

Action verbs and the primary motor cortex: A comparative TMS study of silent reading, frequency judgments, and motor imagery

Barbara Tomasino^{a,b,*}, Gereon R. Fink^{a,b,c}, Roland Sparing^{a,b,c},
Manuel Dafotakis^{a,b}, Peter H. Weiss^{a,b}

^a Cognitive Neurology, Institute of Neuroscience and Biophysics - Department of Medicine (INB-3), Research Centre Juelich, Germany

^b Brain Imaging Centre West (BICW), Research Centre Juelich, Germany

^c Department of Neurology, University Hospital, Cologne, Germany

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Abstract

Single pulse transcranial magnetic stimulation (TMS) was applied to the hand area of the left primary motor cortex or, as a control, to the vertex (STIMULATION: TMS_{M1} vs. TMS_{vertex}) while right-handed volunteers silently read verbs related to hand actions. We examined three different tasks and time points for stimulation within the same experiment: subjects indicated with their left foot when they (i) had finished reading, (ii) had judged whether the corresponding movement involved a hand rotation after simulating the hand movement, and (iii) had judged whether they would frequently encounter the action verb in a newspaper (TASK: silent reading, motor imagery, and frequency judgment). Response times were compared between TMS_{M1} and TMS_{vertex}, both applied at different time points after stimulus onset (DELAY: 150, 300, 450, 600, and 750 ms).

TMS_{M1} differentially modulated task performance: there was a significant facilitatory effect of TMS_{M1} for the imagery task only (about 88 ms), with subjects responding about 10% faster (compared to TMS_{vertex}). In contrast, response times for silent reading and frequency judgments were unaffected by TMS_{M1}. No differential effect of the time point of TMS_{M1} was observed.

The differential effect of TMS_{M1} when subjects performed a motor imagery task (relative to performing silent reading or frequency judgments with the same set of verbs) suggests that the primary motor cortex is critically involved in processing action verbs only when subjects are simulating the corresponding movement. This task-dependent effect of hand motor cortex TMS on the processing of hand-related action verbs is discussed with respect to the notion of embodied cognition and the associationist theory.

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1. Introduction

Processing sentences or verbs describing actions has been shown to involve, in addition to “classic” language areas, the motor and premotor cortex. Experimental support for this notion comes from a number of neurophysiological, behavioral, and brain imaging studies in which subjects were presented with action-related words. For example, *lexical decisions* about action verbs, i.e., to judge whether a verb is a real word or a pseudo-word, have been found to lead to stronger high-frequency EEG

activity at recording sites located closely above primary motor (M1) cortex (Pulvermüller, Lutzenberger, & Preissl, 1999). Furthermore, if the processed action words are related to movements of different body parts, then the strongest in-going EEG current is detected close to the cortical representation of the respective body part (Pulvermüller, Harle, & Hummel, 2001). Interestingly, such a somatotopic activation of M1 has also been reported when action words related to face, arm, or leg movements are silently read only (Hauk, Johnsrude, & Pulvermüller, 2004) and even when subjects are presented with action words while they are engaged in a distractor task (Pulvermüller, Shtyrov, & Ilmoniemi, 2005a).

Transcranial magnetic stimulation (TMS) studies lend support to the idea that M1 might be involved in processing action words. Sub-threshold stimulation of the hand area of left M1

* Corresponding author. Present address: IRCCS “E. Medea”, San Vito al Tagliamento, PN, Italy. Tel.: +49 2461 61 2073; fax: +49 2461 61 1518.

E-mail address: b.tomasino@fz-juelich.de (B. Tomasino).

leads to a facilitatory effect (i.e., faster response times in a *lexical decision* task) for arm- compared to leg-action-related words, and the opposite effect has been found for leg-action-related words after stimulation of the leg area (Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005b). The excitability of the left M1 hand area (as determined by supra-threshold stimulation and measured by motor evoked potentials, MEPs) is modulated during a *transformation task* involving action words as compared to non-action words (i.e., producing the singular/plural form of nouns or the 3rd person singular/plural form for verbs; Oliveri et al., 2004). Similarly, *listening* to hand-action-related sentences decreases the amplitude of MEPs recorded from hand muscles, while listening to sentences related to foot actions modulates the MEPs recorded from foot muscles (Buccino et al., 2005). Furthermore, functional imaging studies revealed that *listening* to (Tettamanti et al., 2005) and *silently reading* of (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006) mouth-, hand-, and leg-action-related sentences engage the visuo-motor circuits that subserve action execution and observation in a somatotopic fashion.

Furthermore, the processing of action verbs or action-related sentences has been shown to influence overt motor behaviour. Sentences describing a movement in a certain direction can interfere with responses executed in a different direction, as measured by the action sentence compatibility effect (Glenberg & Kaschak, 2002). In the same way, listening to hand-related action sentences leads to slower reaction times for hand responses compared to foot responses (Buccino et al., 2005). Hand responses to sentences describing manual rotation are faster when both the manual response and the sentence have the same direction of rotation than when the response and the sentence differ in rotation direction. Accordingly, it has been suggested that sentences involving rotations activate a motor program for manual rotation in the listener (Zwaan & Taylor, 2006). Finally, processing of action-related verbs interferes with a concurrent reaching task (Boulenger et al., 2006). These authors also showed that the same action-related verbs could facilitate motor performance when they are processed before movement onset, suggesting that the interaction between action execution and processing of action words possesses a critical temporal dynamic. Taken together, these studies suggest that the “mere reading of action-related words activates the motor homunculus” (see de Lafuente & Romo, 2004).

To date, however, the cause of this M1 activation during action word processing remains to be elucidated. Furthermore, the question arises how M1 contributes specifically to the processing of action words. Some authors argue that it is unclear whether the M1 activation is an integral part of language processing or whether it results from a nonspecific spreading of activation from areas involved in language production to motor areas (Tokimura, Tokimura, Oliviero, Asakura, & Rothwell, 1996). Other authors suggested a specific functional connection between language areas and the hand area of the motor cortex (Meister et al., 2003; Sparing et al., 2007). Two further views have been proposed that are consistent with the idea that language understanding is processed in dedicated cortical areas (e.g., Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995;

Martin, Wiggs, Ungerleider, & Haxby, 1996), in contrast to the idea that the meaning of a sentence is accessed through amodal mental representations (e.g., Fodor, 2001; Pylyshyn, 1984). The first view, inspired by associationist theories of Hebbian learning, proposes that if a word is frequently presented together with the corresponding visual stimulus and, therefore, acquires meaning, co-activation of neurons in perisylvian and visual cortices leads to the formation of cell assemblies distributed over these perisylvian and temporo-occipital sites (Pulvermüller et al., 1999). Similarly, words which frequently occur in the context of action execution, causing neurons that process the word form and those that process the corresponding action to fire together and thus become linked, will result in word-related overlapping networks of motor and premotor cortex in a somatotopic fashion (Hauk et al., 2004; Pulvermüller et al., 1999; Pulvermüller et al., 2005a; Pulvermüller et al., 2005b). The second view proposes that the comprehension of action sentences relies on “embodied cognition” (e.g., Barsalou, 1999; Feldman & Narayanan, 2004; Gallese & Lakoff, 2005), meaning 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 (Aziz-Zadeh et al., 2006; Buccino et al., 2005; Tettamanti et al., 2005).

“Embodied cognition” refers also to mental simulation. Processing action words may result in M1 activation, because action words could trigger motor simulation, a process known to activate M1 cortex somatotopically (e.g., Ehrsson, Geyer, & Naito, 2003; Stippich, Ochmann, & Sartor, 2002). Motor representations may be implicitly triggered during action word processing, because subjects, although not explicitly instructed to imagine themselves or somebody else performing the movements, might implicitly simulate the respective action when processing action words. In fact, the above-mentioned studies did not control for putative motor imagery processing. Modulations of M1 activity contingent upon action word processing may be found even in the absence of specific cognitive demands, e.g., as it happens during silent reading tasks. In silent reading tasks, subjects are not engaged in any additional cognitive operation with the stimuli and are, therefore, free to think about the corresponding action during or after the silent reading. Thus, they might implicitly simulate the movement described in the action word, which in turn may activate M1. The idea that language understanding may trigger mental simulation (motor and visual type) is not new (e.g., Barsalou, 1999; Feldman & Narayanan, 2004; Gallese & Lakoff, 2005; Glenberg & Robertson, 2000).

Taken together, previous studies have shown that reading action words as well as motor imagery may activate the hand area of left M1. To date, however, the relationship between these two observations has not been investigated within the same experiment. Therefore, we have chosen to examine the specific contribution of M1 to action word processing by comparing the effects of single pulse TMS while right-handed subjects performed different cognitive tasks using identical hand-action-related verbs. In particular, we investigated whether sub-threshold TMS of the left M1 hand area differentially mod-

ulates task performance. For control, TMS was delivered to the vertex. The silent reading of hand-action-related verbs, which were presented in the infinitive form (e.g., “aufschrauben”, i.e., “to screw”), was kept constant across conditions, whereas the cognitive operation performed during the reading varied: subjects (i) indicated when their silent reading was completed; (ii) mentally simulated the actions, and (iii) estimated the word frequency. Unlike the above-mentioned studies, in which, during silent reading, subjects were not asked to perform any specific cognitive operation other than reading (i.e., they had the time and were free to think about/simulate the respective actions), the purpose of the mental simulation and the frequency task employed in our study was to control the cognitive set. In fact, the question about hand rotation that subjects had to answer in the mental simulation condition prompted subjects to perform motor imagery. In contrast, the question about word frequency led subjects to concentrate on the meaning of the verb and, in addition, prevent them from *implicitly* performing imagery.

According to a previous TMS study of reading action words (Pulvermüller et al., 2005b), sub-threshold TMS, when applied early (at about 150 ms above M1), should produce a facilitatory effect on action word processing. We reasoned that if reading of action verbs *per se* triggers M1 activation, a similar (facilitatory) effect of TMS to M1 (TMS_{M1}) should be found for all three tasks, since all tasks involve action verb reading. In contrast, if a specific task component activates M1, then we expected to observe task-dependent differential TMS effects on subjects' performance. Although based on different assumptions, the two theoretical accounts mentioned above (i.e., embodied cognition theory and associationist theory) lead to identical predictions with respect to the results of our study, since both accounts hold that the language and motor systems share overlapping neuronal representations. The only difference between these two accounts is *why* M1 activation occurs. Both accounts predict that reading *grasp the bottle* will activate the motor plan for “grasping the bottle” in the listener either by the observation–execution–matching system (embodied cognition) or as the result of Hebbian learning (associationist theory). Crucially, both accounts predict a facilitatory effect of TMS to M1 for all three tasks. Alternatively, M1 might be involved in semantic processing of action words through motor imagery. If this hypothesis holds true, then we should observe a differential facilitatory effect of hand motor cortex TMS on the imagery task and no effect on the pure silent reading task and the frequency judgments. Such a pattern of results would imply that M1 activation found in previous studies might have resulted from the subjects' strategy to mentally simulate the movements during the processing of action words (Tomasino, Werner, Weiss, & Fink, 2007).

2. Method

2.1. Participants

Twenty healthy men (mean age 27.4 ± 7.7 years) gave informed consent to participate in the study. They were all right-handed (Edinburgh Inventory test;

Oldfield, 1971), native German speakers with comparable levels of education. None of the subjects had a history of neurological or psychiatric disorders. The study was approved by the local ethics committee.

2.2. Procedure

Throughout the experiment, subjects sat in a comfortable reclining armchair in front of a computer screen at a distance of 57 cm. Stimuli were presented on a white background of a 19" LCD monitor by Presentation software (Neurobehavioral Systems Inc., CA/USA, version 9.90), used also for TMS triggering and response recording. The subject's head was restrained by a fitted support, and a mechanical arm held a figure-of-eight coil over the cortical focus for TMS. Subjects were instructed to keep their hands still and to be as relaxed as possible. They responded by pressing two keys of a custom-made foot response device with the left, i.e., ipsilateral with respect to TMS, foot, indicating yes/no answers. Ipsilateral foot responses were chosen to minimize interference between motor response preparation and execution and task-related activity in M1 hand area.

2.3. Transcranial magnetic stimulation

Transcranial magnetic stimulation was applied with a Dantec MagPro stimulator (Skovlunde, Denmark) using a figure-of-eight coil. Stimulation of the left M1 was carried out over the optimal location for stimulation of the right first dorsal interosseus (FDI) muscle. The coil handle was held tangentially to the subject's skull at a 45° angle pointing lateral-occipitally. Once the “optimal location” was found, the coil was fixed using a mechanical coil holder. The resting motor threshold was defined for each participant as the lowest stimulator output that elicited a visible motor twitch in the contralateral FDI muscle in at least 5 of 10 trials. Then, we decreased the stimulation intensity just below the sensory threshold of the subject to recognize the corresponding muscle twitch. This procedure (*sub-threshold TMS*), which has successfully been used in a number of other studies (e.g., Brasil-Neto, Pascual-Leone, Valls-Sole, Cohen, & Hallett, 1992; Cohen et al., 1997; Pascual-Leone et al., 1992; Pascual-Leone & Walsh, 2001; Silvanto et al., 2005), aimed at preventing a possible interference between overt muscle twitches and task performance. Using supra-threshold TMS would have resulted in muscular twitches in the (right) hand, for which subjects were performing motor imagery at the same time. In addition, *sub-threshold TMS* enabled us to replicate Pulvermüller et al.'s (2005) RTs findings, who also used *sub-threshold TMS* and to further address the nature of the observed facilitatory effect found in that study. The recording of overt muscle responses (i.e., MEPs) as a measure of corticospinal excitability would furthermore require a complete relaxation of the subjects. However, to assure that subjects made use of imagery in one condition and not in the other, we needed to record subjects' responses and the corresponding RTs. Finally, using *supra-threshold TMS*, we would not have been able to record qualitative responses (and thus no RTs), because a *supra-threshold stimulus* would have interfered with motor preparation and execution, resulting in delayed RTs (Ziemann, Tergau, Netz, & Homberg, 1997), and, in turn, any response execution may interfere with MEP amplitudes.

For the control condition, the coil was placed over the vertex to avoid any significant stimulation of M1 neurons by the induced magnetic field. Nevertheless, the sound and sensory sensation produced by the coil during TMS_{vertex} was comparable to that in the TMS_{M1} condition (see, e.g., Bestmann, Thilo, Sauner, Siebner, & Rothwell, 2002; Koch, Franca, Albrecht, Caltagirone, & Rothwell, 2006), especially because we stimulated sub-threshold, i.e., at a weak intensity.

For each trial, the computer generated a TTL output pulse that randomly triggered the Dantec stimulator at 150, 300, 450, 600 or 750 ms after stimulus onset. The choice of these TMS delays was based on previous studies showing that (i) TMS of the M1 cortex has a facilitatory effect on action words processing already at 150 ms after stimulus onset (Pulvermüller et al., 2005b); (ii) event-related potentials in response to a lexical decision task were recorded approximately at 500–800 ms after stimulus onset (Pulvermüller et al., 1999); (iii) stimulation of the M1 cortex at 500 ms after stimulus onset increases MEPs elicited on action vs. non-action word trials (Oliveri et al., 2004). In addition, since one of the current tasks involved motor imagery, our TMS onset times were also based on previous motor imagery studies, in particular those in which TMS was used to investigate the simulation of hand rotational movements showing

a TMS effect at 650 ms (Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000) or already at 400 ms (Tomasino, Borroni, Isaja, & Rumiati, 2005).

2.4. Stimuli

First, 90 German verbs related to *hand* movements were selected from a dictionary. Many of them, by their nature, were implicitly object-related actions. Verbs were divided by the experimenter into verbs that describe actions which require rotational hand movements (i.e., “rotation-related verbs”, e.g., “aufschrauben”, i.e., “to screw”) and actions that do not (i.e., “non-rotation-related verbs”, e.g., “hämmern”, i.e., “to hammer”). Second, the selected verbs were divided according to their written frequencies (CELEX database, Baayan, Piepenbrock, & Gulikers, 1993) into verbs with high (e.g., “schreiben”, i.e., “to write”) or low (e.g., “rasieren”, i.e., “to shave”) written frequencies. This stimulus selection and classification was controlled for in a pilot study in which we presented these 90 verbs to 12 native German speakers who judged whether each verb requires a hand/wrist rotation or not (i.e., “presence of rotational wrist/hand movements” question) and whether it has a high or a low-written frequency (i.e., “frequent verb” question). The ratings of the pilot study confirmed the experimenter’s division of the stimuli. Those items which had been classified as “rotation-related verbs” by the experimenter elicited indeed significantly more “Yes” (78.7%) than “No” (21.3%) responses ($t(11)=7.8, p<0.001$) to the “presence of rotational wrist/hand movements” question, whereas the opposite pattern was found for the “non-rotation-related verbs”, with more “No” (73.4%) than “Yes” (26.6%) responses ($t(11)=-7.2, p<0.001$). Those verbs with a high-written frequency, as documented in the CELEX database, elicited significantly more “Yes” (74.6%) than “No” (25.4%) responses ($t(11)=6.8, p<0.001$) to the “frequent verb” question, whereas verbs with a low-written frequency induced more “No” (82.4%) than “Yes” (17.6%) responses ($t(11)=-8.9, p<0.001$; see Fig. 2a). None of the 12 subjects involved in the pilot study took part in the TMS study.

For the TMS experiment, 70 verbs with a 95–100% agreement among the ratings of the subjects of the pilot study were selected from the 90 verbs used in the pilot study and were presented in their infinitive form. The number of rotation vs. non-rotation stimuli was unequal, as was the number of high vs. low frequency words both in the pilot and in the TMS study. Stimuli, although being unbalanced (in number) were accurately controlled for. First of all, the same set of 70 stimulus verbs (albeit in a randomized order) had been used in all three tasks. Thus, any differences in stimulus characteristics were identical across the three tasks. Regarding the frequency distribution among the rotation and non-rotation stimulus verbs, the ratios were as follows: the 27 “rotation-related verbs” contained 18 low (66.7%) and 9 highly frequent (33.3%) verbs (as assessed by the CELEX database). Among the 43 “non-rotation-related verbs”, 30 were low (69.8%), and 13 were highly frequent (30.2%). Thus, the frequency distributions were similar between rotation and non-rotation verbs ($\chi^2=0.2, p=0.6$). On the other hand, 18 of the 48 low frequency verbs were rotation verbs (37.5%), while 30 low frequency words were non-rotation verbs (62.5%). The 22 high frequency verbs could be divided into 9 rotation (40.9%) and 13 non-rotation verbs (59.1%). Again, the ratios of rotation vs. non-rotation verbs were similar between low and high frequency verbs ($\chi^2=0.2, p=0.6$). The unbalanced number of stimuli was not considered a confound in the experimental design, since our motivation was to control the cognitive set and operations performed during the silent reading of the action verbs, rather than individual answers. Nevertheless, task performance of our subjects should indicate that they correctly followed task instructions (as they did—see the behavioral data below). In fact, the “rotation” question should prompt subjects to perform motor imagery of the actions denoted by the stimulus verbs. The “frequency” question was used to draw the subjects’ attention to the linguistic content of the stimulus verbs. The rotation vs. non-rotation verbs were matched as carefully as possible for letter length (non-rotation verbs: 7.6 ± 2.03 vs. rotation verbs: 8.55 ± 2.38), and written frequency (non-rotation verbs: 182.92 ± 487.15 opm vs. rotation verbs: 124.10 ± 343.31 opm, CELEX database, Baayan et al., 1993). As far as high vs. low frequency verbs (low frequency verbs: 26.41 ± 38.6 opm vs. high frequency verbs: 428.17 ± 676.4 opm) are concerned, our stimuli were closely matched for letter length (low frequency verbs: 8.05 ± 2.3 vs. high frequency verbs: 7.91 ± 2.1). Overall, the average word length of the 70 verbs was 8 ± 2.19 letters, and their mean written frequency was 156.5 ± 425 (occurrences per million). In addition, the image-ability

of the stimuli was matched as carefully as possible during the pilot study. All 70 stimulus verbs had been rated during the preparation of the stimuli according to image-ability by 10 German native speakers who decided how clearly they could form a mental image on a 1–7 scale (see also Tomasino et al., 2007). The mean image-ability ratings did not differ between the rotation (4.87 ± 0.69) and non-rotation (4.98 ± 0.52) verbs (two-sample *t*-test, $t(68)=0.77, p=0.44, n.s.$) or between the low frequency (4.85 ± 0.55) and high frequency (5.14 ± 0.64) verbs (two-sample *t*-test, $t(68)=-1.88, p=0.63$).

2.5. Task

The same set of verb stimuli ($N=70$), which were randomly presented across participants and tasks, was used in each of the 3 tasks in a block design. The order of tasks was counterbalanced (see Fig. 1 showing one possible counterbalanced combination). The task instructions (8 s) common to all three tasks were: “Silently read the verb”. In addition, subjects were instructed to (i) “Press the right button when you are done” [silent reading (SR) task], (ii) “Imagine yourself performing the action. Does it require a hand rotation? Yes/No” [imagery (I) task], and (iii) “Is this a word you would frequently read in newspapers? Yes/No” [frequency judgment (FJ); see Fig. 1]. Prior to the experiment, subjects were asked “to give a very intuitive and direct answer about whether the given stimulus is a word which would be often found in a newspaper” in the FJ task. The response was quite obvious, both for verbs with low-written frequency (e.g., “to iron”), as these verbs hardly appear in newspapers, and for those with high-written frequency (e.g., “to clap”), as these verbs often appear in newspapers. In addition, subjects were given some examples, e.g., “klatschen” (“to clap”), “knipsen” (“to photograph”), or “boxen” (“to box”), which are words that are likely to appear in newspapers and, therefore, require a “yes” answer for the FJ task. On the contrary, it is unlikely to find the following words in a newspaper: “aufschrauben” (“to screw”), “bügeln” (“to iron”), or “hämmern” (“to hammer”), thus triggering a “no” answer for the FJ task. Subjects responded in the intended manner (see the proportion of “yes”/“no”-answers below). Furthermore, the RTs for the frequency judgement task, which were shorter than for the imagery task, indicated that our subjects gave, in fact, an intuitive response rather than evaluating extensively the written frequency distribution of a given verb.

2.6. Experimental design

We used two TMS conditions counterbalanced across subjects: TMS applied above the left M1 hand area [TMS_{M1}] and, for control, TMS applied above the vertex [TMS_{vertex}]. We stimulated *left* M1 cortex, because all subjects were right-handed. Thus, the action verbs related to hand movements triggered right (dominant) hand motor imagery in our subjects. TMS pulses were randomly given at 150, 300, 450, 600, 750 ms after stimulus onset (DELAY).

We used three TASKS (motor imagery, silent reading and frequency judgment). The three TASKS (SR, I and FJ) were presented in a counterbalanced order across subjects. Identical verb stimuli ($N=70$) were presented in random order in the three TASKS (SR, I and FJ), once during TMS_{M1} and once during TMS_{vertex} , resulting in a total of ($3 \times 2 \times 70 =$) 420 trials. Stimuli were counterbalanced within tasks and between subjects.

Each cell of the design included 14 trials (=420 divided by 2 stimulation conditions, by 3 tasks, and by 5 stimulation delays). In a given trial, the stimulus verb was presented for 900 ms and was followed by a fixation cross lasting 4700 ms. The minimal inter-trial interval between two consecutive TMS pulses was 5 s, to avoid carry-over effects between consecutive stimuli (see Fig. 1). Each block lasted 21 min. The whole experimental session lasted about 80 min (i.e., 21 min for each of the two TMS conditions and the training session plus 1 min rest between tasks, 5 min rest between the TMS conditions, and a few minutes for checking the position of the coil).

To familiarize subjects with the experimental set-up and minimize serial effects during the TMS sessions, all subjects performed a training session with the same stimuli and tasks employed in the two TMS sessions prior to the TMS experiment. The training served two purposes: (i) to familiarize subjects with the experimental set-up and tasks, and (ii) to provide individual mean baseline latencies for all three tasks. These baseline measures may help to differentiate between a facilitatory effect of TMS_{M1} and a possible inhibitory effect of TMS_{vertex} . Furthermore, the analysis of the subjects’ responses during the

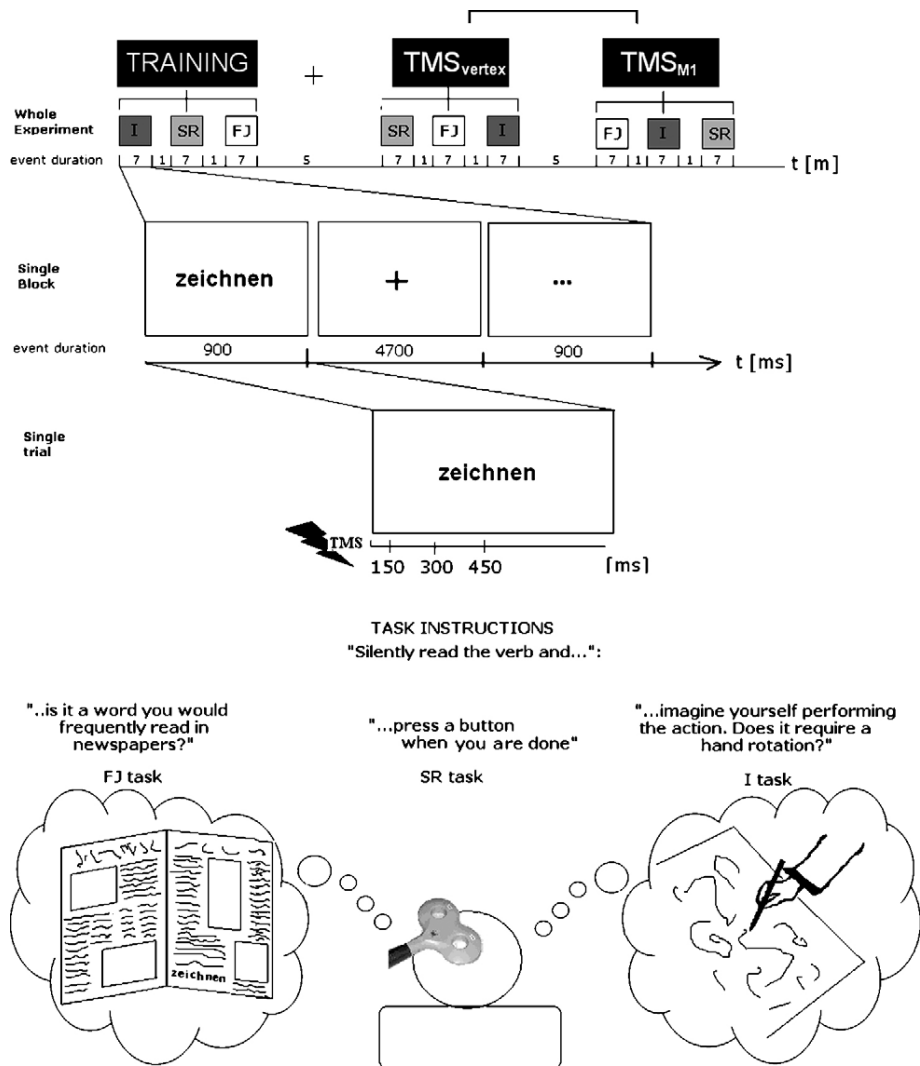


Fig. 1. Experimental design. The upper part (*whole experiment*) exemplifies, using one possible counterbalanced order, the experimental design which involved two stimulation conditions (TMS_{M1} and TMS_{vertex}), three TASKS (silent reading, SR, vs. imagery, I, vs. frequency judgment, FJ) and three TMS DELAYS (150, 300 and 450 ms after stimulus onset). In the lower part (*single block and single trial*), the sequence of events in the experiment and the task instructions are illustrated.

training session would indicate whether the experimental subjects classified the stimulus verbs similarly as the pilot subjects.

2.7. Data analysis

Before the final data analysis, *anticipated responses* (11.2% of trials) were removed by excluding all trials in which the participants' responses occurred *before* the TMS stimulation. In the SR task, there were more anticipated responses at 750 ms delay (67.5%) and at 600 ms delay (51.07%) than at 450 ms delay (32.67%), 300 ms delay (4.1%), and 150 ms delay (0%) (TASK × DELAY, $F(8,152) = 32.83, p < 0.001$). This pattern of anticipated responses implies that we could compare all three tasks only at the earlier three stimulation delays of 150, 300, and 450 ms (with less than 50% anticipatory responses for all three tasks). At the later time points (600 and 750 ms), only the I and the FJ tasks could be compared. Therefore, we conducted the main analysis on all three experimental tasks for only the early stimulation delays (150, 300, and 450 ms), as well as an additional analysis exclusively on the I and FJ tasks for all five stimulation delays (including the late stimulation delays of 600 and 750 ms).

The amount of anticipated responses for the stimulation delays above 300 ms are consistent with electrophysiological studies showing that visual words can be recognized in approximately 150–300 ms (e.g., Pulvermüller et

al., 2005a). As one of the main interests of our study was motor imagery, we included the later stimulation delays, since previous studies revealed that the effect of TMS above M1 on motor imagery occurs at about 500 ms (e.g., Ganis et al., 2000; Tomasino et al., 2005), and other authors found a modulatory effect of TMS_{M1} on processing of action words also at later latencies, i.e., at 500–700 ms after stimulus onset (Buccino et al., 2005; Oliveri et al., 2004).

Furthermore, *outliers* (3.4% for TMS_{M1} and 3.5% for TMS_{vertex}, with no significant difference across experimental conditions, tasks, or TMS delays, all $p > 0.05$, n.s.) were removed by excluding any trial in which the participant's RT was above or below two standard deviations of that participant's mean RT for the condition in which the trial occurred (Ratcliff, 1993). Seven subjects who showed, due to the removal of anticipated responses and outliers, empty cells for at least one experimental condition were excluded from the final analyses. Thus, the final analyses included complete data sets from 13 subjects.

2.8. Training session

2.8.1. Subjects' judgments

Subjects' judgments were analyzed by means of a one-way analyses of variance (ANOVA), with TASKS [I and FJ] as factor, the percentage of "Yes" and "No" responses to the "presence of rotational hand movements" question for

rotation- and non-rotation-related verbs, and the percentage of “Yes” and “No” responses to the “frequent verb” question for high- and low-written frequency verbs as dependent variables. The SR task was not included in this ANOVA, since for the SR task the responses did not express subjects’ judgments but indicated only the time point when they finished silently reading the stimulus verbs.

2.8.2. Response times

We then analyzed how RTs varied according to the task in the training session by means of one-way ANOVA with TASKS [I, FJ and SR] as factor. In addition, we examined whether the intrinsic characteristic of the stimuli (i.e., rotation-relatedness and frequency distribution) influenced the RTs by means of a repeated-measure ANOVA with rotation-relatedness [rotation vs. non-rotation movements] and frequency distribution (low-frequency vs. high-frequency) as factors.

2.9. TMS sessions

2.9.1. Subjects’ judgments

The percentage of “Yes” and “No” responses to the “presence of rotational wrist/hand movements” question for rotation- and non-rotation-related verbs and the percentage of “Yes” and “No” responses to the “frequent verb” question for high- and low-written frequency verbs were compared by means of a repeated-measure ANOVA on subjects’ percentage of “Yes” and “No” judgments, with CONDITION [Training, TMS_{M1} and TMS_{vertex}] and TASKS [I and FJ] as factors.

2.9.2. Response times for the early TMS stimulation delays (all tasks)

In order to measure potential inhibitory or facilitatory effects of TMS, we performed a repeated-measures 3 × 3 ANOVA, with TASK (motor imagery, silent reading, and frequency judgment) and DELAY (TMS stimulation at 150, 300, and 450 ms after stimulus onset) as factors. We assumed that the expected differential effect of TMS_{M1} or TMS_{vertex} depended on the cognitive operations (tasks) performed on the stimulus verbs, rather than on the individual responses, i.e., whether after performing the task the ‘correct’ or ‘incorrect’ response was given. Thus, the analysis was initially performed between tasks and not between stimulus classes, e.g., rotation vs. non-rotation or high vs. low frequency verbs. The dependent variable was the degree of change in mean RT for each participant (expressed as percent change in latency):

$$\left[\left(\frac{RT_{TMS_M1}}{RT_{TMS_vertex}} \right) \times 100 \right]$$

which directly estimates the amount and direction of the RT changes due to TMS_{M1} with respect to TMS_{vertex}. Furthermore, it allows reducing inter-subject variability, since, for every single subject, the individual mean RT during TMS_{M1} is divided by the individual mean RT during TMS_{vertex}. In addition, we introduced in this ANOVA a covariate (of no interest), with the differential RT value between the first and the second TMS session calculated for each subject, independent of the type of stimulation which took place during the sessions, to single out artifacts due to order effects. Again, we performed an additional analysis excluding this covariate (of no interest), which revealed the same pattern of results as the below reported analysis with the covariate (of no interest).

2.9.3. Response times for all TMS stimulation delays (imagery and frequency judgement tasks only)

We also performed an additional analysis for all five time intervals (i.e., including the late stimulation delays of 600 and 750 ms). At these later time points, only the I and the FJ tasks could be compared, due to the high incidence of anticipated responses for the SR task at these later stimulation delays.

For both analyses, the *F*-test was adjusted by the Greenhouse–Geisser correction when the Mauchly sphericity test was significant.

3. Results

3.1. Training session

3.1.1. Subjects’ judgments

In the I task, consistent with the results of the pilot study, “rotation-related” verbs elicited significantly more “Yes” (71.7%) than “No” (28.3%) responses to the “presence of rotational wrist/hand movements” question ($t(12) = 9.0, p < 0.001$), whereas the opposite pattern was found for the “non-rotation-related” verbs (more “No” [86.1%] than “Yes” [13.9%] responses, $t(12) = -7.8, p < 0.001$). In the FJ task, consistent with the CELEX database, verbs with a high-written frequency elicited significantly more “Yes” (67.4%) than “No” (32.6%) responses to the “frequent verb” question ($t(12) = 3.07, p < 0.05$), whereas the opposite pattern was found for the verbs with a low-written frequency (more “No” [84.3%] than “Yes” [15.7%] responses, $t(12) = -7.7, p < 0.001$; see Fig. 2a).

3.1.2. Response times

We found a significant main effect of TASK ($F(2,20) = 37.29, p < 0.001$). RTs were significantly shorter in the SR task (mean 745 ± 226 ms), both with respect to the I task (1721 ± 180 ms, $t(12) = -5.83, p < 0.001$) and to the FJ task (1537 ± 421 ms, $t(12) = -7.68, p < 0.001$), whereas mean RTs in the FJ task, although faster, were not significantly different from mean RTs in the I task ($t(12) = 1.96, p > 0.05, n.s.$; see Fig. 2c).

Analysis of the RT data of the imagery and frequency judgement tasks during the training dividing the stimulus verbs by frequency and presence of rotation revealed that, for the imagery task, RTs were similar for rotation and non-rotation verbs ($F(1,19) = 2.52, p = 0.12$) as well as for high vs. low frequency verbs ($F(1,19) = 0.42, p = 0.52$), and there was no interaction ($F(1,19) = 1.29, p = 0.27$). Similarly, for the FJ task, the RTs did not differ for rotation vs. non-rotation verbs ($F(1,19) = 0.51, p = 0.5$) or for high vs. low frequency verbs ($F(1,19) = 0.29, p = 0.6$). Again, the interaction was not significant ($F(1,19) = 1.12, p = 0.3$). Since there was no effect on task reaction times depending on the word frequency and the presence of a rotation component during training, we performed the RT analyses in the TMS experiment without dividing our stimuli into rotation-related and non-rotation-related or in low-frequency and high-frequency words.

3.2. TMS sessions

3.2.1. Subjects’ judgments

As expected, TMS_{M1} or TMS_{vertex} did not affect subjects’ responses in the three tasks (main effect of CONDITION [TRAINING/TMS_{M1}/TMS_{vertex}]: $F(2,20) = 1, p = 0.386, n.s.$, and CONDITION × TASK interaction: $F(2,20) = 0.38, p = 0.68, n.s.$). Subjects’ judgments in the TMS sessions were very similar (percentage of “yes and “no” answers in response to the “presence of rotational hand/wrist movements” and “frequent verb” questions) to the pattern of responses observed in the pilot study and in the training (see Fig. 2b), showing that there was no significant effect of TMS on performance accuracy. Therefore,

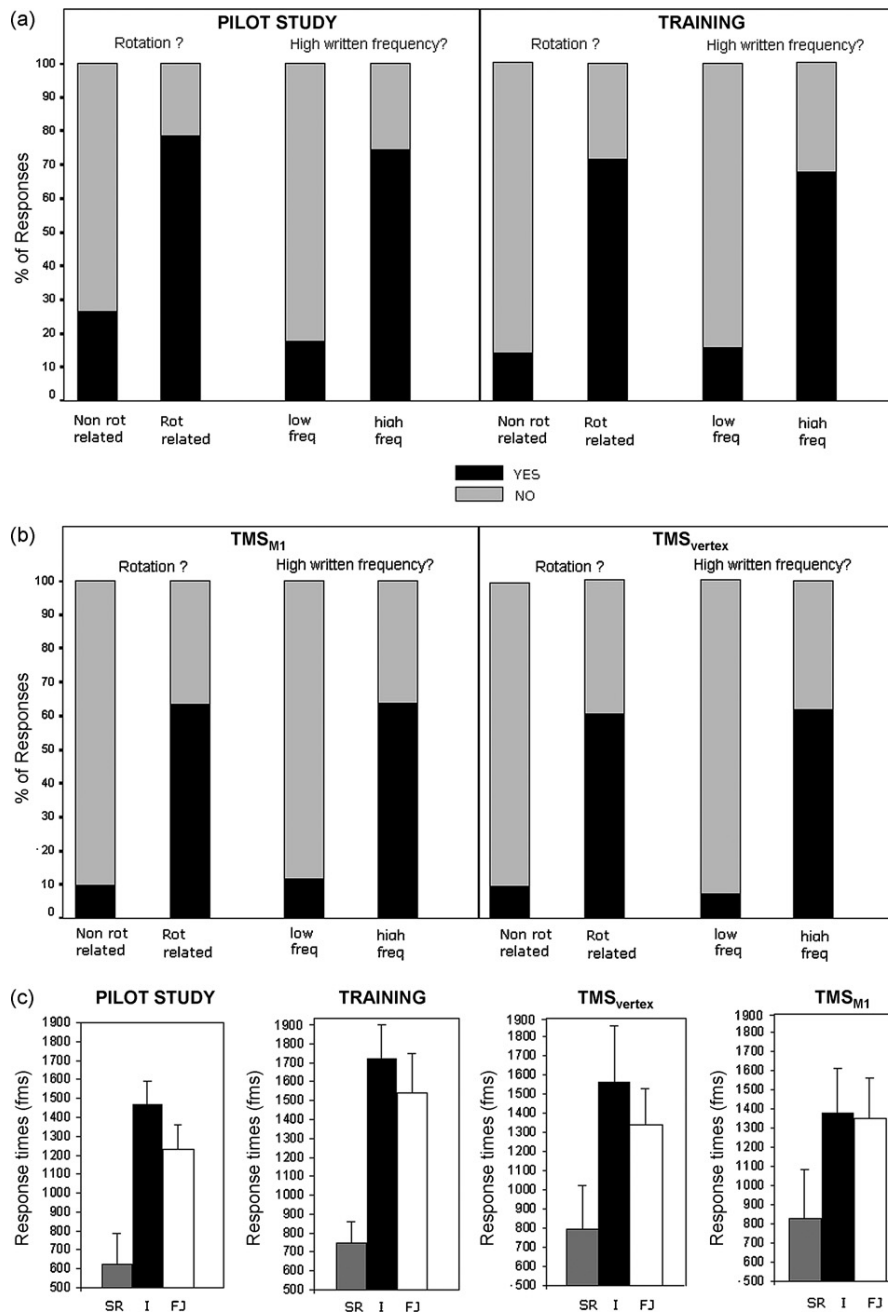


Fig. 2. Subjects' response characteristics in the imagery and frequency judgment tasks and the corresponding reaction times. Percentage of "Yes" and "No" responses to the "presence of rotational wrist/hand movements", the "frequent verb" questions for rotation- vs. non-rotation-related verbs, and for high- vs. low-written frequency verbs, respectively: (a) data for the pilot study and the training; (b) data from the TMS experiment (TMS_{M1} and TMS_{vertex}); (c) mean response times in the pilot study, in the training and in each TMS block (error bars represent standard deviation).

we analyzed the RT data irrespective of the correctness of the responses.

3.2.2. Response times for the early TMS stimulation delays (all tasks)

The calculation of the relative change in mean RT $[(RT_{TMS_M1}/RT_{TMS_vertex}) \times 100]$ (expressed as percent) directly estimated the amount and direction of any RT change due to TMS_{M1} relative to the TMS_{vertex} (i.e., a value of 100%

representing no RT change, a value >100% representing slower, and one <100% indicating a faster mean RT for TMS_{M1} than for TMS_{vertex}). For the first three TMS stimulation delays, there was a differential modulation of the relative change in mean RT dependent upon task (TASK, $F(2,22) = 3.88$, $p < 0.05$: RTs in the I task were about 88 ms faster after TMS_{M1} compared to TMS_{vertex}). The factor DELAY ($F(2,22) = 0.342$) and the TASK \times DELAY interaction ($F(4,44) = 0.284$) were not significant (all $p > 0.05$, n.s.). Although there was a significant main

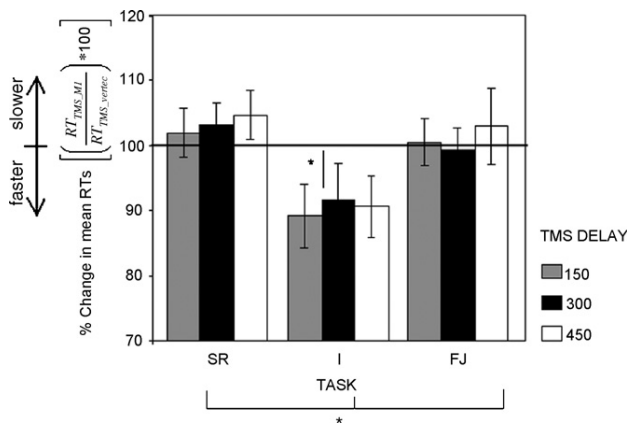


Fig. 3. Degree of change (in percentage) in mean RTs collected during TMS_{M1} with respect to mean RTs collected during TMS_{vertex} . The formula, $\left[\left(\frac{RT_{TMS_{M1}}}{RT_{TMS_{vertex}}}\right) \times 100\right]$, directly estimates the amount and direction of any change of the TMS_{M1} RTs with respect to the TMS_{vertex} RTs (with a value of 100% representing no RT change between TMS_{M1} and TMS_{vertex} , values greater than 100% representing slower RTs for TMS_{M1} than for TMS_{vertex} , and values smaller than 100% indicating faster RTs for TMS_{M1} than for TMS_{vertex}). Data are plotted as a function of the type of task and TMS delay. Error bars represent standard deviations. The asterisk at the bottom of the figure indicates a significant main effect of task: RTs for the I task significantly differed from RTs for the FJ and SR tasks. The second asterisk denotes that the relative change in mean RT for the I task ($90.45 \pm 4.5\%$) was significantly different from 100% (with 100% representing no relative RT change).

effect of the order effect covariate ($F(1,11) = 11.19$, $p < 0.01$), the interactions of the covariate with TASK ($F(2,22) = 1.7$, $p > 0.05$, n.s.), of the covariate with DELAY ($F(2,22) = .24$, $p > 0.05$, n.s.), and the three way interaction of the covariate with TASK and DELAY ($F(4,44) = 1.08$, $p > 0.05$, n.s.) were not significant.

Post hoc analysis of the significant main effect of TASK at the first three TMS stimulation delays revealed that the degree of relative changes in mean RT for TMS_{M1} with respect to the mean RT during TMS_{vertex} were: $90.45 \pm 4.5\%$ for the I task, $100.9 \pm 4.2\%$ for the FJ task and $103.2 \pm 3.4\%$ for the SR task (see Fig. 3). The degree of relative change for the I and the FJ tasks ($t(12) = -2.12$, $p < 0.05$) and for the I and the SR tasks ($t(12) = -2.42$, $p < 0.05$) were significantly different, whereas the relative change for the SR and the FJ tasks were not significantly different ($t(12) = .48$, $p > 0.05$, n.s.).

In addition, the relative change in mean RT for the I task ($90.45\% \pm 4.5\%$) was significantly different from 100% (with 100% representing no relative RT change, $t(12) = -2.19$, $p < 0.05$). Thus, for the I task only, TMS_{M1} sped up subjects' responses (i.e., a facilitatory effect). By contrast, the relative changes in mean RT for the FJ task ($100.9\% \pm 4.2\%$) and for the SR task ($103.2\% \pm 3.4\%$) were not significantly different from 100% ($t(12) = 0.24$, $p > 0.05$, for the FJ task and $t(12) = 0.9$, $p > 0.05$, for the SR task, all n.s.). Therefore, TMS_{M1} (vs. TMS_{vertex}) did not modulate the mean RT during the FJ and the SR tasks.

3.2.3. Response times for all TMS stimulation delays (imagery and frequency judgement tasks only)

The additional analysis conducted exclusively on the I and FJ task data for all five TMS stimulation delays (including the two late stimulation delays of 600 and 750 ms) produced the same pattern of results as the analysis for the early stimulation delays (150, 300, and 450 ms): there was a differential modulation of the relative change in mean RT according to the task (TASK [I vs. FJ], $F(1,12) = 5.3$, $p < 0.05$). The factor DELAY ($F(4,48) = 0.96$) and the TASK \times DELAY interaction ($F(4,48) = 0.22$) were not significant (both $p > 0.05$, n.s.). In addition, the relative change in mean RT for the I task ($89.9 \pm 4.0\%$) was significantly different from 100% (with 100% representing no relative RT change, $t(12) = -2.49$, $p < 0.05$). Thus, for the I task only, TMS_{M1} sped up subjects' responses at all five stimulation delays.

4. Discussion

4.1. Task-dependent modulation of reaction times after TMS_{M1} : facilitation

In this TMS study, we investigated the nature of the previously reported primary motor cortex (M1) involvement in the processing of action words (e.g., Hauk et al., 2004). To examine whether reading of action words *per se* or rather certain task components modulate M1 activity, we applied single-pulse TMS above the left M1 (TMS_{M1}) or, for control, the vertex (TMS_{vertex}), while subjects performed three different tasks (silent reading, motor imagery, and frequency judgment). The main finding of the present study was a significant main effect of TASK: TMS_{M1} (compared to TMS_{vertex}) modulated subjects' reaction times for the imagery task only. Similar to the study by Pulvermüller et al. (Pulvermüller et al., 2005b), in which sub-threshold stimulation of the arm area of the left primary motor cortex led to faster response times in a lexical decision task for arm- compared to leg-action-related words, a facilitatory effect was also found in the present study: mean RTs were about 10% faster for TMS_{M1} as compared to TMS_{vertex} . Importantly, however, this facilitatory TMS_{M1} effect was specific for the imagery task. There are other studies who have also reported TMS-induced facilitation of task responses (e.g., Grosbras & Paus, 2002; Pulvermüller et al., 2005b; Topper, Mottaghy, Brüggemann, Noth, & Huber, 1998; and also Sawaki, Okita, Fujiwara, & Mizuno, 1999). The more commonly observed inhibitory effects of TMS can result from a disruption of neural processing in a given area, when this area is stimulated just *during* information processing. In contrast, TMS-induced facilitation of neural processing may occur if neural activity of a given area is synchronized by TMS stimulation just *before* the relevant information is transferred to this area. In a similar vein, Pulvermüller et al. (2005b) suggested that sub-threshold TMS applied above M1 shortly after the presentation of an action word may result in a priming effect, as do semantically related words when presented prior to the target word presentation. Topper et al. (1998) put forward that focal magnetic stimulation applied over Wernicke's area is able to facilitate lexical processes due to a more general "preactivation" of language-related neuronal networks. Grosbras and

Paus (2002) observed a facilitatory effect on visual processing when TMS was applied over the frontal eye field (FEF) and suggested that TMS increased cortical excitability in the FEF for a brief period of time, so that a stimulus presented just after the TMS pulse elicits a stronger neuronal response in the FEF and, therefore, faster RTs.

It should be noted that our study cannot differentiate whether the specific facilitatory effect of TMS_{M1} on the imagery task is due to direct modulation of primary motor cortex (M1) activity or to indirect modulation of M1 activity by the premotor cortex activated by action words (see for example Fadiga, Craighero, Buccino, & Rizzolatti). In the former case, M1 would directly participate in the processing of action verbs. In the latter case, premotor cortex would be activated by the processing of action verbs (e.g., by the action execution–observation matching system; Aziz-Zadeh et al., 2006; Buccino et al., 2005; Tettamanti et al., 2005). This premotor activity would then facilitate activity in the directly connected primary motor cortex. Thus, when TMS_{M1} occurs, processing is facilitated in M1 due to the previous priming by premotor cortex activity by action verbs. In that case, M1 would only be indirectly involved in the processing of action verbs. However, the current study demonstrates that for the processing of action verbs, task goals can influence the engagement of motor networks, whether they include premotor or primary motor cortex, or both. This task-dependent modulation also corresponds with Eisenegger et al.'s results (2007) showing that the hand motor cortex was activated more strongly during a mental rotation task than during verbal tasks.

4.2. Task-dependent modulation of reaction times after TMS_{M1}: temporal pattern

It should be noted that our study is the first which used different TMS delays within the same experimental set-up, thus making use of the high temporal resolution of TMS. Our results may shed some light on the question whether explicit motor imagery during processing of action verbs is a 'primary/immediate' or rather a 'secondary' step. In this context, "primary/immediate" means that the effect of motor simulation (as in the I task) occurs already quite early (e.g., at 150 ms). However, even such an early facilitatory effect on reaction times by TMS_{M1} does not imply that language comprehension requires motor simulation. Nevertheless, if motor simulation were involved only in the latter stages of the process (i.e., as a secondary step), then we would expect that the differential modulation of reaction times by TMS_{M1} occurs only at later stimulation times, while early stimulation delays do not affect reaction times. The fact that we observed a specific modulation of response times already at early delays is consistent with studies showing that semantic context influences linguistic processes already at about 150 ms after presentation of a written word (Penolazzi, Hauk, & Pulvermüller, 2007; Pulvermüller et al., 2005b). However, some linguistic processes occur later, as reflected by the N400 component in event-related potential (ERP) studies measured at about 400 ms after presentation of a written word. An early involvement of M1 in cognitive tasks related to movement representations has also been found

during memorization of action sentences via enacted encoding (between 150 and 250 ms after stimulus onset, Masumoto et al., 2006). Recent data revealed a cross-talk between language and motor execution already within the first 200 ms after stimulus onset (Boulenger et al., 2006), whereas in Buccino et al.'s study (2005), TMS pulse delivery occurred on average 500–700 ms after stimulus onset. Similarly, in Oliveri et al.'s study (2004) TMS pulses were given at 500 ms. Furthermore, explicit motor imagery is considered to be a long-lasting process (e.g., Ganis et al., 2000 showed that TMS on M1 cortex affects the simulation of a rotational hand movement at 650 ms after stimulus onset) and thus is likely to occur at all the five stimulation delays assessed in the current study. Consistent with these previous findings, the specific facilitatory effect of TMS_{M1} during the I task (as compared to the FJ and the SR tasks) was found for all stimulation delays in our study (i.e., from 150 to 750 ms).

4.3. Motor simulation and action-related word processing

Our data are in keeping with recent findings showing M1 activation during action word processing (Hauk et al., 2004; Pulvermüller et al., 2001; Pulvermüller et al., 2005a). However, extending previous work, our data suggests that M1 is involved in motor imagery performed on action verbs. Although other researchers already considered the possibility that the M1 activation they detected might be related to motor simulation, none of the previous studies controlled for the possible confound that subjects did (or did not) perform mental imagery. Within the framework of the observation–execution–matching system, it has been suggested that: "the understanding of action-related sentences implies an internal simulation of the actions expressed in the sentences" (Buccino et al., 2005), or "... the activation of sensorimotor circuits might be due to the fact that participants were simply engaged in motor imagery of the actions described by the sentences" (Tettamanti et al., 2005), or "... people understand linguistic descriptions of actions by mentally simulating these actions just like people understand directly observed actions by others through mental simulation" (Zwaan & Taylor, 2006). Other views suggest that motor imagery is a corollary phenomenon to action word processing: "... it is possible that word production sometimes leads to the corollary generation of mental images related to the concept being retrieved ... the motor cortex activation that we observed might not strictly be necessary for action word production" (Oliveri et al., 2004). Finally, some authors consider mental motor imagery to be a side effect of understanding motor-related words: "... these effects could result from side or after-effects of linguistic processes and could thus result from mental motor imagery" (Boulenger et al., 2006). However, our results still do not provide evidence as to whether motor areas are essential for processing action words. Neuropsychological studies show that lesions of the M1 cortex do not predictably cause deficits in action-word processing (De Renzi & di Pellegrino, 1995; Saygin, Wilson, Dronkers, & Bates, 2004; see also Mahon & Caramazza, 2005).

In our experiment, the SR task and the FJ task did not show any modulation of the recorded parameters, whereas the modulation of M1 activity specifically occurred in the context of motor

simulation. Therefore, motor resonance seems to be related to subjects performing mental simulation rather than action meaning encoding. These results suggest that the relation between action word comprehension and internal motor simulation is not automatic: in order to understand language, subjects do not need to run a mental simulation of the word content. Rather, the modulation of M1 activation during action-related word understanding depends on whether or not, during reading, subjects simulate the movement the words are referring to. This may help to explain why previous studies reported modulations of M1 activity contingent upon action word processing even in the absence of specific cognitive demands. In the work by, e.g., Hauk et al. (2004) and Pulvermüller et al. (1999), subjects were performing silent reading tasks with no other cognitive operation specified. However, during reading, subjects might have imagined themselves performing the action, which in turn could have activated M1. Furthermore, in other functional imaging studies in which tasks involving action word stimuli have been used to investigate other aspects of language (e.g., morphology, grammar, category specificity), M1 was (e.g., Frings et al., 2006) or was not (e.g., Longe et al., 2007; Perani et al., 1999) activated in the critical comparisons involving processing of action verbs. This inconsistent pattern of M1 activations may also be explained by the fact that subjects did or did not perform mental simulation.

Why then did our subjects not perform motor simulation during the FJ task or SR? Our finding of a differential modulation of reaction times by TMS_{M1} in the I task only strongly suggests that cognitive processing of the same verbal stimuli can be modulated by explicit instructions (Fink et al., 2002). The semantic task (FJ) used here was designed to require a purely lexical judgment that did not encourage image generation. Similarly, the SR task used here should not evoke imagery, as subjects were just required to read the verbs and to press a button as soon as they had finished reading. Secondly, we used explicit instructions in the three task blocks (I, SR and FJ), which were separated in time. In the learning domain (for example, see Fletcher et al. (2005)), it has been shown that explicit processing instructions suppress related implicit processing. With this in mind, we explicitly asked our subjects to perform imagery in one block (I task), therefore, making it unlikely that subjects would (implicitly) use imagery also in the other task blocks (e.g., FJ), in which they were explicitly asked to perform another cognitive operation. Our results show that only under conditions when motor simulation occurred (i.e., during the I task), M1 activity was modulated, suggesting that motor simulation and semantic access *per se* (as in the FJ task) can be disentangled by means of explicit instructions and that only the former triggers M1 activity. In this view, motor resonance is intimately related to subjects (explicitly or implicitly) performing mental simulation but not to action meaning encoding *per se*. Our view is that the presence of M1 activation during action-related word understanding depends on whether or not, during reading, subjects simulate the movement the words are referring to. In this view, mental simulation (and thus M1 activation) would be a *side effect* of or a *corollary* phenomenon to understanding motor-related words, rather than a *requirement* for language comprehension.

With respect to the relationship of our study and the notion of ‘embodied cognition’ (e.g., Barsalou, 1999; Feldman & Narayanan, 2004; Zwaan & Taylor, 2006), our data do not support the notion of embodied cognition, which claims that simulation is an important part of language processing *per se*. In our view, M1 activity is related to (explicit or implicit) motor imagery triggered by action words. The lack of TMS modulation for the FJ task shows that M1 activity is not a requirement for language comprehension. The embodied cognition view assumes that understanding an action (word) relies on mapping the action (word) onto one’s motor representation, e.g., by using mental simulation. This mapping process activates the motor representations and, thereby, leads to activity in M1. Thus, the notion of embodied cognition implies that, *in any case*, action (word) understanding activates M1. However, our data suggest that M1 activity is not required for action word understanding in the context of the FJ task, which certainly requires (action) word comprehension. Rather, a significant modulation of M1 activity only occurred when motor simulation was explicitly required, i.e., during the I task. Nevertheless, both accounts (embodied cognition and our account) have in common that M1 activity is modulated by motor simulation.

In conclusion, our results show that the hand area of the left primary motor cortex is critically involved in processing verbs related to hand action when subjects are explicitly simulating the corresponding hand movement. In contrast, silent reading of hand-related action verbs *per se* or frequency judgments about these action verbs do not seem to be influenced by TMS stimulation of the hand motor cortex. The exact role of motor simulation in processing action-related language deserves, however, further investigation.

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