

On-line Changing of Thinking about Words: The Effect of Cognitive Context on Neural Responses to Verb Reading

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Abstract

Activity in frontocentral motor regions is routinely reported when individuals process action words and is often interpreted as the implicit simulation of the word content. We hypothesized that these neural responses are not invariant components of action word processing but are modulated by the context in which they are evoked. Using fMRI, we assessed the relative weight of stimulus features (i.e., the intrinsic semantics of words) and contextual factors, in eliciting word-related sensorimotor activity. Participants silently read action-related and state verbs after performing a mental rotation task engaging either a motor strategy (i.e., referring visual stimuli to their own bodily movements) or a visuospatial strategy. The mental rotation tasks were used to induce, respectively, a motor and a non-

motor “cognitive context” into the following silent reading. Irrespective of the verb category, reading in the motor context, compared with reading in the nonmotor context, increased the activity in the left primary motor cortex, the bilateral premotor cortex, and the right somatosensory cortex. Thus, the cognitive context induced by the preceding motor strategy-based mental rotation modulated word-related sensorimotor responses, possibly reflecting the strategy of referring a word meaning to one’s own bodily activity. This pattern, common to action and state verbs, suggests that the context in which words are encountered prevails over the intrinsic semantics of the stimuli in mediating the recruitment of sensorimotor regions. ■

INTRODUCTION

The context of a cognitive task corresponds to any external information that channels an individual’s attention to certain aspects of the stimuli, thus guiding the subsequent information process. The internal representation of a context helps generate predictions about the content of stimuli and update task-relevant information for the selection of a response (Fenske, Aminoff, Gronau, & Bar, 2006; Friston, 2003; Büchel & Friston, 1997; Cohen, Servan-Schreiber, & McClelland, 1992). The implication of such top-down modulation of stimulus processing is striking: Neural responses are not invariant to a stimulus and, depending on the context in which they are evoked, differential activity can relate to the processing of identical stimuli (Friston, 2003). This defines the notion of modulability and reversibility of the modality (or strategy) for processing information.

The role of bottom-up and top-down factors has been highlighted in studies addressing whether the recruitment of motor processes in mental rotation depends, respectively, on the nature of the stimuli or on the particular mental operation adopted for solving a task. Top-down control has been examined through the implicit transfer

of strategies, a phenomenon occurring when a processing mode is implicitly transferred from one task to another that does not necessarily require it (Wraga, Thompson, Alpert, & Kosslyn, 2003; Grafton, Fagg, & Arbib, 1998; Pascual-Leone, Grafman, & Hallett, 1994; Willingham, Greeley, & Bardone, 1993). In particular, Wraga et al. (2003) showed that mental rotation of objects, known to rely on visuospatial processing or visuospatial strategy (Zacks, 2008), elicited motor activity when participants had previously performed mental rotation of hands, a task found to engage motor processes or motor strategy (i.e., the internal rotation of one’s own hand; Kosslyn, Ganis, & Thompson, 2001; Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000; Bonda, Petrides, Frey, & Evans, 1995; Parsons et al., 1995). That is, because of the implicit transfer of the motor strategy used during the hand rotation task, participants imagined grasping and rotating objects with their own hands. No motor activity was found when object rotation was not preceded by the hand rotation task. Adopting a strategy to perform a Task A can thus implicitly evoke a “cognitive context” that affects neural responses to a subsequent Task B.

We exploited this cognitive phenomenon to contribute to the current debate on word processing. It has been proposed that processing words denoting motor acts involves accessing stored sensorimotor information (Binder

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& Desai, 2011; Hauk, Johnsrude, & Pulvermüller, 2004; Chao & Martin, 2000; Grabowski, Damasio, & Damasio, 1998) and, possibly, performing an internal simulation of the implied physical act that engages the left fronto-central sensorimotor regions (for a review, see Binder & Desai, 2011). It is unclear to what extent this activity is an invariant component of action words processing or it is dependent on top-down modulation.

Extant literature suggests that the recruitment of these sensorimotor regions may be bounded to task contexts driving an individual's attention toward the motor attributes of a linguistic utterance. Systematic manipulation of the task demand in neuroimaging and TMS studies revealed increased sensorimotor activity when participants thought about the typical scenario (indoor/outdoor) of implied language actions (e.g., "I run"; Tomasino, Werner, Weiss, & Fink, 2007) or when they performed semantic judgments on action verbs (Papeo, Vallesi, Isaja, & Rumiati, 2009), relative to task conditions where the access to meaning was less explicit or only incidental (e.g., letter detection or syllable counting; see also Papeo, Corradi-Dell'Acqua, & Rumiati, 2011; Willems, Toni, Haggort, & Casasanto, 2010; Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008). Moreover, it has been shown that functional connections between language comprehension regions and motor regions were activated when speech was accompanied by semantically relevant hand gestures (Skipper, Goldin-Meadow, Nusbaum, & Small, 2009), suggesting that the cortical network for language understanding is not "static" but changes according to the currently available contextual cues. Finally—and by analogy with Wraga et al.'s (2003) report of sensorimotor activity for the mental rotation of cubes—sensorimotor neural responses to concrete words with no motor content (Postle, McMahon, Ashton, Meredith, & De Zubicaray, 2008; Pulvermüller & Hauk, 2006; Mellet, Tzourio, Denis, & Mazoyer, 1998; D'Esposito et al., 1997) and, sometimes, to pseudowords (Tomasino, Weiss, & Fink, 2010; Postle et al., 2008) further suggest that it is not the type of stimulus, but the type of strategy employed to solve a task, that drives sensorimotor processes.

By using fMRI, the current study investigates the effect of the cognitive context on neural activations related to word processing, while keeping constant the stimuli and the task demand. Following Wraga et al. (2003), two mental rotation tasks (based on motor strategy and on visuospatial strategy, respectively) were used to manipulate the cognitive context of the subsequent word processing. This manipulation rests upon the notion of implicit transfer as a flexible mechanism, which can operate across different types of materials (images of objects to rotate and words) and across cognitive domains (mental rotation and language processing; Willingham, 1997, 1999). Participants performed a block of either motor strategy- or visuospatial strategy-based mental rotation, randomly presented before each block of silently reading verbs describing hand actions or physical/psychological states.

Participants were instructed to read verbs for delayed recognition to ensure attentive encoding of each word meaning.

Word-related neural activations were thus measured in two conditions that were identical, except for the cognitive context (motor or nonmotor) elicited by the preceding task (motor strategy-based or visuospatial strategy-based mental rotation). This experimental design allowed testing the hypothesis that the recruitment of sensorimotor regions reflects one optional strategy for word encoding, and as such, it is not invariantly driven by the bottom-up stimulus features (i.e., the semantic nature of the stimuli). If this hypothesis is correct, sensorimotor responses to action words should be modulated by the cognitive context in which they are evoked. In particular, we predicted that the motor strategy adopted in the rotation task, where participants learnt to relate the stimuli to their own bodily movements, could influence the way participants processed words in the subsequent silent reading, although they received no explicit instructions on relating verb meanings to bodily actions. Crucially, a pivotal influence of contextual factors over stimulus features would be suggested by a transfer of the motor modality of processing to abstract terms (i.e., state verbs), just like in Wraga et al. (2003), the motor strategy of rotation was transferred to stimuli with no sensorimotor components, such as meaningless cubes. Thus, neural responses to state verbs, given the motor context, became a crucial testbed of our hypothesis.

Bilateral hand representation in the motor areas were individually localized with a hand movement task combined with cytoarchitectonic maximum probability maps (MPMs) of human primary motor and premotor cortex (see also Tomasino et al., 2010; Postle et al., 2008).

METHODS

Participants

To avoid gender effects on mental rotation tasks (Jordan, Wustenberg, Heinze, Peters, & Jancke, 2002; Voyer, Voyer, & Bryden, 1995), only healthy university graduate or undergraduate women ($n = 18$, aged 22–28 years) took part in the study. All were right-handed (Edinburgh Inventory; Oldfield, 1971), native Italian speakers, with normal or corrected-to-normal vision and no history of neurological illness, psychiatric disease, or drug abuse and no other counterindication to fMRI. Participants gave written informed consent before the study and were paid for their participation. The study was conducted in accordance with the Declaration of Helsinki and was approved by the local ethics committee.

Stimuli

Stimuli for the silent reading task were 80 hand action-related verbs (e.g., *to stir*) and 80 state/psychological verbs

(e.g., *to adore*) appearing in their infinitive form, one at a time, on a white background (Verdana font, 40-pt). These items were taken from a larger database of verbs classified as either action-related (e.g., *to grasp, pick, write*) or stative (e.g., *to love, belong, contain*), according to the criteria of linguistic tradition (Jackendoff, 1990; Taylor, 1977; Vendler, 1967), and then validated with a rating study involving a panel of 10 subjects (for details, see Papeo et al., 2009). The selected action and state verbs were matched for the percentage of agreement on the category (action vs. state), length (number of graphemes), and written frequency (Laudanna, Thornton, Brown, Burani, & Marconi, 1995), $t(79) < 1$. To obtain a high level baseline, 80 meaningless illegal letter strings (“*csdawq*”), randomly generated and matched for length with the verb list, $t(79) < 1$, were included. In the recognition task administered at the end of the scanning session, a subset of 40 verbs (20 action and 20 state) was randomly selected from the experimental list (“old” list) and presented intermingled with 40 verbs not shown in scanning session (20 “new” action and 20 “new” state) and matched for frequency and length with the “old” list, $t(39) < 1$.

The mental rotation tasks involved color photographs (560×560 pixels) of a hand or a geometrical figure, respectively (Figure 2A), appearing on a white background, in one of six possible orientations: 45° , 90° , 135° , 225° , 270° , or 315° from the upright canonical orientation. Each figure appeared 20 times at each orientation, for a total 120 stimuli for each mental rotation task (120 hands and 120 geometrical figures).

Hand pictures depicted either the right hand (50% of trials) or the left hand (50% of trials); geometrical figures depicted a 3-D two-armed geometrical figure (Shepard & Metzler, 1971) created with Blender software (www.blender.it). The figure, in its upright orientation, had approximately the shape of a “J”, with one longer arm and two shorter arms at the two extremes of the longer one. The figure had a red marker on either shorter arm and a black arrow at the center of the longer arm, heading leftward (50% of the trials) or rightward (50% of the trials) to cue the direction for mental rotation.

Experimental Design and Procedures

We used a 2×2 block design, with Cognitive Context (motor vs. nonmotor, as defined by the preceding motor or visuospatial strategy-based mental rotation task) and Verb Category (action vs. state) manipulated within subjects.¹ This yielded four experimental conditions: silent reading of (1) action verbs or (2) state verbs after motor strategy-based mental rotation (i.e., in motor context) and (3) action verb or (4) state verb after visuospatial strategy-based mental rotation (i.e., in nonmotor context; Figure 2A). Eight trial blocks (17.2 sec each) of either action or state verbs were randomly presented (2 sec per stimulus followed by 150-msec blank), after each block of either motor or visuospatial strategy-based mental rotation,

for a total of 40 blocks (20 silent reading, 50% after the motor, and 50% after the visuospatial strategy-based mental rotations), alternating with 10-sec resting baseline. Before each block, a 5-sec instruction screen informed the participants on the upcoming task.

In the silent reading task, participants were instructed to read carefully each verb to perform a recognition test at the end of the scanning session. In the motor strategy-based mental rotation task, participants were instructed to decide whether each photograph depicted a left hand or a right hand, by imaging moving their own hands until it reached the position of the hand stimulus on the screen (motor strategy). In the visuospatial strategy-based mental rotation task, participants decided whether a red marker on either arm of the 3-D object was at the left or right of the screen midline, after having mentally visualized the object rotating and aligning with the midsagittal line of the computer screen (visuospatial strategy). These two strategies of mental rotation have been found to trigger egocentric perspective taking and sensorimotor activations versus allocentric perspective taking and visuospatial activations, respectively (Zacks, 2008; Tomasino, Borroni, Isaja, & Rumiati, 2005; Kosslyn et al., 2001). Before the scanning session, participants were trained on both mental rotation strategies.

As activity in the hand representation of the left primary motor cortex (M1) and premotor cortex is frequently found during hand rotation, we identified this region, in each individual, by combining the cytoarchitectonically defined MPMs with a functional localizer task that defined functional activations within the anatomically constrained ROI (Grefkes et al., 2008). This task was performed within the scanner after the main experiment. Participants were instructed to perform right- or left-hand clenching movements synchronized with the white-to-red color alternation (1.5 Hz rate) of a circle appearing in the center of a white background. Nine blocks of active movements (15 sec each) were interleaved with baseline resting periods (15 sec each). Each “active” block was preceded by instruction (3 sec) to move either hand. The time between the instruction screen and the onset of the cue stimulus for clenching was jittered (1.5, 2.0, and 2.5 msec; for details, see Grefkes et al., 2008).

In the fMRI scanner, participants laid supine with their head fixated by firm foam pads and their arms along the body with the palms parallel to the legs. Stimuli were projected through a VisuaStim Goggles system (Resonance Technology), and responses to the imagery tasks were given by pressing the keys, placed under the participant’s left toes (left-hand/left-sided marker) and right toes (right-hand/right-sided marker) of an MRI-compatible response device (Lumitouch, Lightwave Medical Industries, Coldswitch Technologies, Richmond, CA). Foot responses were chosen to prevent interference with the task-related activity in the hand motor ROIs.

fMRI Data Acquisition

A 3-T Philips Achieva whole-body scanner was used to acquire T1-weighted anatomical images and functional images using a SENSE Head 8-channel head coil and a custom-built head restrainer to minimize head movements. Functional images were obtained using a T2*-weighted EPI sequence of the whole brain. EPI volumes for the main experiment ($n = 840$) contained 30 transverse axial slices (repetition time = 2500 msec; echo time = 35 msec, field of view = 23 cm, acquisition matrix = 128×128 , slice thickness = 3 mm with no gaps, flip angle = 90° , voxel size = $1.79 \times 1.79 \times 3.3$ mm) and were preceded by seven dummy images that allowed the MR scanner to reach a steady state. EPI volumes for the functional localizer ($n = 265$ images), preceded by five dummy images, were acquired with the same sequence characteristics as in the main experiment, except that each volume contained 21 transversal slices acquired with a repetition time of 1600 sec. Both experiments were included in one single fMRI session. After functional neuroimaging, high-resolution anatomical images were acquired using a T1-weighted 3-D magnetization-prepared, rapid acquisition gradient fast field echo (T1W 3D TFE SENSE) pulse sequence (repetition time = 8.2 msec, echo time = 3.76 msec, field of view = 24 cm, 190 transverse axial slices of 1 mm thickness, flip angle = 8° , voxel size = $1 \times 1 \times 1$ mm) lasting 8.8 min.

Postscanning Recognition Test

The recognition task was administered outside the scanner, at the end of the fMRI session. Participants sat on a chair at about 1 m from an LCD screen that displayed each verb (Verdana font, 45-pt) for 2 sec, followed by a blank that remained on the screen up to 10 sec to allow the response. They were instructed to decide whether the verb was presented during the previous reading task by pressing one of two keys corresponding to yes and no responses. As soon as they provided the response, the new trial began.

Data Analysis

Behavioral Data

Prerequisites for our experimental manipulation were that participants performed above chance on the motor and visuospatial strategy-based mental rotation tasks and on the postscanning verb recognition test, ensuring that they had attentively processed each word. Binomial tests were used to compare each participant's performance against chance (50% accuracy). Successful (above chance) performance on these three tasks was the criterion for including a participant in the subsequent analysis of behavioral and imaging data.

Reliable indication that individuals use the motor strategy of rotation is provided by the effect on RTs of the

arm-hand bio-mechanical constraints that apply to real movements (Parsons, 1994). Faster RTs for imagined hand movements toward the body's midsagittal plane (medial orientation) than away from it (lateral orientation) are expected in the motor but not in the visuospatial strategy of rotation. Both strategies are instead characterized by a linear relation between RTs and the amplitude of the rotation angle. To test for these effects, a repeated-measures ANOVA was performed on RTs with within-subjects factors Mental Rotation Strategy (motor vs. visuospatial), Orientation (lateral vs. medial), and Angle (small vs. medium vs. large). For further details on the analysis, see Supplementary Materials. Trials in which participants provided an incorrect response (12% for motor rotation and 18% for visuospatial rotation) and those with RTs 2 *SDs* above or below the individual condition mean (6% of correct responses for the motor rotation and 9% for the visuospatial rotation) were discarded from the analysis (Ratcliff, 1993). All post hoc comparisons were performed with Fisher's least significant difference (LSD) test ($\alpha \leq 0.05$).

Mean accuracy rates and RTs obtained in the recognition test were submitted to a 2 Cognitive Context (motor vs. nonmotor) \times 2 Word Category (action vs. state) repeated-measures ANOVA.

fMRI Data Processing

The fMRI data preprocessing and statistical analysis were performed on UNIX workstations (Ubuntu 8.04 LTS, i386, www.ubuntu.com/) using MATLAB r2007b (The Mathworks, Inc., Natick, MA) and SPM5 (Statistical Parametric Mapping software, SPM; Wellcome Department of Imaging Neuroscience, London, U.K. www.fil.ion.ucl.ac.uk/spm/). Six dummy images were discarded before further image processing. Preprocessing included (i) spatial realignment of the images to the reference volume of the time series, (ii) segmentation producing the parameter file used for normalization of EPI data to a standard EPI Montreal Neurological Institute (MNI) template provided by SPM5, (iii) resampling to a voxel size of $2 \times 2 \times 2$ mm, and (iv) spatial smoothing with a 8-mm FWHM Gaussian kernel to meet the statistical requirements of the general linear model and to compensate for residual macroanatomical variations across participants.

A whole-brain random effects analysis was performed. A general linear model for block designs was applied to each voxel of the data by modeling the activation and the baseline conditions for each participant and their temporal derivatives by means of reference waveforms that correspond to boxcar functions convolved with a hemodynamic response function (Friston, Frith, Turner, & Frackowiak, 1995; Friston, Holmes, Worsley, Poline, & Frackowiak, 1995).

The presentation of motor strategy-based mental rotation blocks, visuospatial strategy-based mental rotation blocks, reading blocks (action and state verbs in motor

and nonmotor context), resting blocks, and instructions were modeled as the regressors of main interest. To correct for motion artifacts, we included six additional regressors of no interest, which modeled head movement parameters obtained from the subject-specific realignment parameters. All regressors were convoluted with a canonical hemodynamic response function. Low-frequency signal drifts were filtered using a cutoff period of 128 sec.

At 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 each subject, we first calculated the contrast images to define the network for mental rotation (mental rotation > baseline) and for silent reading (reading > baseline) and ascertain that participants were actually engaged in those tasks. We then assessed activations specific to either mental rotation strategy (motor strategy-based mental rotation > visuospatial strategy-based mental rotation and vice versa), the effect of cognitive context on verb processing (reading in motor context > reading in nonmotor context and vice versa), the effect of the verb category (action > state verbs and vice versa), and the interaction between cognitive context and verb category interaction [(action > state)_in motor context > (action > state)_in nonmotor context and vice versa].

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 the contrast at the group level (threshold $p < .05$, family-wise error [FWE] corrected; height threshold $p < .001$, uncorrected). For each activated region, t tests were performed over the extracted averaged parameter estimates to investigate the functional properties of the areas of activation. Statistical analysis was performed with SPSS 14.0 software (SPSS, Inc., Chicago, IL). Significant results of the random effects analysis were compared with the cytoarchitectonic maps using the SPM Anatomy toolbox (Eickhoff et al., 2005).

In the hand localizer task, identical preprocessing and first-level analysis procedures were used as in the main experiment. A design matrix, which comprised contrasts modeling alternating intervals of “activity” (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. Individual ROIs in the bilateral hand M1 were identified considering all contiguous voxels significantly more active during clenching than resting (threshold, $p < .05$, FWE corrected), falling within the cytoarchitectonically defined MPMs of M1 (Grefkes et al., 2008).

Differently than others’ previous studies in the field relying on subject-specific activations (e.g., Willems et al., 2010; Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006),

we defined individual ROIs according to the activity clusters obtained with the standard whole-brain group analysis of the hand movement localizer. Functional activations were then combined with the MPMs to ensure that, in each individual, the activity peak fell within the cytoarchitectonically defined M1 and premotor cortex (see also Tomasino et al., 2010; Postle et al., 2008). Although both approaches have their own advantages and disadvantages (for a discussion, see Fedorenko, Hsieh, Nieto-Castanon, Whitfield-Gabrieli, & Kanwisher, 2010; Duncan, Pattamadilok, Knierim, & Devlin, 2009; Nieto-Castanon, Ghosh, Tourville, & Guenther, 2003), subject-specific ROIs are held to be more sensitive than group-based methods. Therefore, we reasoned that any effect observed with our preferred approach would be robust and would have been even stronger, if the alternative approach was applied.

RESULTS

Behavioral Results

Binomial tests comparing each participant’s performance against chance (50% accuracy) showed that all performed at criterion on all tasks ($ps < .05$), but three ($ps > .05$): those who failed the motor strategy-based mental rotation, the visuospatial strategy-based mental rotation, and both, respectively. These participants were discarded from the subsequent analyses.

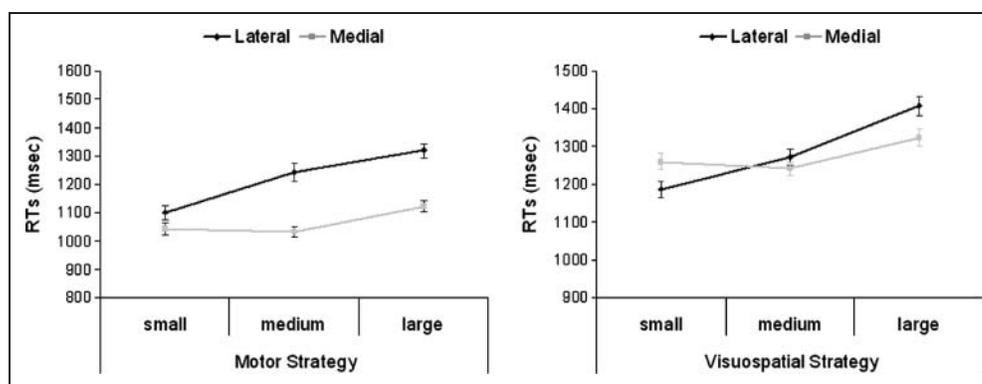
The ANOVA revealed a significant effect of the Angle, $F(2, 28) = 78.95, p < .001$, small angles being processed faster than medium angles ($p < .001$), and the latter, faster than large angles ($p < .001$). Importantly, this effect applied to both the motor and the visuospatial strategy-based mental rotation (i.e., Angle \times Mental Rotation Strategy interaction, $F(2, 28) < 1, ns$). As expected, a significant interaction between Mental Rotation Strategy and Orientation, $F(1, 14) = 12.32, p < .01$, revealed that responses were faster to medial than to lateral orientations during motor strategy-based mental rotation ($p < .001$), but not during visuospatial strategy-based mental rotation ($p = .6$; Figure 1). This finding maintains that participants correctly switched between the two strategies. Please refer to Supplementary Materials for the other main effects and interactions. The analysis of the recognition test revealed no significant effect or interaction (all $ps > .05$).

Neural Activations

Mental Rotation

The whole-brain random effects analysis revealed typical activations for mental rotation (see Wraga, Shephard, Church, Inati, & Kosslyn, 2005; Kosslyn et al., 2001), in addition to differential activations specific to motor and visuospatial strategy-based mental rotation, indicating that participants switched between the two strategies (Table 1; Figure 2B and C).

Figure 1. Behavioral results of the mental rotation tasks: RTs increased linearly with the angle of rotation (small, medium, large) in both the motor strategy and the visuospatial strategy mental rotation; only in the former task RTs were significantly faster for medial than for lateral orientations. Vertical bars denote SEM.



As activity in the hand representation of the left primary motor cortex (M1) is frequently found during hand rotation (motor strategy), we used a hypothesis-driven ROI-based approach (Friston et al., 1997) and performed a small volume correction (SVC) analysis within a spherical ROI (8-mm radius corresponding to the smoothing kernel used in the single subject analysis), centered on the x , y , and z coordinates derived from the hand movement localizer task, averaged across participants (Figure 2F; mean MNI coordinates: $-38, -26, 60$; see Supplementary Table 1 for individual coordinates). A region encompassing the left postcentral gyrus (Area 1) and left precentral gyrus (Area 4a of hand M1) showed greater activity during the motor than during the visuospatial strategy of rotation (peak coordinates: $-38, -30, 66$; $p < .05$, FWE corrected for the ROI; Figure 2B). A second SVC analysis in an 8-mm spherical ROI centered in the left premotor cortex focus (Area 6, mean MNI coordinates: $-45, -11, 55$; see Supplementary Table 1 for individual coordinates), revealed greater activity for motor, relative to visuospatial strategy-based mental rotation at $-44, -12, 58$ peak coordinates ($p < .05$, FWE corrected for the ROI).

Finally, in a second analysis, we used an “inclusive mask” ($p < .05$, FWE corrected) that determined the regions of activation common to both hand movement execution and motor strategy of mental rotation. By using the MPMs of the left and right Area 4a and Area 4p (M1), significant activation was found in the left hand M1 ($-40, -22, 58$, Area 4a) and in the right hand M1 ($34, -22, 52$). By using the MPMs of the left and right Area 6 (premotor cortex), significant activation was found in the left ($-34, -18, 66$) and right ($36, -22, 64$) premotor cortex (Supplementary Figure 1). The reversed contrast revealed no differential activation in these ROIs.

Silent Reading Task

The brain network for silent reading (Figure 2D; Table 2) overlapped with neural activations typically related to the semantic analysis of visual words (Friederici, Opitz, & Von Cramon, 2000; Price, 2000; Fiez & Petersen, 1998).

Activations specific to action verbs (vs. state) and to state verbs (vs. action; Table 1) replicated previous observations of extensive, bilateral neural responses to concrete meanings, relative to more strongly left-lateralized responses to abstract meanings (e.g., Binder, Medler, Desai, Conant, & Liebenthal, 2005).

The following results revealed how the cognitive context influenced neural responses to reading verbs. Irrespective of the verb category (action or state), reading in the motor context (after performing motor strategy-based mental rotation), as compared with reading in the nonmotor context (after performing visuospatial strategy-based mental rotation), revealed two activation clusters centered in the left precentral gyrus ($-30, -24, 62$, Area 6 and Area 4a of M1, according to the cytoarchitectonically defined MPMs) encompassing the postcentral gyrus ($-30, -34, 62$, Areas 3b and 2 of SI), and in the right precentral gyrus (Area 6; Figure 2E; Table 2). In a second analysis, we used an “inclusive mask” that determined the regions of activation common to both silent reading and hand movement execution ($p < .05$, FWE corrected). Relying on the MPMs of the left and right Areas 4a and 4p (M1), significant activation was found in the left ($-38, -20, 52$, Area 4a) and in the right ROIs ($36, -22, 56$). By using the MPMs of the left and right Area 6 (premotor cortex), significant activation was found in the left ($-34, -18, 66$) and right ROIs ($34, -22, 56$; see Supplementary Figure 1). The reversed contrast (reading in nonmotor vs. motor context) revealed no differential activation in the same ROIs.

Lastly, the interaction between Cognitive Context and Verb Category (Figure 3; Table 2) revealed greater activity for action verbs than for state verbs during reading in the nonmotor context, in a cluster centered in the left precentral gyrus, $p = .01$, whereas the difference between verb categories was abolished in the motor context, $p = .15$. Likewise, a second cluster centered in the right postcentral gyrus showed greater activity during reading action verbs, relative to state verbs, in the nonmotor context, $p = .002$; in the motor context, the activity for state verbs increased to the extent that it was greater than the activity for action verbs, $p = .006$. The reverse contrast

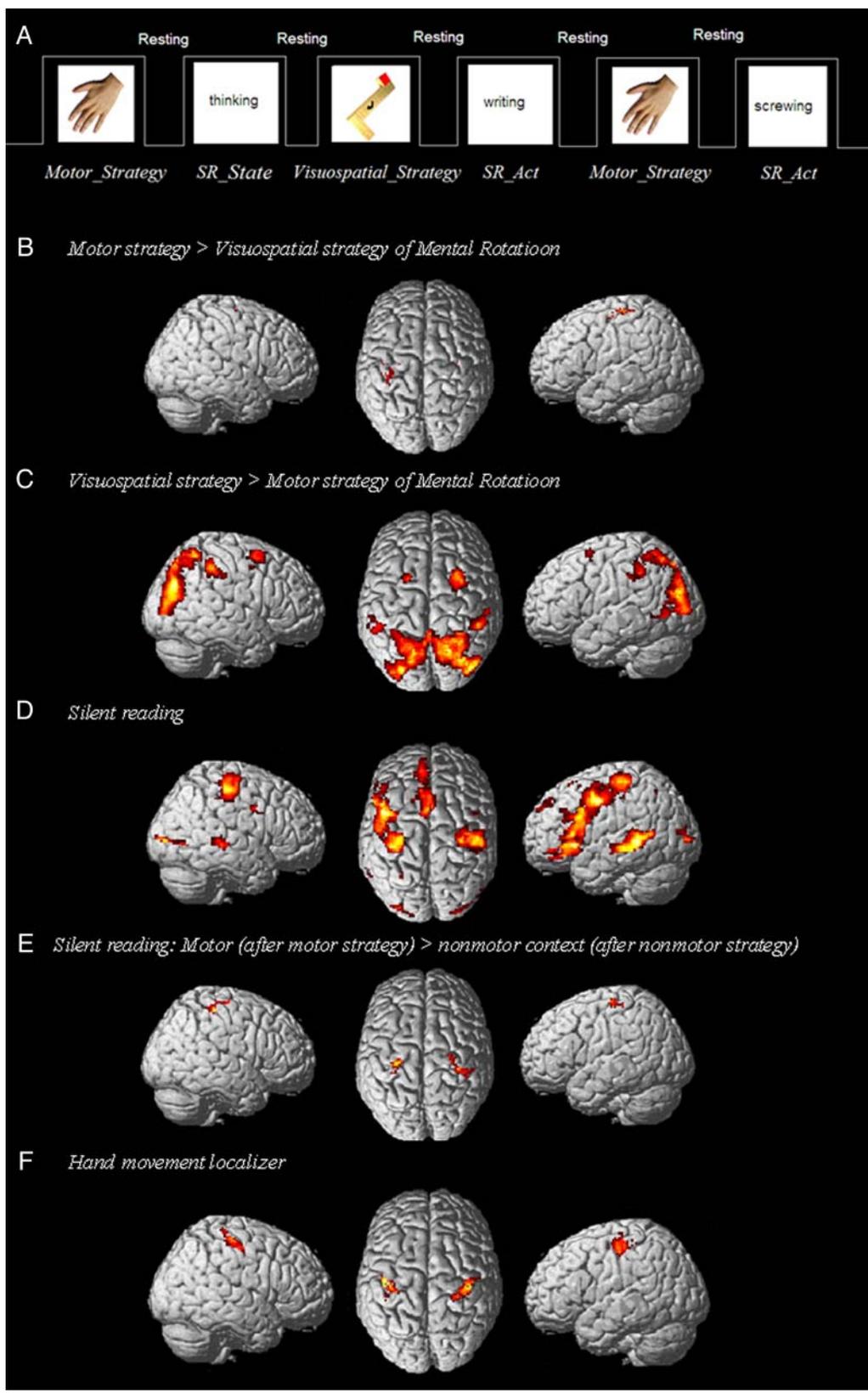


Figure 2. (A) Experimental design: Each block of silent reading of either action (“SR_Act”) or state verbs (“SR_State”) was preceded by one block of either motor or visuospatial strategy-based mental rotation. (B) Motor strategy versus visuospatial strategy mental rotation. (C) Visuospatial strategy mental rotation versus motor strategy mental rotation. (D) Network for silent reading of verbs. (E) Main effect of the context (motor > nonmotor context) on silently reading of verbs. (F) Hand movement localizer task: Hand representation in the left and the right primary motor cortices (M1) displayed on a rendered template brain.

Table 1. Whole-brain Analysis: Brain Responses to Mental Rotation and Specific to Motor Strategy Mental Rotation and Visuospatial Strategy Mental Rotation

Region	Side	MNI			Z	Cluster Size Voxel
		x	y	z		
<i>Imagery Task: (Motor + Visuospatial) vs. Baseline</i>						
Precentral gyrus (Area 6)	L	-30	-4	62	5.87	4811
Superior frontal gyrus	L	-22	-4	50	5.70	
Inferior frontal gyrus (pars opercularis)	R	54	8	28	5.18	979
Precentral gyrus	R	44	4	32	4.97	
Middle frontal gyrus	L	-42	36	34	3.77	70
Inferior frontal gyrus (pars triangularis)	L	-40	28	26	3.62	
Insula	R	30	20	4	5.19	540
Insula	L	-34	16	4	5.15	290
Thalamus	L	-18	-24	10	5.95	3381
Thalamus	R	18	-24	10	5.52	
Putamen	L	-24	10	4	3.98	70
Middle occipital gyrus	L	-32	-92	6	6.98	15495
Cuneus	R	18	-98	14	6.27	
parietal lobule	L	-24	-64	-52	6.07	
Parietal lobule	R	12	-70	-50	6.07	
<i>Motor Imagery (vs. Visuospatial)</i>						
Superior frontal gyrus	R	18	60	18	4.51	82
Middle frontal gyrus	R	24	54	22	3.87	
Inferior frontal gyrus (pars orbitalis)	L	-42	36	-6	4.06	99
<i>Primary motor cortex, hand area</i>	<i>L</i>	<i>-38</i>	<i>-30</i>	<i>66</i>	<i>3.58*</i>	<i>15</i>
Superior occipital gyrus	L	-14	-96	20	4.43	761
Cuneus	R	4	-92	14	4.26	
<i>Visuospatial Imagery (vs. Motor)</i>						
Middle frontal gyrus	R	30	4	56	4.56	531
Middle frontal gyrus	L	-20	2	44	3.95	135
Superior parietal lobule	R	18	-60	56	5.92	8273
Inferior parietal lobule	L	-52	-42	46	4.25	221
Thalamus	R	18	-30	14	6.04	150
Thalamus	L	-20	-34	14	4.30	70

Regions and MNI coordinates indicating local maxima of significant activations are tabulated with associated z values ($p < .05$, corrected for multiple comparisons at the cluster level, height threshold $p < .001$, uncorrected) and cluster sizes. L = left hemisphere; R = right hemisphere.

Values in italics refer to the results of the small volume correction (SVC, $p < .05$, corrected for ROI) analysis performed within a spherical ROI centered on the x, y, and z coordinates derived from the hand movement localizer task, averaged across participants.

* $p_{\text{svc}} < .05$, corrected for ROI. Coordinates derived from the localizer task.

Table 2. Whole-brain Analysis: Brain Responses to Silent Reading and Specific to Motor and State Verbs; Effect of the Cognitive Context on Reading Verbs; Interaction between Cognitive Context and Verb Category

Region	Side	MNI			Z	Cluster Size Voxel
		x	y	z		
<i>Silent Reading of Verbs: (Action + State Verbs) > Strings</i>						
Inferior frontal gyrus (pars triangularis)	L	-48	14	26	4.97	1842
Supplementary motor area	L	-4	8	58	4.65	427
Precentral gyrus (Area 4p)	L	-34	-24	54	5.24	248
Precentral gyrus (Area 4a)	L	-36	-30	62	4.30	
Precentral gyrus (Area 6)	L	-30	-20	68	3.52	
Postcentral gyrus (Area 4p)	R	32	-22	44	3.92	72
Precentral gyrus (Area 1)	R	44	-24	56	3.64	
Precentral gyrus (Area 3b)	R	42	-24	44	3.60	
Middle temporal gyrus	L	-66	-44	2	5.16	833
Middle temporal gyrus	R	52	-30	-2	4.53	115
<i>Action Verbs > State Verbs</i>						
Middle frontal gyrus	R	44	12	52	5.44	175
Postcentral gyrus (Area 1)	L	-52	-16	48	5.05	1594
Precentral gyrus (Area 6)	L	-46	0	44	5.05	
Postcentral gyrus (Area 1)	R	50	-22	52	4.57	569
Precentral gyrus (Area 6)	R	36	-16	64	4.23	
Anterior cingulate cortex	R	10	48	18	4.97	613
Frontal superior medial gyrus	R	12	58	18	4.69	
Frontal superior medial gyrus	L	-6	40	36	4.84	1189
Middle orbital gyrus	L	-36	52	-10	4.12	180
Inferior frontal gyrus (pars orbitalis)	L	-42	42	-14	3.95	
Middle orbital gyrus	R	38	44	-10	4.11	168
Inferior frontal gyrus (pars orbitalis)	R	50	40	-8	4.09	
Middle temporal gyrus	R	50	-34	-2	4.79	75
Middle occipital gyrus	L	-32	-94	4	4.65	201
Middle temporal gyrus	L	-46	-54	-2	4.47	166
Middle occipital gyrus	L	-46	-74	0	3.97	
Middle occipital gyrus	R	40	-64	-2	4.43	100
Middle temporal gyrus	R	48	-60	4	3.45	
Middle temporal gyrus	L	-64	-30	-4	4.13	66
Middle occipital gyrus	R	24	-98	4	3.75	125
Paracentral lobule	R	6	-24	66	4.29	108
Angular gyrus	R	58	-56	30	3.66	64
Superior parietal lobule	L	-28	-58	50	3.48	60

Table 2. (continued)

Region	Side	MNI			Z	Cluster Size Voxel
		x	y	z		
<i>State Verbs > Action Verbs</i>						
Middle frontal gyrus	L	-30	-8	54	4.24	64
<i>Effect of Cognitive Context (Motor vs. Nonmotor)</i>						
Precentral gyrus (Areas 6, 4a)	L	-30	-24	62	4.65	88
Postcentral gyrus (Area 3b, 2)	L	-30	-34	62	4.07	
Precentral gyrus (Areas 6)	R	26	-16	66	4.02	52
<i>Cognitive Context × Verb Category</i>						
Postcentral gyrus (Area 3a)	R	40	-20	38	4.28	212
Precentral gyrus (Area 6)	L	-52	4	34	3.93	52

Regions and MNI coordinates indicating local maxima of significant activations are tabulated with associated z values ($p < .05$, corrected for multiple comparisons at the cluster level, height threshold $p < .001$, uncorrected) and cluster sizes. L = left hemisphere; R = right hemisphere.

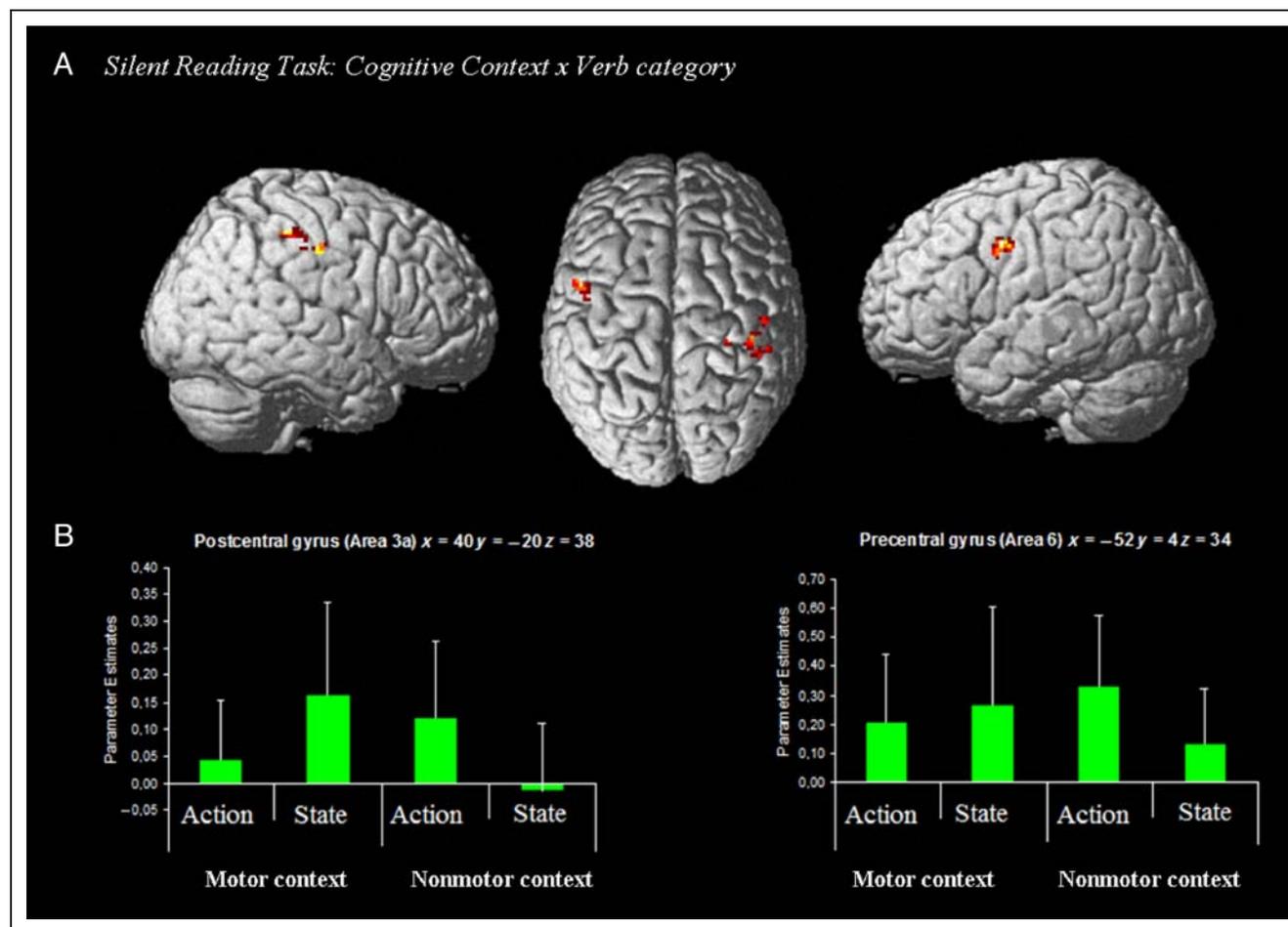


Figure 3. (A) Context × Verb Category interaction. (B) The plots of relative BOLD signal changes in the right postcentral and left precentral gyri. Vertical bars denote SDs.

revealed no significant activation at the predefined statistical threshold.

DISCUSSION

We investigated whether the same verbs could evoke different neural responses as a function of the context in which they were encountered, by combining the paradigm of the implicit strategy transfer of strategies and the fMRI technique to manipulate the cognitive context (motor vs. nonmotor) in which participants read verbs. We found that the cognitive context induced by the preceding task (motor or visuospatial strategy-based mental rotation) modulated the recruitment of sensorimotor regions—but not of other language-related regions—during silent reading of verbs.

Given our prediction that the reliance on either strategy of mental rotation could vary the cognitive context of the subsequent reading task, a crucial prerequisite of our study was that participants performed the motor and visuospatial strategy-based rotation tasks according to the instructions. Behavioral performance, together with neural responses, including hand motor activity, maintained that in the former, but not in the latter task, participants adopted the strategy of rotation based on the internal transformation of their own body (Ehrsson, Geyer, & Naito, 2003; Kosslyn et al., 2001; Jeannerod & Decety, 1995).

To relate our study to previous research on action word processing (e.g., Tomasino et al., 2010; Hauk et al., 2004), we used a silent reading task. During this task, we found activation in a widespread neural network including the classic language processing regions (i.e., left posterior temporal and inferior frontal areas; e.g., Price, 2000; Price, Wise, & Frackowiak, 1996) and the frontocentral sensorimotor regions. Importantly, only activity in the frontocentral sensorimotor regions was modulated by the cognitive context. This result confirmed our a priori hypothesis and, as such, will be the focus of the following discussion.

In keeping with numerous previous reports, in the current study, the processing of verbs denoting motor events (vs. states) evoked greater activity in sensorimotor regions (Rueschemeyer, van Rooij, Lindemann, Willems, & Bekkering, 2010; Hauk et al., 2004; Grabowski et al., 1998; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Petersen, Fox, Posner, Mintun, & Raichle, 1988). As a new finding, we showed that activity in these regions, specifically in the left M1, bilateral dorsal premotor cortex, and left SI, was significantly enhanced, when participants read the verbs after performing the motor mental rotation task (i.e., in the motor context), relative to when they read the same stimuli after performing the visuospatial mental rotation task (i.e., in the nonmotor context). Most crucially, the modulation of sensorimotor activity in the

motor context took place irrespective of whether verbs implied actions or states.

The results of the interaction between Cognitive Context and Verb Category go along with an increased sensorimotor recruitment for state verbs appearing in the motor context. In two clusters centered in the left precentral and right postcentral gyri, the activity was reduced for state verbs as opposed to action verbs, during reading in the nonmotor context. In contrast, during reading in the motor context, the activity for state verbs increased and turned comparable to (in the left precentral gyrus) or even greater than (in the right postcentral gyrus) the activity for action verbs.²

These results demonstrate that the processing modality adopted in the mental rotation task successfully elicited a cognitive context that implicitly transferred to word processing, despite differences in materials (pictures vs. verbs) and cognitive domain (imagery vs. language) between the preceding phase and the subsequent one. That is, the experimental manipulation of the cognitive context through implicit transfer met our goal to vary neural responses to linguistic stimuli. One cluster of activity found during reading in motor context encompassed the hand representation in the left M1 (Area 4a), as defined by the cytoarchitectonic MPMs. The cytoarchitectonic Area 4a, the rostral component of M1, is thought to mediate the stage immediately before the execution of movements under the direct control of higher-order motor areas, from which it receives extensive cortico-cortical projections (Geyer et al., 1996; Porter & Lemon, 1993; Strick & Preston, 1982). A similar dynamics, with premotor areas exerting a top-down influence on M1 (preferentially, Area 4a; Ehrsson et al., 2003), operates in motor simulation (Passingham, 1997). Accordingly, just like in Area 4a, the activity in a portion of the bilateral dorsal premotor was modulated by the context. The effect of the context extended to the left SI (Area 3b), another correlate of the generation and transformation of mental motor images (Lorey et al., 2011; Lamm, Fisher, & Decety, 2007; Porro et al., 1996). Thus, as an effect of the motor context, the activity in an important part of the network for motor simulation increased during word processing.

Our study provides new insight into the question as to whether language-related sensorimotor activity is entirely dependent on the (action-related) nature of the stimuli or whether other (top-down) factors need to be considered, if one wishes to come up with a full account of this phenomenon. The current results pave the way to the second possibility.

The main effect of action verbs on a cluster centered in the ventral premotor cortex, at first sight, might suggest that some sensorimotor regions are driven by the action-related semantics of the stimuli in itself. However, as already pointed out, tasks soliciting the processing of semantic features promote sensorimotor activations for words with salient motor components (Papeo et al.,

2009; Tomasino et al., 2007; Grabowski et al., 1998). This leaves open a possibility that the sensorimotor activity that we observed for action verbs was specific to the present task context, where the instruction to read verbs for delayed recognition was given to participants with the specific purpose to elicit deep encoding of word meanings.

Previous studies suggested that the mere exposure to action-related words even in “shallow” semantic tasks (e.g., lexical decision; see Willems, Labruna, D’Esposito, Ivry, & Casasanto, 2011; Willems et al., 2010) is necessary and sufficient to trigger motor activity. However, first, careful task analysis of available (or future) studies would be required to assess—and eventually exclude—that stimulus-independent elements in the task context contributed to sensorimotor activations. For instance, one may consider whether and to what extent sensorimotor activity could be explained by attentional biases or expectations, implicitly introduced when participants are instructed to perform the experimental (linguistic) task together with the action execution/observation localizer task, before entering the MRI scanner, or to what extent, when embedding the localizer task in a factorial design (Poldrack, 2007; Saxe, Brett, & Kanwisher, 2006), a block of action execution affects neural processes in the subsequent block of a different task. Second, whether or not sensorimotor activity is an automatic response to action words neither changes nor conflicts with our observation that top-down factors, such as the task context, have modulatory effect on it.³ Third, although our data do not allow ultimately adjudicating between the effect of action-stimuli and the effect of task demand, a particular susceptibility of sensorimotor activity to contextual factors earns credence when considering that no other (classic) language-related region underwent the effect of cognitive context and instead showed invariant responses to action verbs.

The reported neural responses to state verbs provide a decisive direction to this issue. This linguistic category typically serves as the “control” condition, against which action verbs are contrasted to highlight sensorimotor activations. Here we showed that, given the motor cognitive context, sensorimotor activations could also be elicited for state verbs: This is unambiguous demonstration that sensorimotor activity is tightly dependent on the cognitive context in which verbs are read and rather independent of the specific attributes of the stimuli. Non-specific (i.e., non-action verb specific) activity has been reported (Tomasino et al., 2010; Postle et al., 2008). Relevant for our discussion is the observation by Tomasino et al. (2010) that, whereas motor activations for action verbs varied according to whether those items were presented in a positive or in a negative phrase, pseudowords activated motor areas, irrespective of the linguistic context. In other words, motor activity is not a neural signature to distinguish action verbs from other word categories; it is rather the systematic modulation of this activity by contextual factors that define its involvement in conceptual tasks.

In a broader perspective, our observation extends the view that computations in brain regions are not solely driven by bottom-up stimulus features, but they also rely on “predictions” generated at higher levels of processing, exerting a top-down influence on the way stimuli are encoded (Egner, Monti, & Summerfield, 2010; Friston, 2003). Available information in the context of stimulus encoding plays a central role in the process of generating predictions about bottom-up inputs. In fact, top-down effects are often emphasized by showing how the context interacts with the content of representations and modulates neural responses to the same stimuli (Friston, 2002; Büchel & Friston, 1997).

How the context actually changed the content of state verb representations is an open question. We argue that participants implicitly applied the strategy of relating each verb’s meaning to one’s own bodily action, as learned in the preceding motor strategy-based rotation task, just like in Wraga et al. (2003), after using a motor strategy of rotation, they imagined grasping and rotating abstract objects instead of applying the expected visuospatial strategy. It is worth to recall from the Introduction that the notion of “strategy” here denotes a neural mechanism for processing information, which is susceptible to top-down (contextual or stimulus-independent) modulation.

Whereas the content of the motor simulation appears intuitive for verbs such as “grasping,” the motor specification of an act such as “desiring” is less obvious. Yet, we are all capable of readily linking a motor act to the abstract concept of “desiring.” Overall, the polysemy—the ability of a word to convey multiple meanings and subsume novel usage given a context—applies to both concrete and abstract words (Lee, 1990). Psycholinguists have widely documented contextual effects on the activation of specific, even nondominant, secondary or unusual attributes of word meanings (Tabossi, Colombo, & Job, 1987). Likewise, extra-language contextual factors, such as the explicit involvement of motor skills in linguistic tasks (e.g., specific movements for responding) might explain motor facilitation, even when processing language with abstract meaning (Glenberg & Kaschak, 2002; for a discussion, see Louwerse & Jeuniaux, 2008). Finally, it is held that the argument structure of verbs makes them particularly prone to cue event representations implying relations, such as an agent acting over something/someone else (Gillette, Gleitman, Gleitman, & Lederer, 1999).

In conclusion, our results contribute by defining motor simulation in language as the strategy of referring a given meaning to one’s own bodily action. This strategy can be spontaneously applied to the processing of words with obvious motor components and can also be readily extended to the processing of nonaction verbs. The cognitive context in which words are encountered prevails over the bottom-up stimulus features in determining whether this strategy is engaged or not. The top-down contextual effect thus influences neural responses to words, mediating changes

in the recruitment of “extra-language” (sensorimotor) regions, beyond the classic language processing regions.

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Notes

1. Although both block and event-related designs have proven successful to identify verb meaning-specific motor activity (for block designs, see Postle et al., 2008; Tomasino et al., 2007; Aziz-Zadeh et al., 2006; for event-related design, see Carota, Moseley, & Pulvermüller, 2012), our choice of a block design was motivated by its well-known superior efficiency in detecting subtle differences in BOLD signal across test conditions (Bandettini & Cox, 2000; Friston, Zarahn, Josephs, Henson, & Dale, 1999). Moreover, the analysis of the same data set as block or event-related design has revealed comparable results, with an advantage for the former method in terms of amplitude of neural response (Postle et al., 2008; see also Chee, Venkatraman, Westphal, & Siong, 2003).

2. Notice how, against the consistent increase of activity for state verbs, the activity in the two clusters (within the left precentral and right postcentral gyri) showed a qualitative decrease for action verbs, from the nonmotor context to the motor context. In neither cluster, however, this comparison approached significance ($ps > .05$), implying a null effect of the context for action verbs, at these sites. This observation in no way contradicts our claim for increased sensorimotor activity to both verb categories, when encoded in the motor context. These two clusters were indeed anatomically far from the regions—including those identified with the hand movement localizer (M1 and premotor cortex)—where the main effect of the context was found.

3. The automaticity of sensorimotor activity in response to action words tightly relates to the debate on its functional relevance for word processing. We refer to research in cognitive neuropsychology as the most fruitful soil, to date, for a deep understanding of the issues related to this debate (e.g., Kemmerer, Rudrauf, Manzel, & Tranel, 2012; Papeo, Negri, Zadini, & Rumiati, 2010; Grossman et al., 2008; for a recent review, see Papeo & Hochmann, 2012).

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