, the scalp distribution of the N400 effect to verbs appears comparable to the standard N400 effect to filler items.

Commonality of N400 effects

To investigate the commonality of the standard N400 effect to filler items and the N400 effect obtained for verbs presented in an animal context, a correlation analysis was conducted. For each subject, the average N400 effect was calculated by taking the average ERP amplitude in the interval in which the effects were

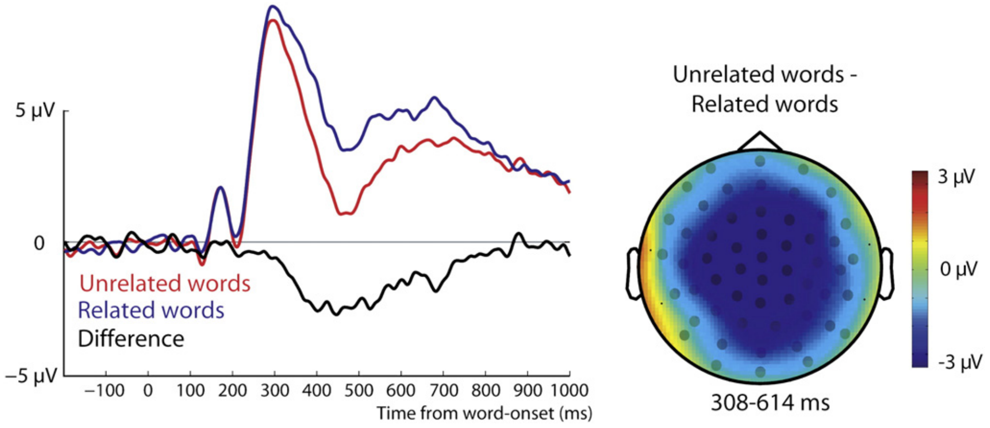


Fig. 1. N400 effect for filler items. ERPs relative to word onset for related filler items and unrelated filler items (left side) and the distribution of the standard N400 effect between unrelated and related filler items (right side). Electrodes showing significant differences between conditions are marked in grey.

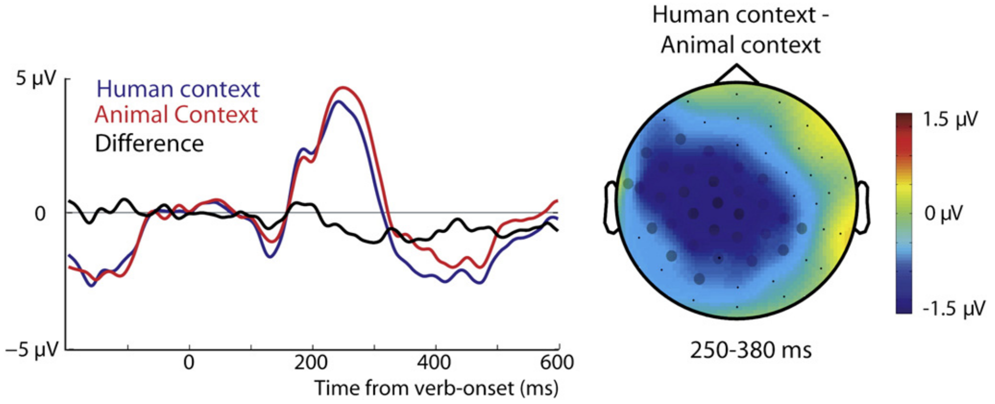


Fig. 2. N400 effect for action verbs. ERPs relative to word onset for verbs presented in an animal context and in a human context (left side) and the distribution of the N400 effect between verbs in an animal and a human context (right side). Electrodes showing significant differences between conditions are marked in grey.

found significant. The correlation between the standard N400 effect (unrelated–related filler words) and the N400 effect for verbs presented in a human compared to an animal context was calculated across subjects, using Pearson's *r*. As can be seen in Fig. 3, a significant correlation was observed between the individual standard N400 effect size and the N400 effect for verbs presented in a human context, $r = .572$, $p < .005$.

To investigate the overlap in scalp distribution of both N400 effects, the effects were compared across the entire set of electrodes using the average value per electrode calculated from the interval in which the N400s were found significant, as entries to calculate Pearson's correlation. A strong correlation was observed between both N400 effects, $r = .705$, $p < .001$ (see Fig. 3). In a subsequent analysis, Pearson's correlation was calculated for a subset of electrodes that was found significant for the standard N400 effect. For this subset of electrodes, again a significant correlation was observed between both N400 effects, $r = .573$, $p < .001$.

To further test the overlap between both effects, two rectangular 3×3 electrode grids were projected overlying central areas (cf. Praamstra et al., 2005). A repeated measures analysis was conducted on the mean amplitudes of the N400 effects with the factors Effect, Hemisphere (Left vs. Right), Anterior–Posterior axis (3 levels) and Medial–Lateral axis (3 levels). First, a main effect of Effect indicated that the N400 effect for filler items was stronger than the N400 effect for verbs, $F(1,23) = 11.6$, $p < .005$. A significant interaction was observed between Effect and Medial–Lateral axis, $F(2,22) = 9.2$, $p < .001$, indicating that the N400 effect for filler items was more laterally distributed than the N400 effect for verbs. A significant three-way interaction between Effect, Hemisphere and Medial–Lateral axis, $F(2,22) = 3.5$, $p < .05$, indicated that the N400 effect for verbs was slightly lateralized to the lateral part of the left hemisphere, compared to the N400 effect for filler items. Finally, a significant four-way interaction between Effect, Hemisphere, Anterior–Posterior axis and Medial–Lateral axis, $F(4,20) = 3.6$, $p < .05$, indicates that the N400 effect for verbs was slightly stronger at anterior left lateral sites compared to the N400 effect for filler items. In sum, the correlation analysis suggested a considerable overlap in the distribution of both N400 effects, but the N400 for verbs appeared to be more strongly lateralized to the left anterior hemisphere compared to the N400 for filler items.

Time-frequency effects for verbs

As can be seen in the upper part of Fig. 4, the onset of the verb was accompanied by a strong increase in power from 8 to 24 Hz in the first 200 ms after verb presentation, likely related to the processing of the preceding noun. Next, a desynchronization in the mu- and beta-frequency bands was observed from about 200 to 600 ms. After 600 ms, the next word appeared on the screen, which was accompanied by an increase in power from about 600 ms.

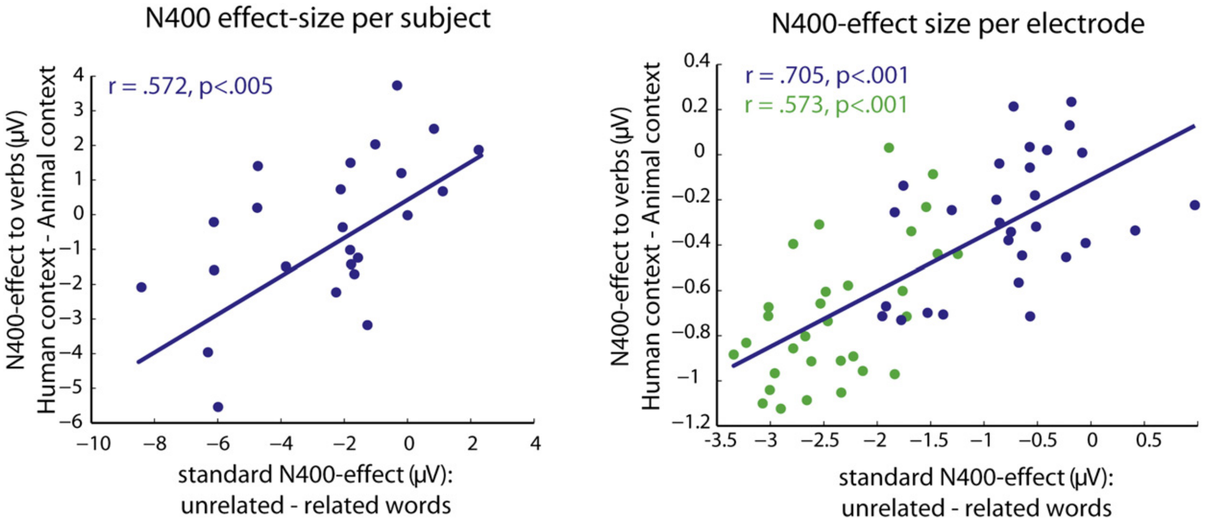


Fig. 3. N400 correlations. Correlation between the N400 effect for filler items and for verbs presented in a human compared to an animal context (left side). Correlation of scalp topography between both N400 effects for all electrodes (right side: blue and green dots) and for a subset of electrodes (green dots). Electrodes showing significant differences between conditions are marked in grey.

The comparison of the power spectra of verbs presented in a human and an animal context indicated a stronger relative decrease in the mu- and beta-frequency bands for verbs presented in an animal compared to a human context (see Fig. 4, middle part). Cluster-level randomization tests indicated a significant difference between both conditions in the mu-frequency band (10–14 Hz) from 160 to 520 ms after verb onset, $p<.01$. This difference was found maximal at frontal–central scalp regions (Fig. 4, lower part). In addition, a significant difference was observed in the beta-frequency band (20–30 Hz) from 500 to 600 ms after verb onset, $p<.01$, and this difference was found maximal over central electrodes (Fig. 4, middle part).

Source analysis

The sources accounting for the modulation in the mu- and beta-frequency bands were characterized by comparing the 10- to 14-Hz and the 20- to 30-Hz activity between verbs presented in an animal compared to a human context during the interval in which the effects were found significant. The sources accounting for the mu-effect (12 ± 2 Hz) for verbs presented in an animal compared to a human context were localized in BA 4 around the medial part of the precentral gyrus ($x=10$, $y=-25$, $z=70$; see Fig. 5). The sources accounting for the beta-effect (25 ± 5 Hz) for verbs presented in an animal compared to a human context were localized in BA 6 around the left dorsal premotor cortex ($x=-30$, $y=-5$, $z=68$; see Fig. 5).

Cloze probability of the noun–verb pairs

The pre-test indicated that the animal noun–verb pairs had a higher cloze probability than the human noun–verb pairs. Therefore, the smaller N400 and the stronger mu- and beta-desynchronization for verbs presented in an animal context likely reflected the facilitated retrieval of action semantic information (Kutas and Hillyard, 1984). To obtain further evidence that the cloze probability of the noun–verb pairs is the driving factor of the N400 effect and the mu/beta-effects, in a subsequent analysis we directly compared noun–verb pairs with a low and a high cloze probability.

Based on the pretest, all human and animal noun–verb pairs were classified according to the cloze probability of the items (high or low; see Table 2). The averaged N400 amplitude was calculated over the time interval and electrodes for which the effects of the main analysis were found significant and were analyzed using a repeated measures ANOVA with the factors Context (Human vs. Animal) and Cloze Probability (High vs. Low). As expected, a main effect of Context indicated a stronger N400 amplitude for verbs presented in a human compared to an animal context, $F(1,24)=4.3$, $p<.05$ (see Fig. 6). In addition, a main effect of Cloze Probability indicated that verbs with a low cloze probability resulted in a stronger N400 amplitude than verbs with a high cloze probability, $F(1,24)=4.7$, $p<.05$. No interaction was found between Context and Cloze Probability. These findings confirm the interpretation that the stronger N400 amplitude for verbs in a human compared to an animal context reflects the lower cloze probability for human verb–noun combinations.

To investigate whether the differences in the mu- and beta-frequency band reflected the strength of the semantic associations between the noun and the verb, the averaged mu- and beta-power were calculated over the intervals and electrodes for which the main effects were found significant and were analyzed using a repeated measures ANOVA with the factors Context (Human vs. Animal) and Cloze Probability (High vs. Low).

For the mu-power, a main effect of Context indicated a stronger mu-desynchronization for verbs presented in an animal compared to a human context, $F(1,24)=7.7$, $p<.01$ (see Fig. 6). No effect of cloze probability was observed and no interaction was found (F's<1). For the beta-power, a main effect of Context indicated a stronger beta-desynchronization for verbs presented in an animal compared to a human context, $F(1, 24)=11.9$, $p<.005$ (see Fig. 6). In addition, a significant effect of Cloze Probability, $F(1, 24)=6.3$, $p<.05$, indicated a stronger beta-desynchronization for items with a high cloze probability compared to items with a low cloze probability (see Fig. 6). No interaction effect was found ($F<1$). These analyses indicate that overall a stronger motor activation was found for verbs in an animal context compared to a human context, as reflected in a stronger mu- and beta-desynchronization. Interestingly, the beta-effect appeared to be driven by the cloze probability of the noun–verb pairs as well, with a stronger beta-desynchronization for noun–verb pairs with a high cloze probability.

To sum up, verbs presented in animal sentences had a higher cloze probability than human sentences and generated a reduced N400 amplitude and stronger motor activation, as reflected in desynchronization in the mu- and beta-frequency bands.

Peak latency analysis

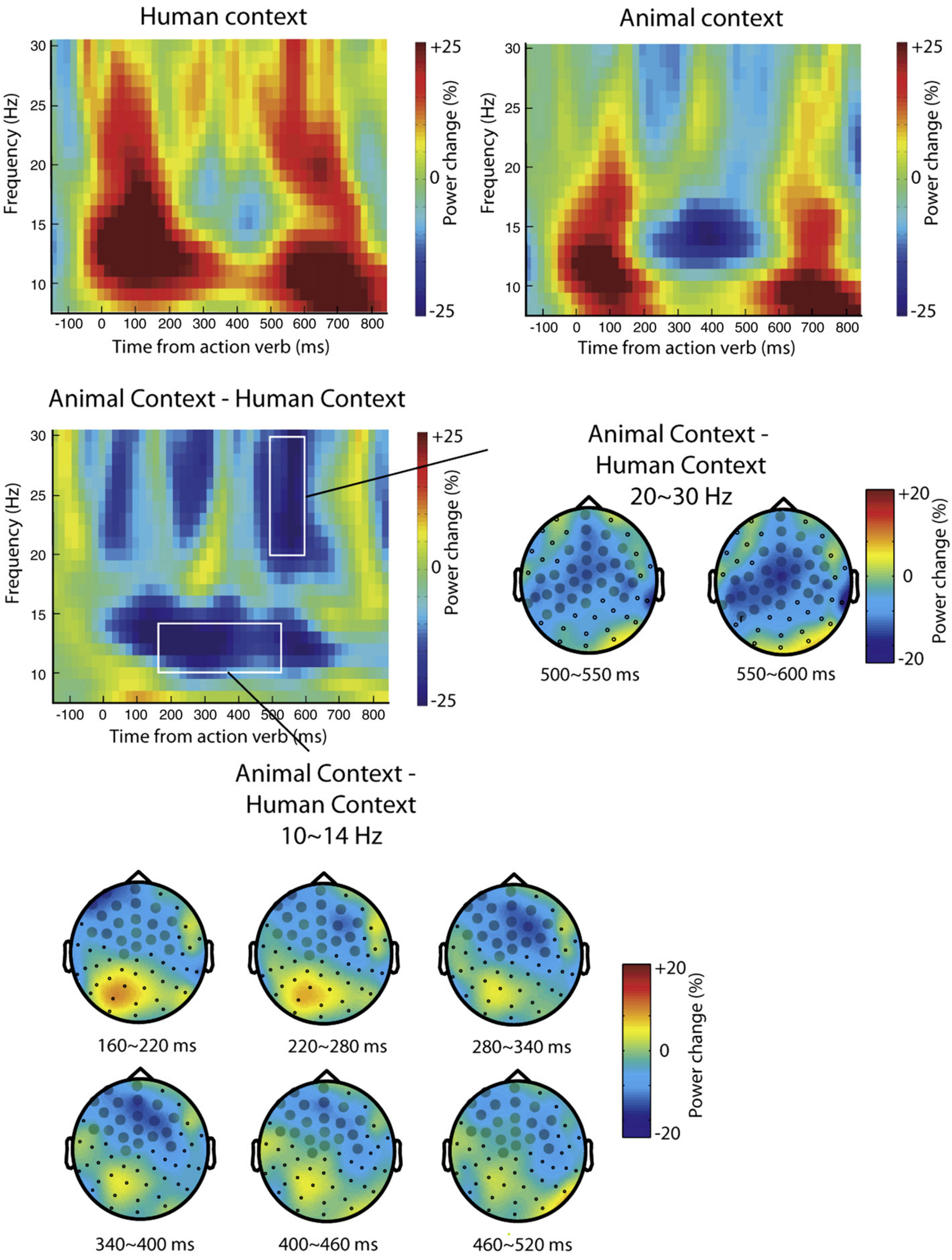
We were interested in the question whether motor activation precedes or follows classical measures of semantic integration. Therefore, a correlation analysis was conducted on the peak latencies of the N400 and the mu- and beta-effects to determine the relation between a classical measure of semantic processing, as reflected in the N400 and modality-specific brain activations, as reflected in the mu- and beta-frequency bands. For each subject, the peak latency of the N400 component was identified separately for verbs presented in an animal and a human context. Furthermore the peak latency of the desynchronization in the mu- and beta-frequency bands was identified separately for verbs presented in an animal and a human context. Interestingly, a significant correlation was found between the N400 peak latency and the mu peak latency both for verbs presented in an animal context, $r=.424$, $p<.05$, and for verbs presented in a human context, $r=.464$, $p<.05$ (see Table 3). No significant correlation was observed between the N400 peak latency and the beta peak latency.

To further investigate the relation between the N400, the mu-power and the beta-power, the peak latencies were directly compared using t-tests. A significant difference was observed between the peak latencies of the N400 (460 ms) and the mu-power (367 ms) for verbs presented in an animal context, $t(23)=5.5$, $p<.001$. In addition, a marginally significant difference was observed between the peak latencies of the N400 (450 ms) and the mu-power for verbs presented in a human context (409 ms), $t(23)=2.1$, $\mathrm{p}=.051$. Furthermore, a significant difference was observed between the peak latencies of the N400 (460 ms) and the beta-power (365 ms) for verbs presented in an animal context, $t(23)=3.4$, $p<.005$, and a significant difference was found between the peak latencies of the N400 (450 ms) and the beta-power (380 ms), $t(23)=4.6$, $p<.001$, for verbs in a human context (see Table 3). No significant differences were found between the peak latencies of the mu- and beta-power ($p>.15$).

In sum, a significant correlation was observed between the peak latency of the N400 component and the mu-power. Importantly, the peak latencies of the mu- and beta-power preceded the peak latencies of the N400 component by about 70 ms.

Control for temporal smearing

The onset of the mu- and beta-effects that were obtained using the multitaper method should be handled with caution. That is, the width of the wavelet (7 cycles) leads to severe smearing out of the time course of the power changes (i.e. one wavelet at 10 Hz is 700 ms long). To control for the possible confound that the early onset of the mu-effect may have been caused by temporal smearing, an additional conventional frequency analysis was conducted. EEG data were first band pass filtered (10–14 and 20–30 Hz) and the amplitudes were squared and averaged across trials (cf. Pfurtscheller and Klimesch,


Human context
Animal context
Frequency (Hz)
30
25
20
15
10
-100 0 100 200 300 400 500 600 700 800
Time from action verb (ms)
Power change (%)
+25
0
-25
Animal Context - Human Context
Animal Context - Human Context 20~30 Hz
500~550 ms
550~600 ms
+20
0
-20
Animal Context - Human Context 10~14 Hz
160~220 ms
220~280 ms
280~340 ms
340~400 ms
400~460 ms
460~520 ms

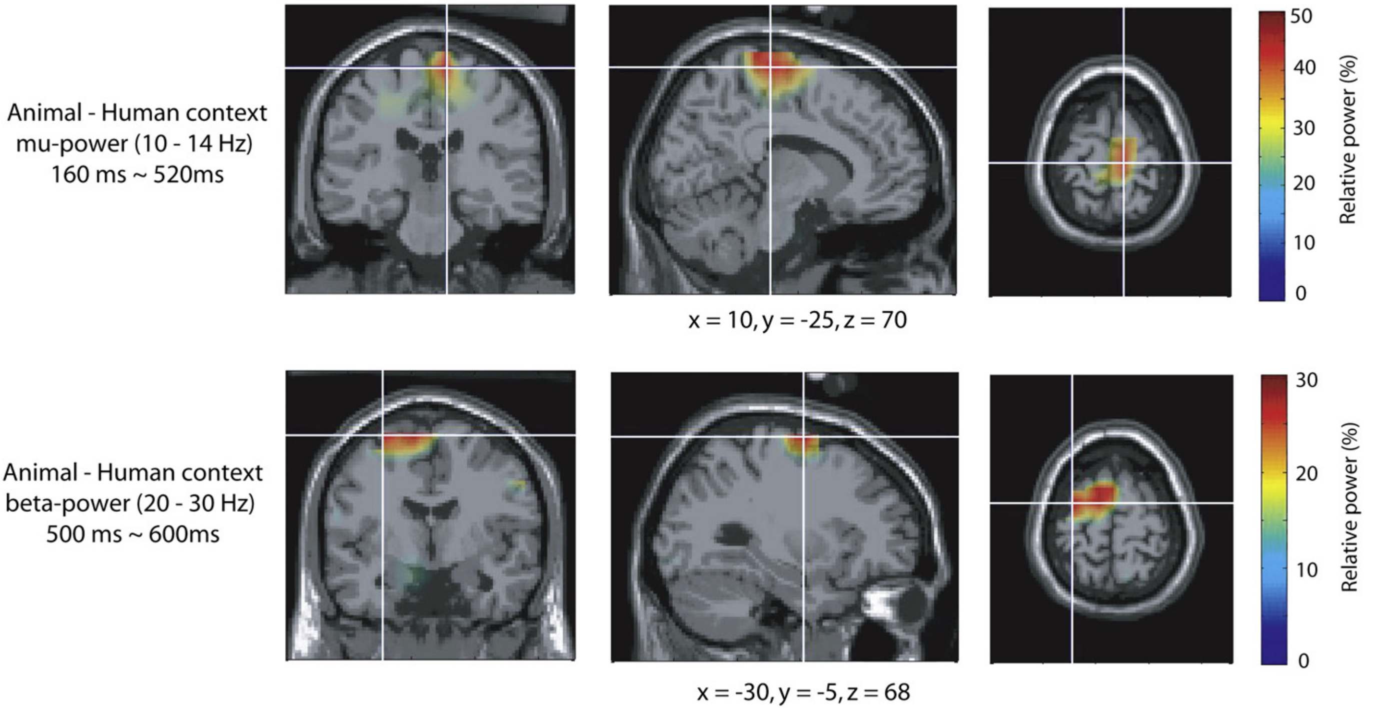


Fig. 5. Source analysis. Source reconstructions accounting for the mu-effect and the beta-effect for verbs presented in an animal compared to a human context. Sources accounting for the mu-effect were found around the medial part of the precentral gyrus (BA 4). Sources accounting for the beta-effect were found in the left superior frontal gyrus (BA 6). Source activation is projected on a standard brain (MNI).

1990). Differences between verbs presented in an animal compared to a human context were assessed by applying *t*-tests to subsequent 2-ms time bins on the same cluster of electrodes that was used for the main analysis of the mu- and beta-effects. A criterion of 10 subsequent time bins showing a significant difference ($p<.05$) between verbs presented in an animal compared to a human context was adopted to correct for multiple comparisons.

The earliest difference in mu-power was observed 152 ms after stimulus onset, reflected in a stronger desynchronization for verbs presented in an animal compared to a human context. The earliest difference in beta-power was observed 508 ms after stimulus onset, also reflected in a stronger desynchronization for verbs presented in an animal compared to a human context. These results indicate that the multitaper method and conventional frequency analysis yield comparable outcomes, with only a slight difference (<10 ms) in the onset of the effects. Thereby, this analysis provides a strong cross-validation of the main findings and suggest that the early onset of the mu-effect cannot be attributed to temporal smearing due to the use of multitapers.

Discussion

The present study investigated the functional role of motor activation during language processing. The main finding is that verbs presented in an animal context elicited stronger early motor activation than verbs presented in a human context. In addition, motor activation was found modulated by the cloze probability of the noun–verb pairs and preceded the N400 by about 70 ms. These findings make a strong argument for the notion that language-induced motor activation primarily reflects the retrieval of lexical-semantic information associated with the verb rather than post-lexical motor imagery of specific kinematics.

The present findings are in line with the suggestion that language processing occurs at different – though complementary – functional levels (Hagoort and van Berkum, 2007). At a referential level, readers construct a model of the referential situation that is described in the sentence (Zwaan and Kaschak, 2009). For instance, at a visual level subjects generate a detailed visual representation of the objects that are described in a sentence (Zwaan et al., 2002). In a similar fashion, at a motor level readers represent the actions that are described in the sentence (Glenberg and Kaschak, 2002). At a lexical-semantic level, readers continuously update their expectations about upcoming words, based on the semantic associations between different words (Kutas and Hillyard, 1984). For example, the word “duck” is more strongly associated with the verb “swimming” than the word “woman” and “swimming”. The cloze probability reflects the strength of the semantic associations between two different words. In the present study, the context manipulation (human vs. animal context) resulted in verbs presented with a high cloze probability (animal context) or a low cloze probability (human context). That is, animals have only limited action capabilities (e.g. a duck can “swim”, “fly”, “squack” or “waddle”), whereas a human could perform an endless range of different actions. Of course the lexical-semantic and the referential level are closely related because co-occurring words also have co-occurring references in the real world. For instance, we most often see ducks swimming and these real-world relations are reflected at a lexical level as well in the association between “duck” and “swimming”. Accordingly, the cloze probability is driven by both the referential representation (i.e. the situation model) and by the lexical co-occurrences of words (Zwaan and Kaschak, 2009).

The size of the N400 amplitude and the beta-power for verbs were driven primarily by the cloze probability of the noun–verb pairs, reflecting subjects' expectations about upcoming words during the natural reading process. Apparently, the action semantic information

Fig. 4. Mu- and beta-power for action verbs. Time-frequency representations for verbs presented in a human context (upper part, left side) and in an animal context (upper part, right side). Power differences are reflected in a stronger desynchronization in the beta-frequency band (middle part) and a stronger desynchronization in the mu-frequency band (lower part) for verbs presented in an animal compared to a human context. Electrodes showing significant differences between conditions are marked in grey.

Table 2
Example of stimulus materials with a low cloze probability (upper part) or a high cloze probability. Critical verbs and words are marked in bold.

Low cloze probability	
Human context	
Dutch	De wetenschapper **pakt** een biertje.
English	The scientist **grabs** a beer.
Animal context	
Dutch	De kat **likt** aan zijn pootje
English	The cat **is licking** its paw.
High cloze probability	
Human context	
Dutch	De baby **huilt** in zijn wiegje.
English	The baby **is crying** in its cot.
Animal context	
Dutch	De lama **spuugt** naar de man.
English	The llamas **spits** at the man.

Table 3
Correlations between peak latencies of the N400 and the mu- and beta-power.

Peak latencies	Pearson's *r*	*p*
N400 × Mu power animal context	.424	<.05*
N400 × Mu power human context	.464	<.05*
N400 × Beta-power animal context	−.001	.995
N400 × Beta-power human context	−.110	.609

associated with the verb may be more easily retrieved for verbs presented in an animal compared to a human context, as reflected in the smaller N400 and the relative decrease in mu- and beta-power. These findings suggest that motor activation in language processing is sensitive to the lexical-semantic relations between consecutive words in a sentence and supports semantic integration and anticipation rather than explicit motor imagery of the kinematics implied by the sentence (i.e. re-enactment of familiar actions). This interpretation is further supported by the finding that the peak latency of the motor activation preceded the peak latency of the N400 component. The finding that motor activation supports lexical-semantic integration goes well with the notion that the motor representations cued by verbs must be underspecified enough to allow the accommodation of new incoming information. For instance, the verb "to open" is ambiguous with respect to the type of movement implied and only words following the verb allow to specify the precise action (e.g. "to open a door" involves different kinematics than "to open a jar"; Taylor et al., 2008; Taylor and Zwaan, 2008). The possibility that the motor representations that are activated during language processing show an incremental specialization as the sentence's meaning unfolds opens interesting avenues for future research.

If motor activation reflects the activation of lexical-semantic features, an intriguing question is how motor activation could support the understanding of sentences describing animal actions. That is, most animals' bodies and the way in which they move are highly dissimilar from humans' bodies and their action repertoire. Studies on the observation of human actions typically report stronger motor activation for observation of familiar actions that can be directly mapped onto one's own motor repertoire (Calvo-Merino et al., 2006; van Elk et al., 2008b). For example, when expert dancers were observing familiar dance sequences, this resulted in a stronger activation of premotor areas in the brain (Calvo-Merino et al., 2005). Furthermore, when humans observed movements of a different species, such as monkeys

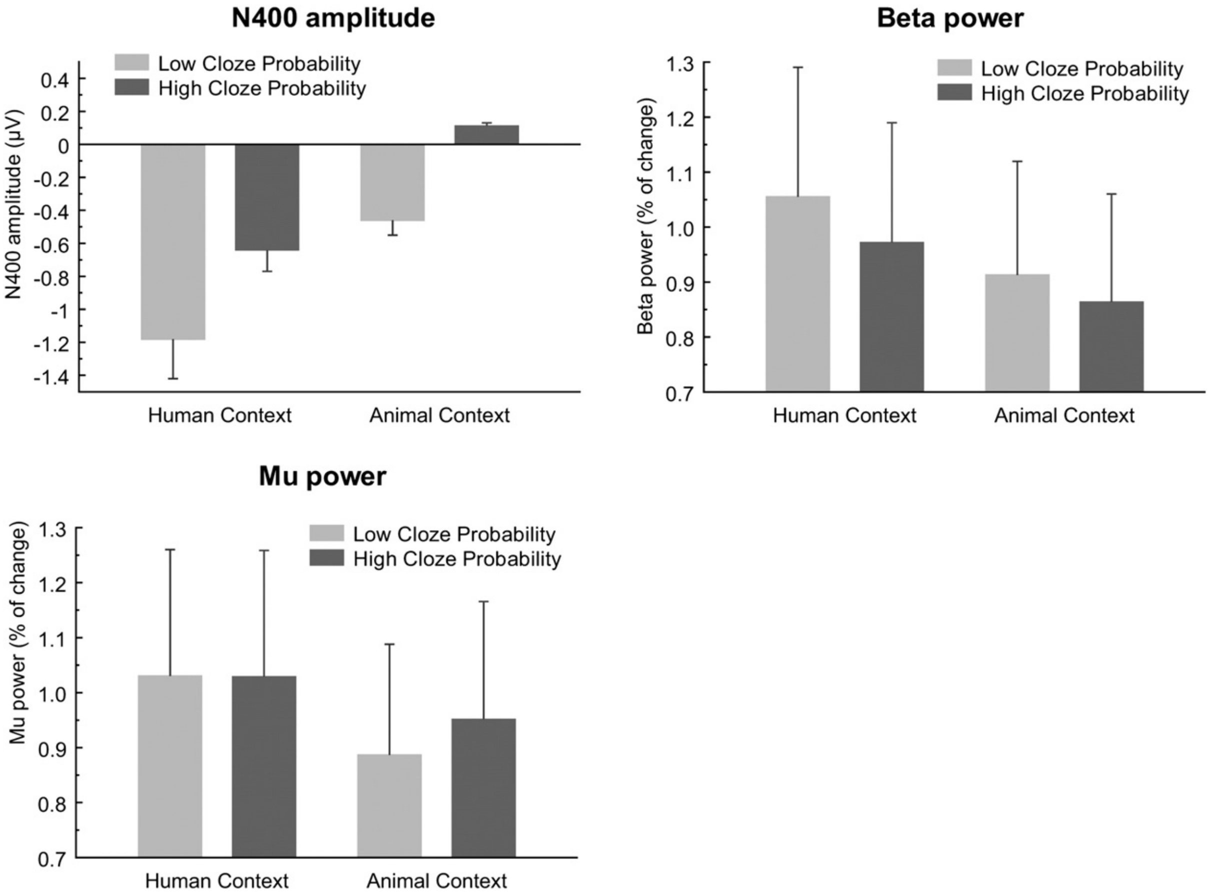


Fig. 6. Effects of cloze probability and context. The average N400 amplitude (upper left graph), beta-power (upper right graph) and mu-power (lower left graph) for noun–verb pairs with a low cloze probability (dark bars) or a high cloze probability (light bars) for verbs presented in a human context (left side of graph) or an animal context (right side of graph).

or dogs, this resulted in a decrease in activation of the mirror neuron system (Buccino et al., 2004). In sum, these studies show that during action observation the motor system is more strongly activated for observation of familiar compared to unfamiliar actions.

However, other studies indicate that the motor system is activated during the observation of actions that extend beyond one's action repertoire as well (Aglioti et al., 2008; Avenanti et al., 2007; Costantini et al., 2005; Gazzola et al., 2007a,b; Romani et al., 2005). For instance, the observation of biomechanically impossible finger movements resulted in a comparable activation of the motor system as the observation of biomechanically possible finger movements (Avenanti et al., 2007; Romani et al., 2005). Furthermore, in an fMRI study, a stronger activation of motor-related brain areas was found in response to the observation of a robotic arm grasping objects (Gazzola et al., 2007a) and in aplasic subjects the motor system was activated during the observation of human grasping actions that the subjects were unable to perform themselves (Gazzola et al., 2007b). Although the motor system appears to respond more strongly to the observation of familiar actions (Buccino et al., 2004; Calvo-Merino et al., 2005, 2006), motor activation has also been reported for the observation of actions that are beyond one's own action repertoire. Similarly, in the present study, the stronger motor activation for processing verbs in an animal context suggests that motor activation may support the understanding of actions that one is unable to perform oneself. In line with this suggestion, in a recent study, a differential activation of premotor and primary motor cortex was observed for experts compared to novices in association with the reading of action sentences describing hockey events (Beilock et al., 2008). In sum, these studies provide tentative support for the suggestion that subjects may recruit their motor system in order to understand actions that are beyond one's own motor repertoire.

In the present study, the mu- and beta-effects were localized to the medial part of the precentral gyrus (BA 4) and to dorsal premotor areas (BA 6), thereby directly supporting the notion that the processing of action verbs is accompanied by motor activation. The activation in these motor-related areas for the processing of action-related information is in line with previous studies that have consistently shown the involvement of primary motor and premotor regions during the processing of action verbs (Papeo et al., 2009; Pulvermuller, 1999; Willems et al., 2009; Raposo et al., 2009; Tomasino et al., 2008). Previous studies have shown a selective activation of the primary motor cortex only when subjects were required to explicitly process the meaning of the verb (Papeo et al., 2009; Tomasino et al., 2008), thereby further corroborating the supportive role of this area in semantic processing. In addition, other studies have shown that the dorsal premotor cortex represents actions primarily in terms of the intended outcome, rather than the precise kinematics required to attain the outcome (Hoshi and Tanji, 2006; Majdandzic et al., 2009). Although speculative, one intriguing possibility is that the retrieval of action semantic information, as reflected in the early mu-power localized to primary sensorimotor cortex, may actually precede the representation of actions at a higher level, as reflected in the later beta-power localized to the dorsal premotor cortex. Suggestions for the involvement of both fast and slow modality-specific brain activations have thus far only been made for the visual domain (cf. van Schie et al., 2005) and the present study extends these findings to the motor domain.

The present study provides new insight in the relation between classical measures of semantic processing, such as the N400 component, and the activation of modality-specific brain areas, as measured in power changes in the mu- and beta-frequency bands. The involvement of the N400 in the retrieval of action semantic information is corroborated by two recent studies in which the planning of meaningful actions was found accompanied by a modulation of the N400 component (van Elk et al., 2008a, in press). Furthermore, Davidson and Indefrey (2007) report a comparable inverse relation between ERP amplitude and power magnitude changes for processing semantic and syntactic violations. The present study extends these findings, by showing how the retrieval of action semantic information as reflected in a suppression of the mu- and beta-frequency bands is inversely related to the amplitude of the N400 component.

A significant correlation was observed between the peak latencies of the N400 component and the mu-effect for verbs in both an animal and a human context, suggesting a functional relation between motor activation and lexical-semantic integration. On average, the peak latencies of the mu-effect preceded the peak latencies of the N400 component by about 70 ms. In addition, the onset of the mu-effect was quite early, around 160 ms after the presentation of the verb, which is in line with previous studies showing motor effects at a comparable early latency during the processing of action verbs (Hauk and Pulvermuller, 2004; Pulvermuller et al., 2001). Accordingly, the present findings could reflect that the activation in modality-specific brain areas may actually precede the activation of higher-order brain structures, typically associated with the retrieval of semantics. Importantly however, rather than reflecting the automatic bottom-up activation of neuronal cell assemblies associated with the verb (Pulvermuller, 2005), the present study shows that early motor activation during language processing is dependent on the preceding linguistic context and thus supports lexical-semantic integration.

The finding that language-induced motor activation is primarily related to lexical-semantic constraints does not preclude the notion that motor activation may reflect motor imagery as well. As indicated in the introduction, many studies have shown that language processing often involves specific imagery of implied actions (Glenberg and Kaschak, 2002; Zwaan and Taylor, 2006). Furthermore, motor imagery may be induced for actions that are relatively unfamiliar (Beilock et al., 2008) and even during the observation of animal actions (Buccino et al., 2004). As such, an alternative explanation for the present findings might be that the stronger motor activation in to action verbs in animal context represents an interpretative process in which subjects recruit their motor system in order to make sense of actions that are difficult to understand (see also Koelewijn et al., 2008; Stapel et al., submitted for publication). However, the early onset of the motor effects in the present study and the clear relation of these effects with the preceding semantic context (i.e. cloze probability) clearly argue against this interpretation and in favor of a lexical-semantic interpretation.

Whereas in action-oriented studies, a decrease in power in the mu and beta-frequency band consistently reflects activation of the motor system for either action observation or action execution (Babiloni et al., 2002; Caetano et al., 2007; Koelewijn et al., 2008; Muthukumaraswamy and Johnson, 2004; van Elk et al., 2008b), language-oriented studies have suggested that beta-oscillations during language processing reflect syntactic unification operations (Bastiaansen and Hagoort, 2006; Bastiaansen et al., in press). More specifically, a stronger increase in beta-power has been observed for the processing of correct sentences compared to sentences with a word-category violation (Bastiaansen et al., in press). In the present study, the onset of the verb resulted in an initial increase in beta-power as well, which was likely related to the presentation of the preceding noun. In contrast, rather than reflecting syntactic processing, we suggest that the stronger relative decrease in power for verbs presented in an animal compared to a human context reflects motor activation. First, if the beta-effect could be attributed to differences in syntactic unification, this should have become apparent in the ERP as well in the so-called P600 effect. However, the difference between verbs in a human compared to an animal context was reflected in a stronger N400-component, reflecting a semantic integration process. Second, the scalp distribution of the mu- and beta-effects were in line with previous studies, showing comparable effects above central brain areas reflecting motor activation (Babiloni et al., 2002; Muthukumaraswamy and Johnson, 2004).

Third, the sources accounting for the mu- and beta-effects were localized to the dorsal primary motor and premotor cortex, which fits nicely with results of previous reports on the processing of action verbs. These findings provide a strong argument for the notion that desynchronizations in the mu- and beta-frequency bands, previously associated with action execution and observation (Babiloni et al., 2002; Caetano et al., 2007; Koelewijn et al., 2008; Muthukumaraswamy and Johnson, 2004; van Elk et al., 2008b), reflect motor activation during the processing of action verbs as well. Apparently, modulations in the beta-frequency band during language processing may reflect different functional processes, related to either the retrieval of action semantic information or syntactic unification. More research is needed to elucidate the precise functional role of beta-oscillations in language processing and it could well be that different neural generators contribute to either syntactic- or motor-related beta-effects.

Conclusions

In the present study, we showed that the processing of action verbs is accompanied by early motor activation, as reflected in a desynchronization in the EEG mu- and beta-frequency bands. Furthermore, it was found that motor activation during language processing was driven by the cloze probability of the verb rather than the familiarity of the action implied by the verb. Finally, our data suggest that motor activation as reflected in motor-cortical oscillations precedes classical measures of semantic integration, such as the N400 component. In sum, the present study suggests that motor activation in language processing supports lexical-semantic integration rather than post-lexical motor imagery.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2009.12.123.

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