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TO MOVE OR NOT TO MOVE: IMPERATIVES MODULATE ACTION-RELATED VERB PROCESSING IN THE MOTOR SYSTEM

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Abstract—It has been suggested that the processing of action-related words involves activation of the motor circuitry. Using fMRI (functional magnetic resonance imaging), the current study further explored the interaction between action and language by investigating whether the linguistic *context*, in which an action word occurs, modulates motor circuitry activity related to the processing of action words. To this end, we examined whether the presentation of hand action-related verbs as positive or negative imperatives, for example, "Do grasp" or "Don't write," modulates neural activity in the hand area of primary motor cortex (M1) or premotor cortex (Pm). Subjects (n = 19) were asked to read silently the imperative phrases, in which both meaningful action verbs and meaningless pseudo-verbs were presented, and to decide whether they made sense (lexical decision task). At the behavioral level, response times in the lexical decision task were significantly longer for negative, compared to positive, imperatives. At the neural level, activity was differentially decreased by action verbs presented as negative imperatives for the premotor and the primary motor cortex of both hemispheres. The data suggest that context (here: positive vs. negative imperatives), in which an action verb is encountered, modulates the neural activity within key areas of the motor system. The finding implies that motor simulation (or motor planning) rather than semantic processing *per se* may underlie previously observed motor system activation related to action verb processing. Furthermore, the current data suggest that negative imperatives may inhibit motor simulation or motor planning processes. © 2010 IBRO. Published by Elsevier Ltd. All rights reserved.

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Why do action-related words activate motor areas of the brain? An important debate regarding the neural processes underlying semantic representations of action words and their relation to the neural underpinnings of action processing *per se* persists. Presenting words that describe actions has been shown to activate, among other regions, the motor circuitry. Processing of action words caused high-frequency electro-encephalographic or magneto-encephalographic activity recorded at central sites (Pulvermüller et al., 2001, 2005b), as well as a modulation of cortico-spinal excitability (Oliveri et al., 2004; Buccino et al., 2005; Pulvermüller et al., 2005a). Interactions between action word processing and action execution have also been reported (Glenberg and Kaschak, 2002; Buccino et al., 2005; Zwaan and Taylor, 2006; Boulenger et al., 2006). Furthermore, functional magnetic resonance imaging (fMRI) studies measured action word related increases of BOLD-signal in the left primary motor cortex (M1) (Hauk et al., 2004; Ruschemeyer et al., 2007; Tomasino et al., 2007; Kemmerer and Gonzalez-Castillo, 2010). With the same technique, Tettamanti et al. (2005) showed that listening to sentences expressing actions performed with the mouth, the hand, or the foot led to signal increases in different parts of the left premotor cortex (Pm) depending on the effector involved in the action described in the sentence. Furthermore, Aziz-Zadeh and colleagues (Aziz-Zadeh et al., 2006) found in the left Pm common activations, both during the observation of actions and the processing of sentences expressing those same actions. Taken together, these studies suggest that action words related to different body parts activate the primary motor cortex and the Pm in a somatotopic manner (Hauk et al., 2004; Buccino et al., 2005; Pulvermüller et al., 2005a; Aziz-Zadeh et al., 2006).

Despite growing research efforts, the actual *cause* of the observed motor system activity during action word processing remains elusive (see Kemmerer and Gonzalez-Castillo, 2010). Some authors argue that if a word is frequently presented in the context of action execution and, therefore, acquires meaning, co-activation of neurons in perisylvian language and motor cortices may lead to the formation of action word related overlapping neural networks (associationist theory, Pulvermüller et al., 2001, 2005b; Pulvermüller, 2005). Another hypothesis is that sensorimotor representations are similarly accessed when an action is observed (Buccino et al., 2001) or when an action word is processed using the observation-execution-matching system (Tettamanti et al., 2005; Buccino et al., 2005; Aziz-Zadeh et al., 2006). Within this "embodied cognition" view, some researchers (Barsalou, 1999; Glenberg and Kaschak, 2002; Gallese and Lakoff, 2005) explicitly argue that sensorimotor representations are accessed because processing of action-related words triggers mental simulation (see also Willems and Hagoort, 2007). Mental

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Abbreviations: ANOVA, analysis of variance; CMA, cingulate motor area; FEW, family-wise error; fMRI, functional magnetic resonance imaging; MAP, maximum probability maps; M1, primary motor cortex; Pm, premotor cortex; PW, pseudowords; ROI, region-of-interest; SMA, supplementary motor area; SPM, statistical parametric mapping; TPJ, temporo-parietal junction; W, words.

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simulation of a motor plan has been shown to activate M1 in a somatotopic manner (Stippich et al., 2002; Ehrsson et al., 2003). Evidence for motor and perceptual simulations occurring during language comprehension is provided by several studies (Glenberg and Kaschak, 2002; Borghi, 2004; Kaschak et al., 2005; Zwaan and Taylor, 2006; Tomasino et al., 2007). Sentences describing a movement in a certain direction interfere with responses executed in a different direction as measured by the action sentence compatibility effect (Glenberg and Kaschak, 2002). Accordingly, it has been suggested that sentences involving rotations activate—through motor simulation—a motor program for manual rotation in the listener (Glenberg and Kaschak, 2002), and that this motor program may interfere with the motor program for the response in those situations in which rotation directions are different. Consistent with this, it has been shown that during a semantic decision task about hand-related, foot-related, or abstract verbs, an early delivery of the go signal (during verb processing) slowed down right hand response times when subjects made decisions about hand-related vs. foot-related verbs, whereas a delayed delivery of the go signal (when verbs had already been processed) did not cause differences in response times with respect to hand- vs. foot-related verbs (Sato et al., 2008).

To date, experimental paradigms which allow disentangling under circumstances in which action-related words activate motor areas, for example, whether they are modulated by the linguistic context within which the action word is presented, are lacking. Thus, in the present event-related fMRI study, we further investigated the interaction between motor and language processes by adopting a novel paradigm. As in previous studies (Pulvermüller et al., 2001, 2005a), subjects performed a lexical decision task, whereas neural activity was measured by fMRI. Subjects were asked to silently read imperative phrases, in which both meaningful action verbs (W) and meaningless pseudo-verbs (pW) were presented, and to decide whether they made sense. As a new feature, we introduced a specific linguistic context, that is, presented the hand-related action verbs (and the pseudo-verbs) in their negative and positive imperative forms, for example, "Don't grasp," "Do grasp."

There is a rich literature on negation within cognitive psychology. However, previous studies did not specifically focus on action words processing. These studies revealed longer processing times and higher error rates for negative vs. affirmative sentences (Carpenter and Just, 1975; Kaup et al., 2007; Ludtke et al., 2008). It was suggested that such type of sentences trigger a two-step simulation process: the evocation of a simulation of the negated state of affairs (e.g. "John has not left") and a simulation of the actual state of affairs (e.g., "John has left;" [Kaup et al., 2007; Ludtke et al., 2008]).

Note that recently Tettamanti et al., (2008) also used negative and positive linguistic material for investigating the involvement of the motor system in the processing of action verbs. However, different types of stimuli were used in their and in our study: Tettamanti et al. used sentences explicitly including objects (e.g., "Now I push the button" [action sentence containing a manipulable object], "Now I don't appreciate loyalty" [control sentence containing an abstract object]), thereby triggering object-related activation in the Pm. In contrast, our study employed action verbs describing hand movements which were presented in isolation (not embedded in a sentence structure and without a related object). Second, Tettamanti et al.'s subjects were asked to passively listen to the sentences describing actions. Therefore, no behavioral data, like reaction time (RTs) or accuracy rates, could be provided. In contrast, we employed an active lexical decision task in the present study. Thus, our results extend those of Tettamanti et al. by providing RT and accuracy data in addition to brain responses with respect to a positive vs. negative linguistic context. Third, the analyses of the fMRI data differ in an important aspect. Tettamanti et al. (2008) adopted a small volume correction approach using a mask derived from their previous study on language (Tettamanti et al., 2005). Note that the peak activations of Tettamanti et al. (2005) are outside of the cytoarchitectonically defined (motor) areas 4 or 6 (see Fig. 1 on page 636 of Postle et al., 2008). In contrast, for our experiment, we used a specific functional localizer of the motor system (i.e., hand clenching movements) to derive anatomically-constrained functional region-of-interest (ROIs) for each individual subject (see later in the text). Note that the use of maximum probability maps (MPMs) in conjunction with a functional localizer task was originally advocated by Postle et al. (2008) and has also recently been applied by Willems et al. (in press). This combined approach is required for a satisfactory test of the associational hypothesis that proposes that the same neurons involved in executing a movement are involved in processing the meanings of related action words. The localizer tasks used in the aforementioned studies as well as in the current study consisted of intransitive movement(s) (see also Hauk et al., 2004). Although our experimental task (as well as the experimental tasks of the other studies [Hauk et al., 2004; Postle et al., 2008; Willems et al., in press]) involved the processing of *transitive* action verbs, we decided to use a transitive movement for the functional localizer for the following reasons. Previous studies showed that (pantomiming of) transitive movements, that is, object-related actions, yielded strongly left-lateralized activation patterns (Moll et al., 2000; Choi et al., 2001). Moreover, object-related (transitive) movements led to stronger activations in Pm (Moll et al., 2000; Tettamanti et al., 2005) than intransitive movements which rather activated the M1. As we were mainly interested in the M1 and moreover aimed at examining motor regions of both hemispheres, we adopted a localizer task with a simple, intransitive movement leading to a bilateral activation pattern including M1. Nevertheless, the use of different localizer tasks (e.g., including transitive and intransitive verbs) constitutes a promising approach for future studies because localizer tasks using intransitive movements only may miss some common activation caused by the processing of transitive action verbs.

Although simulation and associative learning theories are difficult to distinguish (e.g., Keysers and Perrett 2004; Brass and Heyes 2005), the contribution of our experiment is to introduce a context by presenting the verb in a positive or negative context, which might be a promising approach to investigate the interaction between the language and the motor systems. The two theoretical accounts mentioned earlier (i.e., embodied cognition theory and associationist theory) lead to identical predictions with respect to an involvement of M1 (or Pm) for action words presented in an affirmatory context. Both accounts predict that reading "Do grasp" will activate the motor plan for "grasping." The key feature that differentiates these two perspectives is the modulation of motor areas by linguistic context, that is, negative imperatives. The associationist theory assumes that action words trigger neural activity in motor areas because it is the meaning of an action word *per se* that is represented in overlapping networks because of co-activations of neurons in perisylvian and motor cortices. If this prediction were correct, then, independent of whether the verb stimuli were presented as positive or negative imperatives, for example, "Do write" and "Don't write," we should find similar motor system activation for action-related verbs because the linguistic context should not have an effect on the motor system activation (see also Boulenger et al., 2008). By contrast, the embodied cognition framework speaks in favour of a modulation by the positive/negative imperatives because it proposes that when action words are processed, sensorimotor representations and, thus, M1 (and Pm) are activated through the observation-execution-matching system. Because of this intermediate processing step, the activation of the sensorimotor representations may be modulated by lexical context (e.g., imperatives). Processing of action words in an affirmatory, that is, positive context should initiate the activation of sensorimotor representations, whereas a negative context should inhibit the activation of sensorimotor representations. Thus, on the basis of the notion of embodied cognition, one would predict that the M1 (and Pm) activity related to the processing of action verbs is modulated by a preceding negative imperative. Taken together, revealing a modulatory effect of the imperatives on M1 (and Pm) activity during action verb processing would lend support to the embodied cognition view, whereas the absence of such a modulatory effect would strengthen the associationist theory.

To increase the sensitivity of our experimental manipulations, we restricted our stimulus set to verbs related to hand actions (Zwaan and Taylor, 2006; Tomasino et al., 2007). Furthermore, the localization of the ROIs within the motor system (primary motor cortex and premotor cortex of both hemispheres) was individually determined using (i) a functional localizer task based on repetitive hand clenching movements, which all subjects performed *after* the cognitive fMRI experiment, and (ii) the cytoarchitectonically-defined MPMs of the Brodmann areas 4 (M1) and 6 (Pm) provided by the Anatomy toolbox (Eickhoff et al., 2005). This allowed us to individually measure the modulation of neural activity in the hand area of both primary motor and premotor cortices using anatomically-constrained functional ROIs when our right-handed subjects processed positive and negative imperatives of hand-action related verbs (and pseudo-verbs).

Although we were primarily interested in the neural response pattern of the (left) M1 cortex, we also explored the activation patterns in the Pm (Brodmann area 6) of both hemispheres using again anatomically-constrained functional ROIs, because many previous studies also point to an involvement of the Pm in processing action verbs (Tettamanti et al., 2005, 2008; Buccino et al., 2005; Aziz-Zadeh et al., 2006).

EXPERIMENTAL PROCEDURES

Subjects

A total of 19 right-handed (Edinburgh Inventory test, Oldfield, 1971) healthy subjects (mean age ± SD: 17.4±14.2 years; nine females) gave informed consent to participate in the study. The study was approved by the local ethics committee. All subjects were native speakers of English with comparable levels of education, and all except four were monolinguals. All subjects had normal or corrected-to-normal vision and reported no history of neurological illness, psychiatric disease, or drug abuse.

Stimuli

For the generation of the stimulus phrases, 104 English action verbs related to hand movements, for example, "to grasp," "to write," were selected. The verbs were 4–9 letters long, and the average lexical frequency was 257.4±572.5 (occurrences per million, CELEX database; Baayan et al., 1993). The use of the English language allowed us to keep the phrase structure as similar as possible for all experimental conditions, with both positive and negative imperatives beginning with "Do. . . ." Stimulus phrases always consisted of the infinitive form of the verbs without the preposition "to" preceded by "Do" or "Don't," thereby resulting in a positive or negative imperative. Thus, the stimuli containing positive and negative imperatives differed visually by "n't" only. To ensure that any reported difference in neural activity between the conditions was not because of stimulus length differences *per se*, an additional regressor coding for word lengths was included in the statistical parametric mapping (SPM) analysis. It should be noted that this additional regressor removed all variance in the fMRI data that was due to the fact that the imperatives with "Don't" were always longer (by two letters) than the imperatives with "Do." However, this regressor did not explain the variance induced by the experimental factor "imperative" ("Do" vs. "Don't") as stimuli with identical lengths occurred in both imperative conditions (e.g., "Don't hit", "Do grasp"; seven letters each).

Experimental paradigm and task

Because we intended to replicate and extend the findings of previous studies (Pulvermüller et al., 2001) in which participants performed lexical decisions, we adopted a lexical decision task, in which—as a new feature—the stimulus verbs were presented as positive and negative imperatives (see earlier in the text). In addition to the 104 phrases with action-related verbs (W), our event-related fMRI design included 104 phrases with meaningless pseudo-verbs (pW) to accomplish the requirements of the lexical decision task. The pseudo-verbs were generated by substituting or exchanging letters of the corresponding action verbs, for example, "gralp," and were thus in agreement with the phonological and orthographic rules of English. As a prerequisite for the lexical decision task (Pulvermüller et al., 2001), our subjects processed the meaning of the word stimuli, but our study design focused on the effect of the lexical context, that is, positive vs. negative imperatives, on the neural activity in the hand area of the primary motor and premotor cortex during action verb processing.

The fMRI experiment started with an instruction (6 s) requesting that subjects silently read the imperative phrases and decided whether they made sense. The exact task instruction was "Does this phrase make sense: yes / no?" We considered this task to represent a lexical decision task as this task prompts subjects to decide, in the context of the experiment, whether the string in the verb position is a verb or a pseudo-verb. This way the current task was similar to lexical decision tasks used in previous studies (e.g., Pulvermüller et al., 2001). We acknowledge, however, that subjects may have perceived the task as a sensibility judgment task, which might have triggered even deeper linguistic processing. If this was the case, then this would even strengthen our findings (see the following paragraph), because our main result was a differential activity *reduction* for all four motor areas tested in the context of negative imperatives. This finding is not consistent with the associationist theory which proposes that any linguistic processing of action-related words (which might be even deeper when our subjects perceived the current experimental task as a sensibility judgment) should result in an activity *increase* in the motor areas independent of the linguistic context. Subjects reported their yes/no answer for each stimulus by pressing on a pedal with their foot. All experimental trials had a duration of 2 s and were followed by a variable inter-trial interval, with a duration that was jittered between 1750 and 3250 ms, with incremental steps of 500 ms 48 null events (i.e., blank screens), perceived as a prolongation of the inter-trial period, were randomly interspersed among the event trials to increase the power of estimating the BOLD response (Dale and Buckner, 2008). Three pseudo-randomized stimulus sequences were alternated between subjects. To avoid any potential priming effect, trial sequences were shuffled, so that the same verb did not subsequently appear in the two imperative conditions (positive vs. negative imperatives), and that paired stimuli did not subsequently appear in the two stimulus conditions (verbs [W] and pseudo-verbs [pW], e.g., "grasp" before "gralp" and vice versa). In addition, we included 29 randomly-presented recognition trials, in which subjects were asked whether the last phrase started with "Do" (in 15 of the recognition trials) or "Don't" (in 14 recognition trials). In the recognition trials, subjects also indicated their responses by pressing a pedal. The rationale for these recognition trials was to ensure that subjects paid attention to the whole stimulus phrase, especially the "Dos" and "Don'ts", throughout the experiment.

Presentation of the stimuli and their synchronization with the MR scanner was realized by the software Presentation® (version 9.9, Neurobehavioral Systems Inc., CA, USA). Subjects viewed the stimuli through a mirror mounted on the head coil. They were instructed to keep their hands still in a relaxed manner and to respond as quickly as possible with their feet using an MRI-compatible response device (Lumitouch, Lightwave Medical Industries, CST Coldswitch Technologies, Richmond, CA, USA) mounted on a custom-made foot support. Foot responses were chosen to minimize interference between response preparation and execution and the predicted task-related activity in M1 and Pm hand area. All subjects reported that their preferred response for answering whether the phrase made sense was a right foot press ("If the phrase is *right*, I press with my *right* foot"). Therefore, we decided to allow this compatibility between phrase type and foot response, that is, right foot press for real verbs, to reduce the attentional and memory load devoted to the responses. This procedure enabled the subjects to focus their attention on the experimental tasks (lexical decisions, recognition trials) with minimal distraction by the response mode.

Before the fMRI experiment, subjects practiced the experimental task as well as the foot responses outside the scanner. For this purpose, subjects performed the task on 20 action verbs related to face and leg movements and the corresponding pseudo-verbs to avoid biasing the subjects' attention toward the hand-related aspects of the stimuli. These action verbs were, of course, not included in the experiment, which involved hand-action related verbs only.

Statistical analyses of behavioral data

Using the software SPSS for Windows (version 12.0), a repeated measure analysis of variance (ANOVA) with the factors "imperative" (positive ["Do". . .] and negative ["Don't". . .] imperatives) and "stimulus" (W, pW) was performed on the subjects' accuracy and RT data for the lexical decision task. In addition, the error rates for the recognition task, which indicated whether subjects were processing the complete phrase including the preceding "Do" and "Don't" were computed. For the RT data, outliers were removed by excluding any trials in which the participant's RT was greater than two standard deviations above or below that participant's mean RT for the condition in which the trial occurred (Ratcliff, 1993).

fMRI data acquisition

Functional MR images were acquired on a Siemens 3 T MRI whole-body scanner (Siemens Trio, Erlangen, Germany) using a standard head coil and a custom-built head restrainer to minimize head movements. Functional images were obtained using a single-shot gradient echo, echoplanar imaging (EPI) sequence. Each subject was scanned first for the lexical decision experiment and then again for the localizer task. EPI volumes for the main experiment (lexical decision task, $n=1033$) contained 36 axial slices (TR=2200 ms, TE=30 ms, FOV=200.36 mm, matrix: 64×64; slice thickness of 3 mm, 90° flip angle, voxel size: 3.1×3.1×3.3 mm) and were preceded by six dummy images that allowed the MR scanner to reach a steady state. EPI volumes for the functional localizer (N = 159) were acquired with the same sequence characteristics as in the main experiment except for a shorter TR of 1.6 s, fewer (26) axial slices, and five dummy images. Both experiments were obtained in the same fMRI session. The main experiment lasted 37 min and the localizer task 5 min. After functional neuroimaging, high-resolution anatomical images were acquired using *a* T1-weighted 3-D magnetization-prepared, rapid acquisition gradient-echo (MP-RAGE) pulse sequence (TR=2250 ms, TE=3.03 ms, FOV=256 mm, 176 sagittal slices of 1 mm thickness, flip angle=9°, voxel size: 1×1×1).

fMRI data processing and whole brain analysis

All calculations were performed on UNIX workstations (SUN Microsystems Computers, CA/USA) using MATLAB 7 (The MathWorks Inc., Natick, MA, USA) and SPM5 (Statistical Parametric Mapping software, SPM, Wellcome Department of Imaging Neuroscience, London, UK http://www.fil.ion.ucl.ac.uk/spm). Dummy images were discharged before further image processing. Preprocessing included spatial realignment of the images to the reference volume of the time series, segmentation producing the parameter file used for normalization of EPI data to a standard EPI template of the Montreal Neurological Institute template provided by SPM5, re-sampling to a voxel size of 2×2×2 mm, and spatial smoothing with a 6-mm FWHM Gaussian kernel to meet the statistical requirements of the General Linear Model and to compensate for residual macro-anatomical variations across subjects.

To delineate the network involved in the lexical decision task *per se*, we performed a whole brain random effects analysis. Low-frequency signal drifts were filtered using a cut-off period of 128 s. To correct for motion artifacts, subject-specific realignment parameters were modeled as covariates of no interest. The presentation of action verbs as positive and negative imperatives (W_Do, W_Don't) were modelled as the regressors of main interest. Separate regressors modelled the presentation of the pseudoverbs (pW_Do, pW_Don't). An additional regressor of no interest specified the word length of our stimuli (see above). At the single subject level, specific effects were assessed by applying appropriate linear contrasts to the parameter estimates of the experimental conditions resulting in *t*-statistics for each voxel. For the second-level random effects analyses, contrast images obtained from individual participants were entered into a one-sample *t*-test to create a SPM{T}, indicative of significant activations specific for this contrast at the group level. We used a threshold of $P<0.05$, corrected for multiple comparisons at the cluster level (using family-wise error (FWE)), with a height threshold at the voxel level of $P<0.001$, uncorrected.

Hand area localizer and region of interest (ROI) analysis

The individual anatomically-constrained functional ROIs comprising the hand representations within the primary motor cortex (M1) and the premotor cortex (Pm) of both hemispheres were determined in all subjects immediately after the main experiment using a functional localizer task (Grefkes et al., 2008). The localizer always followed the lexical decision experiment to avoid biasing the subjects' attention toward the hand action-related aspect of the verb stimuli.

The localizer scan started with an instruction (3 s) requesting subjects to perform bilateral hand clenching movements in synchrony with a visual stimulus (a red circle) regularly appearing in the center of a white screen, with a frequency of 1.55 Hz. Blocks of active hand movements ($n=9$, 15 s each) were preceded by the instruction (3 s) and were alternated with baseline resting periods ($n=9$, 15 s each), during which subjects performed no movement. The time between instruction and stimulation onset was jittered (1.5, 2.0, 2.5 ms).

Identical pre-processing procedures were used as in the main experiment. We modeled the alternating epochs by a simple box-car reference vector. A general linear model for blocked designs was applied to each voxel of the functional localizer data by modeling the activation and the baseline conditions for each subject and their temporal derivatives by means of reference waveforms which correspond to boxcar functions convolved with a hemodynamic response function (Friston et al., 1995a,b). Furthermore, we included six additional regressors that modeled head movement parameters obtained from the realignment procedure. Accordingly, a design matrix, which comprised contrasts modeling alternating intervals of "activation" (hand clenching) and "baseline" (no movement), was defined. Specific effects were assessed by applying appropriate linear contrasts to the parameter estimates of the experimental condition and the baselines resulting in *t*-statistics for each voxel.

Using Marsbar written by Matthew Brett (http://marsbar.sourceforge.net/), ROIs comprising the hand representations within the left and right hemispheres were defined for each subject as the set of all contiguous voxels that were significantly more active for performing clenching hand movements vs. baseline at a threshold of $P<0.05$, FWE corrected. Thereafter, we considered only these voxels of the functional ROIs that were located within the cytoarchitectonically defined MPMs of the primary motor cortex (Brodmann area 4) or the premotor cortex (Brodmann area 6) provided by the SPM Anatomy toolbox (Eickhoff et al., 2005) to derive the anatomically-constrained functional ROIs of the primary motor or the premotor cortex. This procedure was performed for both hemispheres separately resulting in four anatomically-constrained functional ROIs of the left and right primary motor cortex and the left and right premotor cortex. This combined anatomical and functional approach was necessary because the (anatomical) cytoarchitectonically defined probability maps do not specify the (functional) hand representations within the motor areas. Using functionally and anatomically defined ROIs of premotor and primary motor cortex ensured that the reported data are functionally relevant (only those voxels were included which were significantly more active for hand movements during the localizer task) *and* anatomically specific (only those voxels were included that were located with the MPM of either the premotor cortex or the primary motor cortex). This procedure constitutes an important methodological advance in comparison with previous studies (see also Postle et al., 2008 for a discussion of the advantages of using MPMs of the motor areas in studies on action word processing). Subsequently, the beta values associated with each experimental condition (i.e., W_Do, W_Don't, pW_Do, and pW_Don't) were extracted from all voxels within the individually defined anatomically-constrained functional ROIs. Then, these beta values were entered into an ANOVA with stimulus (verb vs. pseudo-verb) and imperative (positive vs. negative imperative) as within-subjects factors.

RESULTS

Behavioral results

Accuracy data. Average accuracies for the lexical decision task did not differ significantly between positive and negative imperatives ($F(1,18)=0.09$, $P>0.05$, n.s., 92.2% for positive imperatives vs. 92.7% for negative imperatives) or stimuli ($F(1,18)=2.57$, $P>0.05$, n.s., 90.7% for verbs vs. 94.2% for pseudo-verbs; see Fig. 1). In addition, subjects were accurate in performing the recognition task (79.5% correct responses, range: 19/29 to 29/29).

RT data. In contrast, we found a significant effect of the type of imperative on reaction times ($F(1,18)=49.04$, $P<0.001$): RTs were significantly longer for negative (mean and standard deviation: 1177±320 ms) than positive imperatives (1115±307 ms; see Fig. 1). Slower RTs for negative relative to positive imperatives were observed both with verbs [$t(18)=-2.9$, $P<0.01$] and pseudo-verbs [$t(18)=-2.4$, $P<0.05$]. Thus, there was no significant interaction between word type (action verbs and pseudoverbs) and imperative ($F(1,18)=0.03$, $P>0.05$, n.s.).

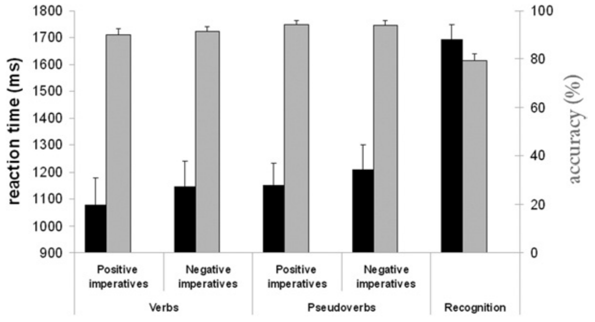

Fig. 1. Behavioral data. Reaction time (black bars) and accuracy (grey bars) data for performing the lexical decision task on action-related verbs and the corresponding pseudoverbs presented as positive and negative imperatives as well as for the recognition trials. Although the subject's accuracy was not influenced by the type of imperative, their mean reaction times (ms) were significantly faster for verbs preceded by a "Do" (positive imperatives) than for those preceded by a "Don't" (negative imperatives, $P<0.05$). There was no significant interaction between the factors word type (verbs vs. pseudoverbs) and imperative (positive vs. negative). Error bars indicate standard error (SEM).

To rule out any relevant effect of differential stimulus length (note that negative imperatives differed from positive imperatives by two letters only, "*n't*", we performed a further ANOVA on the RT data including stimulus length as an additional factor. Although this analysis confirmed the significant main effect of positive ("Do") vs. negative ("Don't") imperatives on reaction times ($F(1,18)=49.46$, $P<0.001$), the interaction "stimulus length" by "imperative" was again not significant ($F(1,18)=0.31$, $P>0.5$, n.s.). Thus, stimulus length did not affect the reaction time pattern.

fMRI results

Brain areas activated by the lexical decision task. The neural network underlying the lexical decision task (i.e., all experimental trials vs. baseline) was assessed by a whole brain random effects analysis ($P<0.05$, FWE corrected for multiple comparisons at the cluster level, with a height threshold at the voxel level of $P<0.001$). The task-related network included activation clusters bilaterally in the: (i) dorsolateral prefrontal cortex (DLPFC); (ii) premotor cortex (Pm); (iii) insula; (iv) superior parietal lobe; (v) temporo-parietal junction (TPJ); (vi) posterior superior temporal gyrus; (vii) ventral occipital cortex; (viii) cerebellar hemisphere; and (ix) primary motor cortex (M1). Furthermore, the anterior superior temporal gyrus, the intraparietal sulcus (IPS), and the posterior medial temporal gyrus (pMTG) of the left hemisphere were activated. Finally, significant activations in the following medial structures were observed: supplementary motor area (SMA), cingulate motor area (CMA), and cerebellar vermis (see Fig. 2a, Table 1).

Analysis of the additional regressor of no interest (coding stimulus length *per se*) revealed differential neural activity in bilateral occipital cortex only ($x=6$, $y=-88$, and $z=2$; $Z=5.17$, and $x=-4$, $y=-86$, and $z=16$; $Z=5.28$).

Region of interest (ROI) analysis of the effect of imperatives on action verb processing in the motor system. With the help of the localizer task based on hand clenching movements, individual anatomically-constrained functional ROIs comprising the hand area of the left and right primary motor cortex (M1) as well as that of the left and right premotor cortex (Pm) were defined in each of the right-handed subjects (see Methods). For a list of the coordinates of the activations peaks within the individual ROIs of the left and right primary motor cortex, see Table 2. The group mean coordinates (± standard deviation) of the peak activations within the anatomically-constrained functional ROI of the left primary motor cortex were −38 (±3.2), −25 (±2.7), and 59 (±5.9); those of the right primary motor cortex ROI were 38 (±2.6), −23 (±2.8), and 58 (±3.5); those of the left premotor cortex ROI were −35 (±5.7), −20 (±3.2), and 68 (±3.5); and those of the right premotor cortex ROI were 40 (±3.4), −18 (±2.9), and 66 (± 2.6; see Table 2). These mean coordinates are in good accordance with the previously published data (Fink et al., 2000; Stippich et al., 2002; Hanakawa et al., 2005). Furthermore, correct localization of the anatomically-constrained functional ROIs was verified for each subject by superimposition on the normalized individual brain (see Fig. 2b for an example).

The ANOVA performed on the beta values extracted from the individual anatomically-constrained functional ROIs comprising the hand area of the *left* primary motor cortex (M1) revealed a significant main effect of stimulus type ($F(1,18) = 916.06$, $P<.001$) and imperative ($F(1,18) = 449.4$, $P<.001$) as well as a significant interaction ([(W_Do - W_Don't] $>$ [pW_Do − pW_Don't], $F(1,18) = 728.21$ $P<.001$; see Fig. 2c). Post hoc *t*-tests revealed a significant difference between W_Do and W_Don't ($t(18)=44.32$, $P<.001$) with a significant decrease of the beta values for W_Don't compared with W_Do. In contrast, the difference between pW_Do and pW_Don't was not significant ($t(18)=0.914$, $P>.05$, n.s). The inverse interaction term was not significant.

The ANOVA performed on the beta values extracted from the individual anatomically-constrained functional ROIs comprising the hand area of the *right* primary motor cortex (M1) revealed a significant main effect of stimulus type ($F(1,18)=73.47$, $P<.001$) and of imperatives ($F(1,18)=98.52$, $P<.001$). In addition, the interaction term was significant too ((W_Do - W_Don't] $>$ [pW_Do - pW_Don't], $F(1,18)=241.92$, $P<.001$; see Fig. 2c. Post hoc *t*-tests revealed a significant difference between W_Do and W_Don't ($t(18) = 11.38$, $P<.001$) with a significant decrease of the beta values for W_Don't compared with W_Do. In contrast, the difference between pW_Do and pW_Don't was not significant ($t(18)=-0.15$, $P>.05$, n.s). The inverse interaction term was not significant.

For the analysis of the premotor cortex activation, the ANOVA performed on the beta values extracted from the individual anatomically-constrained functional premotor cortex ROIs of the *left* hemisphere revealed a significant main effect of stimulus ($F(1,18)=62.24$, $P<.001$) and a significant interaction ([W_Do −W_Don't] $>$ [pW_Do − pW_Don't], $F(1,18)=159.46$, $P<.001$; see Fig. 2c). Post hoc *t*-tests revealed a significant difference between W_Do and W_Don't ($t(18)=6.69$, $P<.001$), again with a significant decrease of the beta values for W_Don't compared with W_Do, and significant difference between between pW_Do and pW_Don't ($t(18)=-17.75$, $P<.001$) with a significant decrease of the beta values for pW_Do compared with pW_don't. The main effect of imperatives and the inverse interaction term was not significant. A similar ANOVA-analysis performed for the individual anatomically-constrained functional ROIs of the *right* premotor cortex revealed a significant main effect of stimulus ($F(1,18) = 61,79$, $P<.001$), of imperative ($F(1,18)=46.5$, $P<.001$), and a significant interaction ([W_Do −W_Don't] $>$ [pW_Do − pW_Don't], $F(1,18)=168.51$, $P<.001$; see Fig. 2c). Post hoc *t*-tests revealed a significant difference between W_Do and W_Don't ($t(18)=9.05$, $P<.001$), whereas the difference between pW_Do and pW_Don't was not significant ($t(18)=.83$, $P>.05$). The inverse interaction term was not significant.

In summary, the ROI-analyses revealed that all four motor areas (left and right primary motor cortex as well as left and right premotor cortex) show a similar modulation of

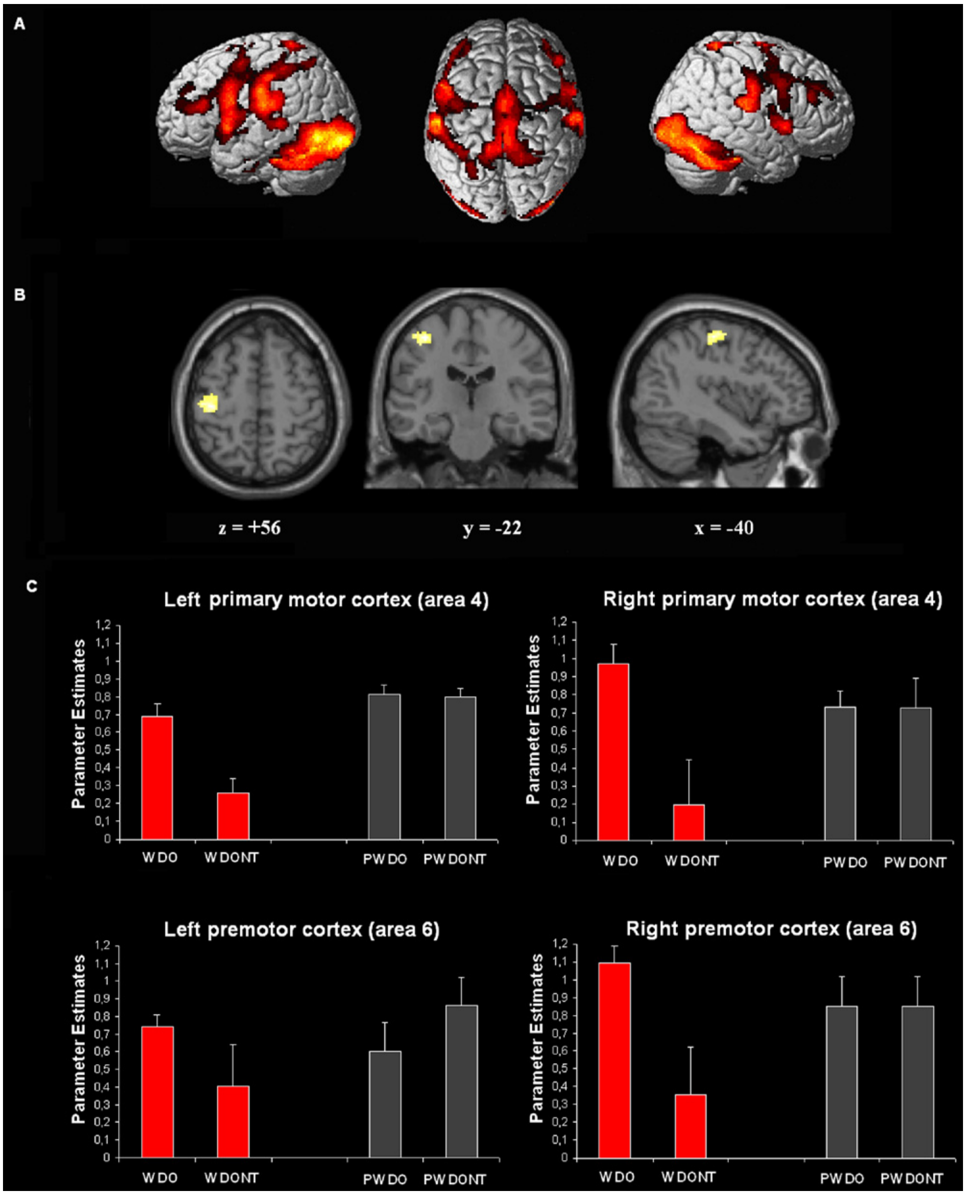

Fig. 2. (A) Common network underlying the lexical decision task as revealed by the whole brain analysis. Relative increases in neural activity associated with the lexical decision task ($P<0.05$, FWE corrected at the cluster level; see Table 2) are displayed on a rendered template brain provided by spm5. (B) An individual left hand M1-ROI (maximally activated voxel at -36, -22, $+52$) is superimposed on an axial, coronal, and sagittal slice of the spatially normalized single subject brain (subject # 1). (C) Group mean beta values extracted from the individual anatomically-constrained functional ROIs comprising the hand representation within the left and the right primary motor cortex (upper row) as well as the left and the right premotor cortex (lower row) separately displayed for action-related verbs (W_Do, W_Don't) and pseudoverbs (pW_Do, pW_Don't) presented in a positive or negative linguistic context.

their activity for action verbs, that is, a reduced activity when the action verbs are presented as negative imperatives (W_don't) compared with a presentation of the action verbs as positive imperatives (W_Do, see Fig. 2c).

DISCUSSION

This fMRI study was designed to further explore the interaction between action and language and, in particular, the nature of the previously reported involvement of the primary motor and premotor cortices in action word processing (Hauk et al., 2004). Specifically, we investigated whether the linguistic context, in which a (hand) action verb occurs (here: negative vs. positive imperatives), modulates the neural activity in the motor system.

Before we address the implications of our main finding, that is, the differential activity decrease in all four motor areas (left and right primary motor cortex as well as left and right premotor cortex) during lexical processing of action-related verbs presented as negative imperatives, we first discuss the neural network involved in the lexical decision task *per se*. The common task-related network in this study predominantly reflected language processing, response

Table 1. Whole brain analysis: brain regions showing significant relative increases of BOLD response associated with the lexical decision task per se

Region	Side	MNI			Z
		x	y	z	
Dorsolateral prefrontal cortex (DLPFC)	L	−44	46	16	5.98
	R	52	16	42	7.98
Posterior superior temporal gyrus	L	−62	−22	20	7.29
	R	66	−22	16	7.6
Anterior superior temporal gyrus	L	−52	16	−10	5.19
Posterior medial temporal gyrus	L	−60	−36	2	5.46
Insula	L	−38	4	6	9.17
	R	48	4	4	6.40
Superior parietal lobe	L	−14	−44	70	6.97
	R	8	−40	72	7.46
Intra parietal sulcus (IPS)	L	−30	−58	54	4.44
Temporo-parietal junction (TPJ)	L	−58	−16	30	8.99
	R	56	−14	30	6.41
Ventral occipital cortex	L	−44	−48	−24	11
	R	46	−48	−24	7.6
Primary motor cortex (M1)	L	−4	−24	70	6.65
	R	6	−26	72	7.62
Premotor cortex	L	−54	10	38	8.12
	R	52	16	42	7.98
Supplementary motor area (SMA)	M	0	4	68	6.93
Cingulate motor area (CMA)	M	−4	−2	42	5.59
Cerebellar vermis	M	4	−58	−36	6.11
Cerebellar hemisphere	L	−36	−50	−30	10.47
	R	38	54	−34	8.88

For each region of activation, the coordinates in MNI space are given in reference to the maximally activated voxel within an area of activation, as indicated by the highest Z-value ($P<0.05$, corrected for multiple comparisons at the cluster level, height threshold $P<0.001$, uncorrected).

L/R, left/right hemisphere; M, medial brain structure.

selection, and motor output-related processes. The activations encompassed areas which have been shown to be involved in lexical-semantic processing by fMRI and PET studies (Price et al., 1996; Perani et al., 1999b; Mechelli et al., 2003): bilaterally the ventral occipital cortex, albeit predominantly left hemispheric, including the "visual word form area" (VWFA; Price et al., 1996; Dehaene and Le Clec'H, 2002], extending to the left anterior superior temporal gyrus, bilateral TPJ, and the left posterior medial temporal gyrus (pMTG) reflecting language processing, especially for sentences with implied motion/action meaning (Wallentin et al., 2005). Furthermore, we found activations in superior parietal cortex bilaterally and in the left intraparietal sulcus in conjunction with bilateral activations of the premotor cortex, confirming earlier reports on a general role of these areas in word processing (Price et al., 1996; Binder, 1997; Tettamanti et al., 2005). Additional activation clusters included the dorso-lateral prefrontal cortex bilaterally, most likely reflecting the supervisory demands of the task. In summary, the lexical decision task adopted in our current study activated neural networks previously associated with lexical decisions on words and pseudo-words (Price et al., 1996; Perani et al., 1999a; Mechelli et al., 2003; Carreiras et al., 2007).

Modulation of motor system activity by linguistic context during processing of action verbs

As in previous studies, in which a functional link between motor and language systems has been demonstrated (Pulvermüller et al., 2001, 2005a,b; Hauk et al., 2004; Oliveri et al., 2004; Aziz-Zadeh et al., 2006; Ruschemeyer et al., 2007; Kemmerer and Gonzalez-Castillo, 2010), we found significant activations of the motor areas (M1 and Pm) during lexical decisions of action words. However, our results extend previous findings by showing that the response of the motor areas was differentially modulated by linguistic context (here: type of imperative), with decreased primary motor and premotor cortex activation for negative imperatives (e.g., "Don't write") compared with positive imperatives (e.g., "Do grasp"). This systematic modulation by the type of imperative occurred for verbs only and was not present for pseudo-verbs. The similar activation patterns for premotor and primary motor cortex jointly support the notion that the activation of the sensorimotor representation has to be inhibited during processing of negative action verb imperatives. This result is consistent with that of Tettamanti et al. (2008), who showed that negative sentences led to a decreased activation in left premotor cortex with respect to affirmative sentences. Moreover, the right primary motor cortex and the right premotor cortex exhibited a similar activation pattern as the left hemispheric motor areas. The activation of right hemispheric motor areas could be due to the fact that many of the hand-related actions described by our stimuli could be performed bimanually (e.g., "Do typewrite," or "Do cut"). Furthermore, this result is in good accordance with previous imaging studies revealing *bilateral* activation of motor areas during action-verb processing (Hauk et al., 2004; Ruschemeyer et al., 2007). The data are also consistent with neuropsychological studies of patients with lesions of right frontal cortex, who showed impaired motor-related verb processing (Neininger and Pulvermuller, 2001, 2003).

Although all motor areas investigated showed a similar modulation of their activity for action verbs, the pattern for the pseudo-word conditions, that is, our control condition—a prerequisite of our experimental task (lexical decision)—was less consistent suggesting that the evaluation of the artificial negative imperatives based on meaningless pseudo-words does not lead to meaningful activity patterns in the motor system. Thus, although pseudo-words (in our study) can activate motor areas, these motor activations are not properly modulated by linguistic context (in contrast to action verbs for which the motor system activations are systematically modulated according to the predictions of the current study). Therefore, we think that the highly consistent modulation of motor system activity by linguistic context, in which action verbs are presented, is a specific effect of action verb processing on the corresponding sensorimotor representations. Note that similar unspecific activations of motor areas have been observed by Postle et al. (2008). These authors showed motor area responses to

Table 2. List of the individual and group mean coordinates (in MNI space) of the maximally activated voxel within the (anatomically-constrained functional) ROIs comprising the hand representation of the left and the right primary motor (M1) and premotor (Pm) cortices obtained by the functional localizer task and the maximum probability maps (MPMs)

Left M1			Right M1			Left Pm			Right Pm		
x	y	z	x	y	z	x	y	z	x	y	z
−40	−28	64	40	−22	60	−42	−22	66	32	−16	72
−36	−24	62	34	−20	58	−40	−14	66	40	−14	66
−36	−22	52	34	−26	62	−30	−20	70	40	−22	68
−38	−28	66	40	−20	58	−30	−16	68	40	−18	62
−36	−28	66	40	−22	62	−26	−24	72	40	−24	68
−38	−22	58	38	−26	56	−34	−16	68	36	−18	68
−38	−28	64	38	−18	52	−36	−24	70	44	−16	64
−42	−24	60	40	−24	60	−42	−20	66	42	−20	66
−38	−22	60	36	−26	60	−40	−18	66	38	−20	64
−40	−28	66	40	−26	62	−44	−16	60	42	−22	66
−36	−24	54	40	−20	52	−36	−20	70	40	−18	68
−38	−24	60	38	−20	60	−36	−20	70	44	−14	64
−40	−28	66	42	−18	56	−42	−22	64	42	−16	66
−34	−30	70	40	−25	62	−28	−26	76	36	−20	70
−42	−22	56	36	−24	58	−36	−18	66	42	−20	64
−38	−22	48	38	−24	58	−34	−20	68	46	−20	64
−30	−24	54	38	−22	54	−42	−20	64	40	−20	66
−44	−26	54	44	−20	54	−26	−24	72	42	−14	62
−36	−24	56	36	−20	64	−36	−20	68	36	−22	68
−38	**−25**	**59**	**38**	**−23**	**58**	**−35**	**−20**	**68**	**40**	**−18**	**66**
3,2	*2,7*	*5,9*	*2,6*	*2,8*	*3,5*	*5,7*	*3,2*	*3,5*	*3,4*	*2,9*	*2,6*

The group mean coordinates are indicated in bold and the respective standard deviations in italics.

imageable concrete words (unrelated to actions) and to "non-words" with regular phonology. Thus, in accordance with our results, the pseudo-words of Postle and co-workers *did* activate motor areas. Furthermore, the pseudo-verbs used in our study were closely matched to the action verbs ("grasp" vs. "gralp"). In fact, this matching of the verb stimuli was comparable with that by Shapiro et al. (2005, see p. 1060). Interestingly, these authors observed a similar activation of a (left) frontal network for their verb stimuli as well as for their pseudo-verb stimuli—a further indication that pseudo-verbs can activate (frontal) cortical areas to a similar extend as verbs (see also Roder et al., 2002). Taken together the previous and our own data, we would like to propose that it is not the activation of motor areas *per se* that distinguishes the effects of action verbs from that of pseudo-verbs, but rather the *systematic modulation* of that motor system activity by the linguistic context which only occurs for action verbs. At variance with the study by Postle et al. (2008), in which generic action word meanings compared with all other classes of lexical stimuli did show increased BOLD signal responses in the pre-SMA, we found that the activation of both primary and premotor cortices was modulated not by the stimulus type *per se* (verbs vs. pseudoverbs), but rather by the linguistic context; more specifically by the interaction of linguistic context and stimulus type (verbs vs. pseudoverbs). Willems et al. (in press) showed that parts of premotor cortex distinguished manual from non-manual actions during both lexical decision and imagery, suggesting that implicit simulation and explicit imagery cued by action verbs may involve different types of motor representations. Our results are not consistent with this view: our data rather suggest that linguistic context might be a critical variable for observing premotor activity overlapping with verb processing (Willems et al., in press).

Revealing a modulatory effect of the type of imperative on primary motor and premotor cortex activity during lexical decisions on action-related verbs does not support the idea that the processing of the action word's meaning directly triggers activity in motor areas. Related to our study, such a direct functional connection between the language and the motor system would predict that reading a verb, for example, "grasp," activates the motor areas of the brain independent of the linguistic context, for example, negative or positive imperative: "Don't grasp" or "Do grasp," in which the verb occurs. We acknowledge, however, that subjects may have perceived the task rather as a sensibility judgment task (than a lexical decision task), which might have triggered even deeper linguistic processing. If this was the case, then this would even strengthen our findings, because our main result was a differential activity *reduction* for all four motor areas tested in the context of negative imperatives. This finding is not consistent with the associationist theory which proposes that any linguistic processing of action-related words (which might be even deeper when our subjects perceived the current experimental task as a sensibility judgment) should result in an activity *increase* in the motor areas independent of the linguistic context.

It is known that sensorimotor representations can be accessed through both the observation-execution-matching system (e.g. Gallese et al., 1996; Rizzolatti et al., 1996;

Buccino et al., 2001) and motor imagery (Decety et al., 1994; Jeannerod and Decety, 1995; Porro et al., 1996). Intending, planning, or preparing to move as well as watching someone else's action with the desire to imitate it, anticipating the effects of an action, or remembering an action may be similar processes, which have been summarized by Jeannerod under a common cognitive state called "motor simulation" (Jeannerod, 2001) or "motor imagery" (Jeannerod and Decety, 1995). It has been suggested these cognitive motor states may serve as "a window into the representational stages of action." According to this view, processing of negative imperatives may inhibit sensorimotor representations resulting in decreased activity in the motor areas.

Although associative learning theories and simulation theories are difficult to distinguish (e.g., Keysers and Perrett, 2004; Brass and Heyes, 2005), our experiment introduces (linguistic) context (by presenting the verb in positive or negative imperative sentences) as an experimental variable, which might be a promising approach to investigate further the interaction between the language and the motor systems. According to the associative learning approach (Pulvermüller, 1999, 2005; Pulvermüller et al., 2001, 2005a,b) the activation of the sensorimotor cortex "should not require people to attend to language stimuli, but should instead be *automatic*" (Pulvermüller, 2005). These sensori-motor areas should play a specific functional role in *recognizing* action words (Pulvermüller et al., 2005b). Those neurons involved in *recognizing* action words should respond anytime when an action verb is recognized. Subjects certainly recognized the action-verbs in the current W_Don't condition (as indexed by their task performance). However, the W_Don't condition led to a *de*crease of the BOLD signal in the hand representation of the motor areas. In contrast, the embodied cognition framework proposes that the activation of the sensorimotor representations may be modulated by linguistic context. Processing of action words in an affirmatory (positive) context should facilitate the activation of sensori-motor representations, whereas a negative context should inhibit the activation of sensori-motor representations.

The differential modulation of the motor system activity by linguistic context (i.e., type of imperative), with decreased motor cortex activation for verbs presented as negative imperatives compared with those presented as positive imperatives shows that motor cortex activity is not a requirement for language comprehension: subjects understood the actions words and correctly performed the lexical decision task for the stimuli presented in the "Don't"-condition, although the activation of the motor areas *de*creased in this condition. Our results show that semantic access *per se* (occurring both for [action] verbs under the "Do" and the "Don't" conditions) does not necessarily increase neural activity in motor areas. In a similar vein, Ruschemeyer and colleagues (2007) reasoned that if action verbs automatically activate the motor circuitry (Ruschemeyer et al., 2007), this should be the case for simple action-related verbs (such as "greifen" [to grasp]) as well as for complex transitive verbs (such as "begreifen" [to comprehend]). By contrast, their data showed that only simple action-related verbs, but not complex verbs, triggered activity in premotor areas. Thus, the activation of the motor circuitry by action verbs depends on the linguistic context, in which the action-related verb is presented. Similarly, Raposo et al. (2009) showed that motor system activity during action verb processing was indeed context-dependent. In that study, authors presented action verbs in isolation, in literal sentential contexts, and in idiomatic contexts and found significant activation in motor regions when action verbs were presented in isolation, and, to a lesser extent, in literal sentential contexts. When the same verbs were presented in an idiomatic context, activation was found in fronto-temporal regions, associated with language processing, but not in motor and premotor cortices. Thus, the data of Ruschemeyer et al. (2007) and of Raposo et al. (2009), as well as our current results, rather support the notion that the motor system is not essential for the processing of action-related verbs *per se*. This is consistent with neuropsychological data showing that lesions confined on the motor system do not predictably cause deficits in action-word processing (De Renzi and di Pellegrino, 1995; Saygin et al., 2004; Mahon and Caramazza, 2005).

Showing that the motor system activation during lexical decisions on action-related verbs is modulated by the lexical context rather favors the notion that this motor system activation is a corollary phenomenon, because the processing of action-related verbs triggers a cognitive set of implicit movement preparation/planning, motor intention, and motor simulation (see also: Oliveri et al., 2004; Boulenger et al., 2006). Therefore, the context-dependent effect on the action verb related motor system activation strengthens the idea of an indirect connection between the motor and language systems through sensorimotor representations. The similar capacity of the observation-execution-matching system (e.g., Gallese et al., 1996; Rizzolatti et al., 1996; Buccino et al., 2001) and of motor simulation (Decety et al., 1994; Stephan et al., 1995; Porro et al., 1996) to activate sensorimotor representations (Jeannerod and Decety, 1995) may point to a common framework explaining motor system activations during action-related word processing. Within this framework, processing of action-related words may (indirectly) activate sensorimotor representations and, thus, primary motor and premotor areas, either through the observation-execution-matching system (e.g., Tettamanti et al., 2005; Buccino et al., 2005; Aziz-Zadeh et al., 2006) or by (implicitly or explicitly) triggering mental simulation (e.g., Glenberg and Kaschak, 2002; Kaschak et al., 2005; Tomasino et al., 2007).

A third explanation for the current pattern of results is that the observed activation of the motor areas is related to motor planning. Previous studies showed that motor planning processes (in the absence of any overt movement) can modulate activity in motor areas (Jeannerod and Decety, 1995; Jeannerod, 2001). The notion that motor planning processes and action-verb processing interact is in line with previous findings (Boulenger et al., 2006). These authors showed that subliminal displays of action verbs have an effect on the neurophysiological correlates of motor planning/preparation and on the kinematics of the subsequent reaching movement. Accordingly, in our study, positive imperatives (e.g., "Do grasp") could have caused excitation of response, whereas negative imperatives (e.g., "Don't grasp") could have caused inhibition of response leading to a decrease of activity in motor areas as a result of the inhibition of sensori-motor representations.

Our behavioral results further indicate that the effect of negative imperatives on response times can be explained by inhibitory mechanisms. As mentioned in the introduction, processing of action verbs or action-related sentences has been shown to influence even overt motor behaviour. However, the current pattern of RTs cannot be attributed to this kind of interference between language processing and response execution. It is known that processing verbally-presented actions activates somatotopically different sectors of the motor system, depending on the effector involved in the movement denoted by the action verb (Hauk et al., 2004). For instance, it has been demonstrated that listening to hand-related action sentences leads to slower reaction times for hand responses compared with foot responses, and that listening to foot-related action sentences leads to slower reaction times for foot responses compared with hand responses (Buccino et al., 2005). In the present experiment, our subjects used their *feet* to press the response buttons while they were performing lexical decisions on imperatives containing *hand*-related verbs and the corresponding pseudoverbs. Taking into account that the increase in response times for a given movement when listening to a related word or sentence is somatotopically specific, that is, hand movements are slowed by hand-related words, this interference effect cannot account for the influence of positive imperatives on foot response times in the current study. Note that in our study, the prolongation of RTs in the context of negative imperatives was present for action verbs and pseudo-words alike. In contrast, there was a decrease of neural activity in the motor areas for negative imperatives of action verbs only. Moreover, subjects were responding with their feet after making lexical decisions about hand action related verbs. Therefore, we think that general inhibition mechanisms (also affecting foot movements) may have been triggered by the negative imperatives resulting in similar RT prolongation for verbs and pseudoverbs. We performed additional analyses of the behavioural and fMRI data to rule out that the reported significant main effect of imperatives on reaction times and BOLD signal changes in the motor areas was due to systematic differences in stimulus length. However, this regressor did not explain the variance induced by the experimental factor 'imperative ("Don't" vs. "Do") as stimuli with identical lengths occurred in both imperative conditions (e.g., "Don't hit" and "Do grasp," both with a length of seven letters). Therefore, we consider an alternative account inspired by the natural use of imperatives. Imperatives are commonly used as commands. Furthermore, if we hear a command (e.g., "Don't move/shoot/hit!"), we refrain ourselves from performing the corresponding action. Thus, while processing a negative imperative, for example, "Don't grasp" an action needs to be withheld. Thus, the activation of the sensorimotor representation has to be inhibited. This view is consistent with Postle et al.'s (2008) study, in which the only region found to be sensitive to the stimulus category (motor vs. control) was the pre-SMA. Postle et al. already suggested that this pre-SMA-activation was due to the imperative form of a verb serving as an instruction cue: "verbs serve as instruction cues by enabling the retrieval of an appropriate motor program, i.e., they [verbs] represent information required for motor planning."

CONCLUSION

In summary, introducing linguistic context (here: negative and positive imperatives) seems to be a promising approach to investigate further the interaction between language and the motor systems. However, more investigations along these lines are necessary to clearly distinguish between the different theories (e.g., embodied cognition framework and associationist theory) proposed to explain activation of the primary motor and premotor cortex during action word processing.

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