Contribution of motor representations to action verb processing

Michael Andres a,b, , Chiara Finocchiaro c, Marco Buiatti b,d, Manuela Piazza b,d

- a Psychological Sciences Research Institute, Université Catholique de Louvain, Place Cardinal Mercier 10, 1348 Louvain-la-Neuve, Belgium
- b Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, 38068 Rovereto, Italy
- c Department of Psychology and Cognitive Science, University of Trento, Corso Bettini 31, 38068 Rovereto, Italy
- d INSERM U992, Cognitive Neuroimaging Unit, CEA/DSV/I2BM/NeuroSpin, Bâtiment 145, Point Courrier 156, 91191 Gif-sur-Yvette, France

a b s t r a c t

Electrophysiological and brain imaging studies show a somatotopic activation of the pre- motor cortex while subjects process action verbs. This somatotopic motor activation has been taken as an indication that the meaning of action verbs is embedded in motor repre- sentations. However, discrepancies in the literature led to the alternative hypothesis that motor representations are activated during the course of a mental imagery process emerg- ing only after the meaning of the action has been accessed. In order to address this issue, we asked participants to decide whether a visually presented verb was concrete or abstract by pressing a button or a pedal (primary task) and then to provide a distinct vocal response to low and high sounds played soon after the verb display (secondary task). Manipulations of the visual display (lower vs. uppercase), verb imageability (concrete vs. abstract), verb meaning (hand vs. foot-related), and response effector (hand vs. foot) allowed us to trace the perceptual, semantic and response stages of verb processing. We capitalized on the psychological refractory period (PRP), which implies that the initiation of the secondary task should be delayed only by those factors that slow down the central decision process in the primary task. In line with this prediction, our results showed that the time cost resulting from the processing of abstract verbs, when compared to concrete verbs, was still observed in the subsequent response to the sounds, whereas the overall advantage of hand over foot responses did not influence sound judgments. Crucially, we also observed a verb- effector compatibility effect (i.e., foot-related verbs are responded faster with the foot and hand-related verbs with the hand) that contaminated the performance of the secondary task, providing clear evidence that motor interference from verb meaning occurred during the central decision stage. These results cannot be explained by a mental imagery process that would deploy only during the execution of the response to verb judgments. They rather indicate that the motor activation induced by action verbs accompanies the lexico-semantic processes leading to response selection.

1. Introduction

Words describing body actions (e.g. to hammer) convey information about concrete gestures that can be performed by every individual, with little variability, because they are constrained by universal biomechanical rules. Recent evi- dence suggests that this tight relationship between action words and bodily experience influences their conceptual representation in the human brain. Indeed, fMRI studies showed that action verb processing induces somatotop- ically organized patterns of activation in the frontal lobe. Verbs describing leg movements elicit activity in the superior frontal gyrus and in the dorso-medial aspect of the precentral gyrus, whereas arm- and face-related verbs activate the middle and inferior frontal gyri (Hauk, Johnsrude, & Pulvermüller, 2004; Pulvermüller, Härle, & Hummel, 2001). Such a homunculus-like activation was also observed when action words were embedded in literal (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Tettamanti et al., 2005) or idiomatic sentences (Boulenger, Hauk, & Pulvermüller, 2009; Boulenger, Shtyrov, & Pulvermüller, 2011). Because no overt move- ments were permitted in these studies, the distinct pattern of frontal activity evoked by action words was assumed to reflect the contribution of motor representations to lexico- semantic processing (Hauk, Shtyrov, & Pulvermüller, 2008; Pulvermüller, 2005).

An alternative hypothesis suggests that the somatotopic activation observed during action verb processing is a by- product of mental imagery of action, which emerges only after the meaning of the action has been accessed (Boulenger et al., 2006; Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008; Willems & Hagoort, 2007). Mental imagery of action is defined as the genera- tion of a complete action plan that is not executed but can facilitate execution by shaping the motor system (Jeannerod, 2001). To date, none of the two hypotheses can be firmly disconfirmed: functional magnetic resonance imaging (fMRI) indicates that, within the primary motor and premotor cortex, there is little overlap in activation induced by lexical decisions on action verbs or explicit mental imagery of the same actions (Willems, Hagoort, & Casasanto, 2010). Transcranial magnetic stimulation (TMS) over the left primary motor cortex was found to facilitate mental imagery of action verbs but not lexical judgments on the same verbs (Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008), although a relative difference was found between arm- and leg-related verbs when TMS was applied distinctively over the hand or foot motor area (Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005). A close look at the time course of body-related changes dur- ing action verb processing also reveals discrepancies. The finding that corticospinal (CS) excitability changes during the latest stages of action word recognition supports the assumption that motor activation arises as a consequence of a mental imagery process emerging only after action identification (Papeo, Vallesi, Isaja, & Rumiati, 2009). How- ever, electroencephalographical (EEG) and magneto- encephalographical (MEG) studies indicate that the motor content of action words already influences frontal activity within 150–250 ms (Hauk et al., 2008; Hauk & Pulvermüller, 2004; Pulvermüller, Härle, & Hummel, 2001; Pulvermüller, 2005; Pulvermüller, Shtyrov, & Ilmoniemi, 2005; Shtyrov, Hauk, & Pulvermüller, 2004; van Elk, van Schie, Zwaan, & Bekkering, 2010). The finding that the subliminal display of hand/arm-related verbs affects the preparation of upcoming hand movements pro- vides further support for an early crosstalk between semantic processing and motor activation, which cannot be ascribed to explicit imagery of the actions (Boulenger, Silber et al., 2008).

In the present study, we used a dual-task experiment to evidence activation of body-specific representations dur- ing action verb judgments and we capitalized on the well-known phenomenon of the psychological refractory period (PRP; Pashler, 1994; Telford, 1931) to test whether such activation emerges at the central stage, during lexico- semantic processing and response selection, or at the motor stage, after the meaning has been accessed and the response selected. When two tasks are presented simultaneously (or sequentially at a short interval), a delay in the execution of the second task is systematically observed. This interference effect (also referred to as the PRP) occurs because the central response selection stage of two tasks cannot occur in parallel. The central response selection stage refers to any process involved in the map- ping of perceptual information onto motor responses, including lexico-semantic processing and selection of the adequate response. In the present experiment, participants had first to decide whether a visually presented verb (displayed in either upper or lower case fonts) was con- crete or abstract by pressing a button or a pedal; second, they had to provide a distinct vocal response to low and high sounds played immediately after the verb display. A stimulus-onset asynchrony (SOA) of 150 ms was used in half of the trials to create interference between tasks, whereas the SOA was set to 900 ms in the other half to obtain a baseline measure of sound discrimination. Sound judgment was used as a probe task to create an attentional bottleneck and differentiate between the central response selection stage and the motor execution stage of the verb judgment task (for a similar approach, see Gaskell, Quinlan, Tamminen, & Cleland, 2008; Sigman & Dehaene, 2005). Within an interference dual-task regime, the pres- ence or absence of a time cost in sound judgment thus indicates whether the processes at work during verb judg- ment reflect either central or motor execution stages of processing.

In the verb judgment task, we expected that lower case stimuli should be processed faster than upper case stimuli for perceptual reasons (Perea & Rosa, 2002), whereas motor conduction times should lead to faster responses with the hand compared to the foot (Rothwell, 1997). In line with the well-established reaction time (RT) advan- tage of concrete over abstract words in lexico-semantic tasks (Binder, Westbury, McKiernan, Possing, & Medler, 2005; de Groot, 1989; James, 1975; Kroll & Merves, 1986; Rubin, 1980; Whaley, 1978), we predicted faster responses to concrete verbs because they are more image- able than abstract ones (Paivio, 1986). Finally, and cru- cially, the somatotopic motor activation hypothesis for action verb processing (Pulvermüller, 2005) predicts that participants should press the pedal faster when concrete verbs describe a foot-related action (e.g. walking), whereas responses to hand-related verbs (e.g. writing) should be faster when they imply a finger press. The aim of this study was first to test this prediction experimentally, and then to determine the locus of this putative verb-response com- patibility effect. A compatibility effect emerging during the central stage would indicate that the motor represen- tations associated with action verbs are active at the time a decision is made about their concrete status and the hand or foot is selected to respond. A compatibility effect emerg- ing during the motor stage would indicate that the motor representations associated with action verbs are activated

during the execution of the response to verb judgments, only after the meaning has been accessed and the correct response selected. According to the PRP model (Hesselman, Flandin, & Dehaene, 2011; Pashler, 1994; Sigman & Dehaene, 2005; Telford, 1931), within an inter- ference dual-task regime, the initiation of the secondary task (i.e. sound processing) should be delayed only by those factors that slow down the sensory and central deci- sion process in the primary task (i.e. verb processing), but not by factors that influence the mere response execution. Thus, sound judgments should be delayed when verbs are more difficult to recognize (lower vs. uppercase) and to understand (abstract vs. concrete), whereas pressing a but- ton or a pedal should not affect the initiation of sound pro- cessing because response programming can proceed in parallel to a secondary task (see Fig. 1). Under the assump- tion that motor activation accompanies the lexico-semantic processes leading to response selection, the verb-response compatibility effect should propagate to subsequent sound judgments. Alternatively, if the verb- response compatibility effect is a by-product of an explicit mental imagery process that takes place at the response execution stage, then sound judgments should reveal equal RTs after compatible and incompatible trials because the conflict between the verb meaning and the response effec- tor is assumed to emerge after the time window concerned by the PRP (see Fig. 1 for a schematic depiction of the predictions of the PRP). After testing these predictions, we conducted correlation analyses to investigate further the propagation of the aforementioned effects from the pri- mary to the secondary task. We reasoned that if an effect emerging at the level of the first task propagates to a subsequent task, the size of the propagation should be pro- portional to the size of the effect itself. In other words, the delay preceding response in the secondary task (sound judgments) should increase as a function of the effect size in the primary task (verb judgments).

2. Methods

2.1. Participants

Sixteen Italian-speaking students of the University of Trento (14 female, right-handed, age: 20 ± 3 years) partici- pated to the dual-task experiment against course credits. Their vision was normal or corrected to normal.

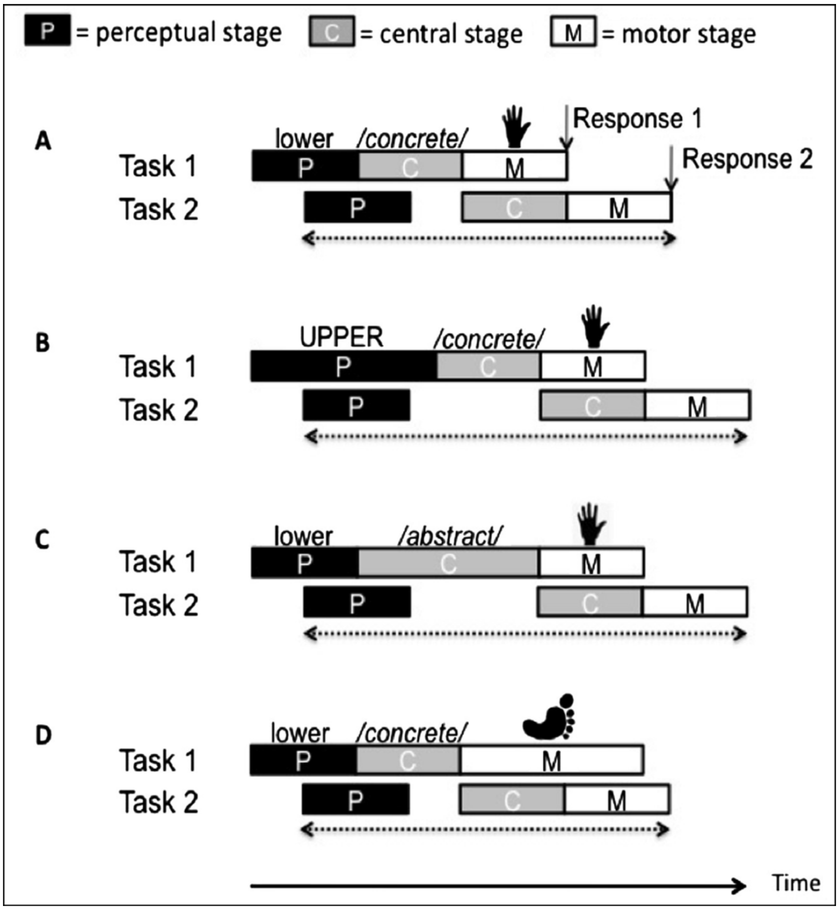
2.2. Stimuli

Verbal stimuli consisted in 48 abstract and 48 concrete verbs presented in the infinitive form either in upper or lower case (Courrier New, 18). Half of the concrete verbs were related to an action performed with the foot and the other half to hand movements. The lemma's frequency was (mean ± SD) 16.6 ± 23.5 for abstract verbs, 17.8 ± 26.7 for foot-related verbs and 17.6 ± 27.6 for hand-related verbs, according to the corpus and frequency lexicon of written Italian (CoLFIS, see http://www.istc.cnr.it/group- page/databases; Laudanna, Thornton, Brown, Burani, & Marconi, 1995). The average number of letters (±SD) was

8.3 ± 1.4 for abstract verbs, 8.5 ± 1.7 for foot-related verbs, and 8.3 ± 1.4 for hand-related verbs. Independent t-tests showed no difference in written frequency or number of letters between the three verb categories ($t < 1$, $p > .5$ for all comparisons). Because the corpus did not provide information about word imageability, we asked eighteen Italian speakers (15 female, age: 22 ± 4 years) who did not partic- ipate in the main study to rate how easily each verb evokes a vivid mental image or a vivid sensory-motor experience (1 = very difficult; 7 = very easy). Independent t-tests showed that abstract verbs (3.2 ± 1) were less imageable than hand-related (5.7 ± 0.9; $t(70) = 14.57$, $p < .001$) and foot-related verbs (5.7 ± 0.9; $t(17) = 15.20$, $p < .001$); no difference was observed between hand-related and foot- related verbs ($t < 1$, $p > .5$). Two sounds varying in pitch (440 vs. 880 Hz) were generated for sound judgments.

2.3. Procedure

In each trial, a verb was displayed for 150 ms on the com- puter screen (1700) in black on a white background (maxi- mum visual angle 5°). A sound was played for 150 ms either 0 or 750 ms after the verb offset. It was followed by a fixation cross that remained on the screen until the partic- ipant's response. Instructions required participants to answer as fast as possible to the verb and then to the sound, while keeping errors at minimum. In total, participants per- formed 768 trials divided in four blocks, resulting in 24 trials for each relevant condition of concrete verb judgments (case verb meaning response stimulus-onset asyn- chrony) and 48 trials for each relevant condition of abstract verb judgments (case response stimulus-onset asyn- chrony). In half of the blocks, participants were asked to press a button with their right hand in response to abstract verbs and to press a pedal with their right foot in response to concrete verbs, whereas the reverse stimulus-response mapping was used in the other half. These instructions were counter-balanced across blocks following an ABBA or BAAB order. Moreover, participants had to say ‘‘bi’’ in response to high sounds and ‘‘bo’’ in response to low sounds. The exper- imenter encoded the response for off-line analysis and trig- gered the next trial. In order to ensure that participants were familiar with the stimulus-response mapping before starting each block, they performed 24 practice trials with different verbs than those displayed in the rest of the exper- iment and instructions were reminded whenever they made errors. No feedback was given to the participants after the practice trials. In each of the four experimental blocks, the 96 verbs were presented twice in a random order; all verbs were first presented once before the repetition of any of them so that repetition was kept orthogonal to all condi- tions. Within a block, each combination of verb case, abstractness, response and stimulus-onset asynchrony (SOA) was presented equally often in association with high or low sounds. The stimulus onset and the recording of man- ual and pedal responses were controlled by the E-prime software (Psychology Software Tools, Sharpsburg, USA). A microphone connected to E-prime was used to detect the onset of verbal responses.



P = perceptual stage
C = central stage
M = motor stage
A
lower
/concrete/
Response 1
Response 2
Task 1
Task 2
B
UPPER
/concrete/
Task 1
Task 2
C
lower
/abstract/
Task 1
Task 2
D
lower
/concrete/
Task 1
Task 2
Time

Fig. 1. Schematic representation of the psychological refractory period in the present experiment (A). Sound judgment (task 2) was used as a probe task to create an attentional bottleneck and differentiate between perceptual, central or motor stages of verb judgment (task 1). Perceptual stages were tracked by indexing the time cost resulting from the display of upper-case (‘‘WRITE’’) vs. lower-case (‘‘write’’) verbs; central stages were tracked by indexing the time cost resulting from the processing of abstract (‘‘think’’) vs. concrete (‘‘write’’) verbs; motor stages were tracked by indexing the time cost resulting from the programming of foot (pedal) vs. hand (button) responses. According to the PRP model, sound judgment should be delayed when verbs are more difficult to recognize (B) and to understand (C), whereas pressing a button or a pedal should not affect the initiation of sound judgment because response programming can proceed in parallel to a secondary task (D).

2.4. Data analysis

Analyses were performed on the median RTs after removing error trials (8%) and trials where the microphone failed to detect the verbal response (3%). Error trials included trials where participants gave an incorrect answer in one or both tasks. RTs refer to the delay between the verb display and the button/pedal response in the pri- mary task, and to the delay between the sound onset and the verbal response in the secondary task. Two participants were discarded from the analysis because their data showed that they did not follow the instructions that required to answer as fast as possible to the verb and then to the sound. One participant answered to the primary task several hundred milliseconds after the sound onset irre- spective of the SOA, whereas the other answered to the secondary task before the primary task in 54% of the trials. For similar reasons, trials where RTs to the primary task were higher than 1500 ms (<3%) and trials where the secondary task was performed first (<2%) were excluded from the analysis. A first ANOVA was conducted on the median RTs in verb judgments with case (lower vs. upper), imageability (concrete vs. abstract), response (button vs. pedal) and SOA (150 vs. 900 ms) as within-subject factors. The RTs measured in response to concrete verbs only were entered in a second ANOVA with verb meaning (hand- related vs. foot-related), response (button vs. pedal) and SOA (150 vs. 900 ms) as within-subject factors. In order to test the predictions of the PRP model, median RTs in sound judgments were analyzed as a function of the same factors as for the primary task. Planned comparisons between foot-related and hand-related verbs were per- formed separately for each response using one-tailed paired t-tests. Because comparisons were orthogonal and did not exceed the number of two, a was set at an uncor- rected level of .05 per comparison. Finally, we measured effect sizes in the two tasks in an interference (SOA 150 ms) or a non-interference regime (SOA 900 ms) by computing individual RT differences (dRTs) between: (1) upper and lowercase conditions; (2) abstract and concrete conditions; (3) incompatible and compatible trials; (4) pedal and button responses. For each effect, subjects (N = 14) were ranked according to the size of their dRTS in verb and sound judgments and the correlation between the two tasks was estimated separately for the interference and non-interference regime using Spearman's coefficient ($p < .05$).

3. Results

3.1. Primary task: verb judgments

There was no RT difference between the verb judg- ments performed in close proximity with the sound onset and those performed with a longer time asynchrony (765 ± 18 versus 778 ± 20 ms), confirming that participants answered to the primary task independently of the sound onset in the secondary task ($F(1, 13) = 2.94$, $p > .1$). Although lowercase words (769 ± 18 ms) were identified faster than uppercase words (774 ± 19 ms), the main effect of case was not significant ($F(1, 13) = 3.4$, $p > .09$). Abstract verbs (790 ± 20 ms) took more time to be processed than concrete verbs (753 ± 20 ms), as evidenced by the main effect of imageability ($F(1, 13) = 6.6$, $p < .02$). The response effect ($F(1, 13) = 60.7$, $p < .001$) showed that foot move- ments (814 ± 20 ms) were executed more slowly than hand movements (728 ± 18 ms). None of these effects interacted with the SOA (all p-values > .1).

In order to test the relationship between the meaning of

action verbs and the motor representations, we conducted a second ANOVA on the RTs gathered in response to con- crete verbs that could be hand- or foot-related. Results showed a main effect of verb meaning ($F(1, 13) = 5.3$, $p < .04$) and response ($F(1, 13) = 7.8$, $p < .02$) as well as an interaction between these two factors ($F(1, 13) = 19.4$, $p < .001$). As shown in Fig. 2, the two-way interaction revealed that participants pressed the button with their hand faster in response to hand- than foot-related verbs ($t(13) = 2.87$, $p < .01$), whereas foot-related verbs led to fas- ter pedal responses than hand-related verbs ($t(13) = 5.01$, $p < .001$). The verb meaning-response compatibility effect did not interact with the SOA ($F(1, 13) = 0.08$, $p > .8$). Over- all, foot-related verbs showed a 42 ± 8 ms advantage over hand-related verbs when the response involved a pedal press, whereas hand-related verbs showed a 25 ± 9 ms advantage over foot-related verbs when the response involved a button press; the verb meaning-response com- patibility effect was more pronounced for pedal than but- ton presses ($t(13) = 2.3$, $p < .05$).

3.2. Secondary task: sound judgments

The first ANOVA performed on sound judgments revealed a main effect of SOA ($F(1, 13) = 982$, $p < .001$) : RTs were longer for an SOA of 150 ms (1176 ± 38 ms) than for an SOA of 900 ms (648 ± 30 ms), indicating that the ini- tiation of the secondary task was delayed by the concur- rent processing of the verb in the primary task at the

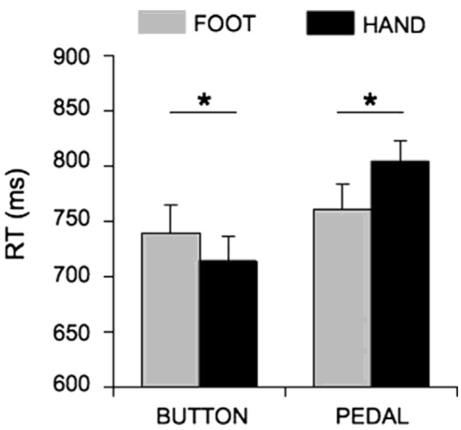


Fig. 2. Interaction between verb meaning and response effector during concrete verb judgments. Error bars show within-subject corrected standard errors (Loftus & Masson, 1994) and asterisks signal significant differences between conditions (⁄p < 0.05).

shortest SOA. Moreover, as predicted by the PRP model, this delay was influenced by the lexico-semantic process underlying response selection in verb judgments. Indeed, a significant interaction between imageability and SOA ($F(1, 13) = 5.5$, $p < .04$) showed that, when sounds and verbs were presented with an asynchrony of 150 ms, abstract verbs slowed down the initiation of sound judgments when compared to concrete verbs ($t(13) = 2.04$, $p < .05$). The relative time cost of abstract verb processing vanished when an SOA of 900 ms separated the two tasks ($t(13) = 1.07$, $p > .2$). Finally, sound judgments were faster after pressing a button (888 ± 32 ms) than after pressing a pedal (936 ± 35 ms; $F(1, 13) = 21.6$, $p < .001$) but, in con- trast with the imageability effect, this response effect was observed irrespective of the time elapsed between the verb and the sound onset ($F(1, 13) = 0.7$, $p > .4$). All other effects and interactions were not significant (all p-values > .1).

The second ANOVA aimed at testing the impact of the

verb meaning-response compatibility effect in trials where the sound was preceded by a concrete verb. Results showed a significant interaction between verb meaning and response ($F(1, 13) = 10.6$, $p < .006$) that was integrated in a three-way interaction with SOA ($F(1, 13) = 5.6$, $p < .04$). The three-way interaction indicated that, when the SOA was 150 ms, the delay induced by the incompatibility between the verb meaning and the response propagated to sound judgments ($F(1, 13) = 11.7$ $p < .005$). As illustrated in Fig. 3, the initiation of sound judgments was delayed when participants had to perform a button press in response to foot-related verbs when compared to hand- related verbs ($t(13) = 2.43$, $p < .015$), whereas verb meaning had the opposite effect in trials where sound judgments followed a pedal response ($t(13) = 2.20$, $p < .025$). Sound judgments were 45 ± 18 ms faster after pressing a button in response to hand-related verbs com- pared to foot-related verbs, whereas a 33 ± 15 ms advan- tage was observed after pressing the pedal in response to foot-related verbs compared to hand-related verbs. The

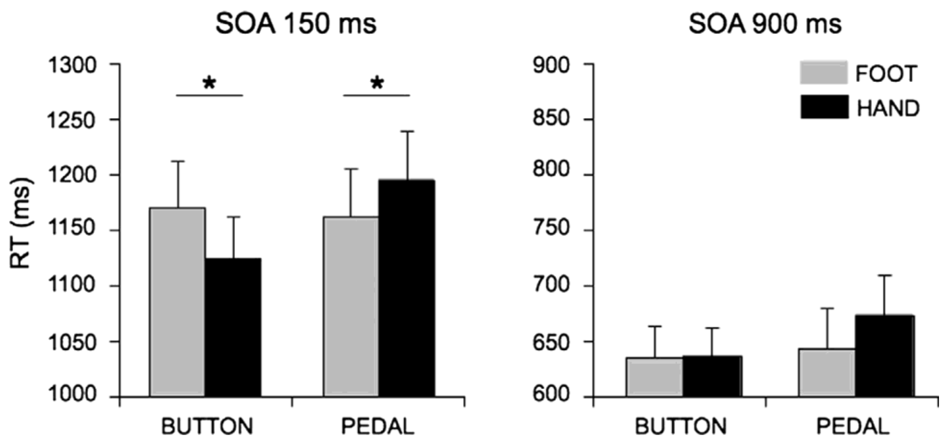


Fig. 3. Verb meaning-response compatibility effect observed in sound judgments following the presentation of concrete verbs in an interference (SOA 150 ms, left panel) or a non-interference regime (SOA 900 ms, right panel).

verb meaning-response compatibility effect had a similar impact on sound judgments whether the response required a button or a pedal press ($t(13) = .49, p > .63$). No compatibility effect was observed with an SOA of 900 ms ($F(1, 13) = 3.4, p > .09$).

3.3. Correlations between tasks

In the short SOA condition, a significant correlation for the case ($r = .66, t(13) = 3.09, p < .009$) and imageability effects ($r = .87, t(13) = 6.19, p < .001$) was found, indicating that, under an interference regime, the impact of linguistic manipulations on individual RTs in the primary task was predictive of individual differences in RTs in the secondary task (see Fig. 4). When the SOA was 900 ms, no correlation was observed between the estimates of the case effect ($r = .07, t(13) = .25, p > .8$), and the correlation between the estimates of the imageability effect was only marginal ($r = .53, t(13) = 2.1, p > .06$). Although previous analyses indicated that response execution did not interfere with the initiation of the secondary task, a weak correlation was found between the response effect when the two tasks were performed with a short SOA of 150 ms ($r = .62, t(13) = 2.72, p < .02$; see Fig. 4). Because this correlation might be influenced by the strength of the compatibility effect during action verb processing, we restricted the analysis to the trials where the sound was preceded by an abstract verb. In these trials, the correlation between the response effects measured in the two tasks did not exceed 0.21 ($t(13) = .74, p > .5$). Finally, individual esti- mates of the verb meaning-response compatibility effect correlated between tasks when the sound was presented 150 ms after the verb ($r = .73$, $t(13) = 3.72$, $p < .003$) but not when it was presented 900 ms later ($r = .46$; $t(13) = 1.77$, $p > .1$; see Fig. 4). When looking at the compat- ibility effect for each type of response effector separately, the correlation was slightly higher for button ($r = .75$, $t(13) = 3.92$, $p < .002$) than for pedal responses ($r = .51$, $t(13) = 2.04$, $p > 0.06$).

4. Discussion

The present study showed that semantic judgments about action verbs induce activation of body-part specific representations. A verb meaning-response compatibility effect demonstrated that hand-related verbs elicited faster hand responses than foot-related verbs, whereas the pro- cessing of foot-related verbs facilitated foot responses when compared to hand-related verbs. Results further indicate that motor representations are activated within the psychological refractory period, thus during the time window where participants are accessing the meaning of verbs and are deciding if they are concrete or abstract. This means that the motor activation induced by action verbs is not an epiphenomenon occurring only after participants have processed verb meaning, while they are executing their response.

Our paradigm required performing button or pedal

presses in response to concrete or abstract verbs and then to provide a distinct verbal response to low and high sounds. In the primary task, the SOA did not affect verb judgments, confirming that subjects answered as fast as possible irrespective of the sound presentation. Access to the semantic representation of abstract verbs was assumed to be more difficult because these verbs are less imageable than concrete verbs (Paivio, 1986). Results showed that lexico-semantic processing was indeed slower for abstract than concrete verbs. Moreover, response execution was slower with the foot than with the hand, reflecting longer conduction times for lower limb movements (Rothwell, 1997). We thought that manipulating the verb case would allow us to interfere with perceptual processes because letters are easier to discriminate in lowercase than in uppercase words (Perea & Rosa, 2002). In the present task, lowercase verbs were processed faster than uppercase verbs but the difference was not significant, probably due to the high automatization of upper-case reading in our highly educated subjects. Importantly, judgments of con- crete verbs were faster when the verb meaning and the motor response implied a movement of the same body

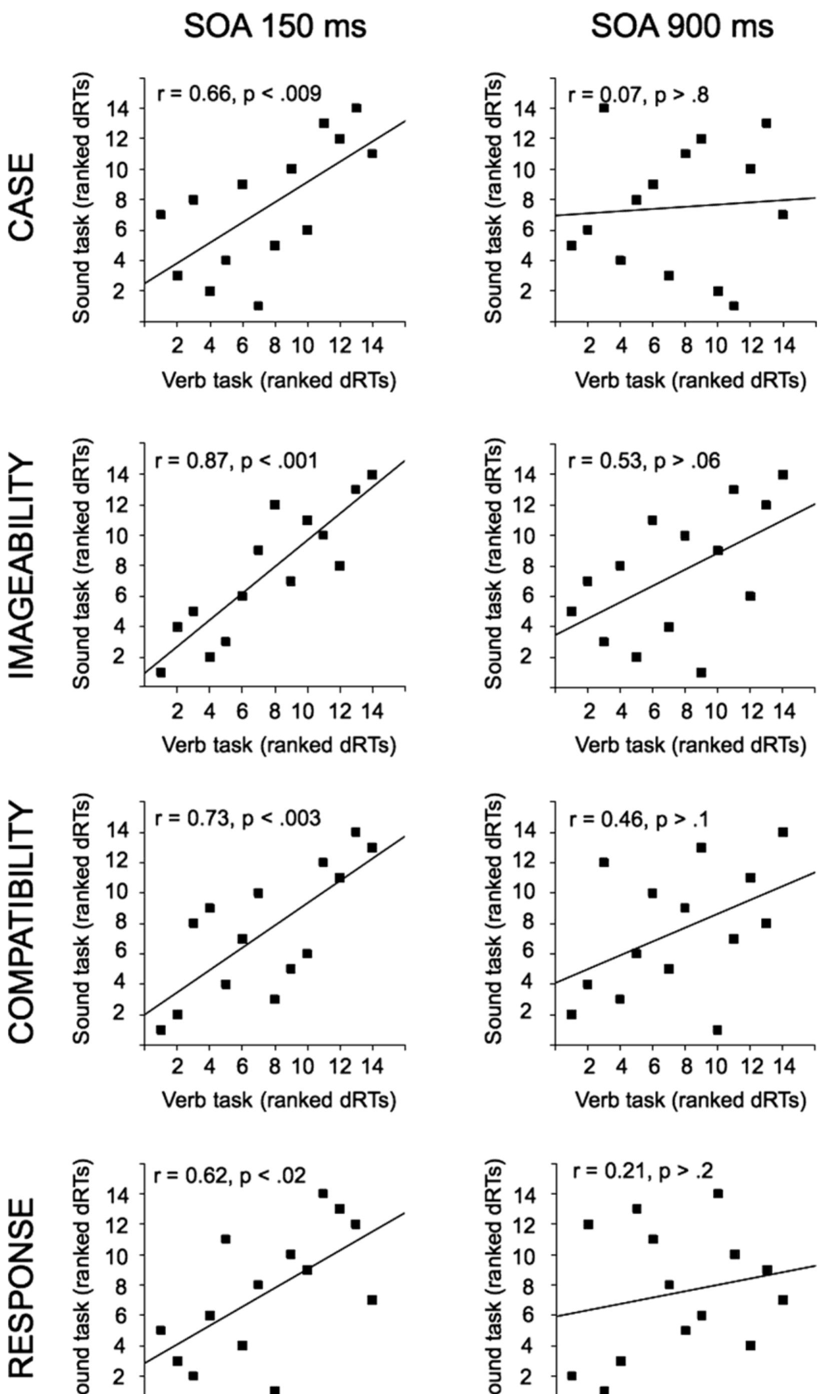

SOA 150 ms
SOA 900 ms
CASE
IMAGEABILITY
COMPATIBILITY
RESPONSE
r = 0.66, p < .009
r = 0.07, p > .8
r = 0.87, p < .001
r = 0.53, p > .06
r = 0.73, p < .003
r = 0.46, p > .1
r = 0.62, p < .02
r = 0.21, p > .2
Sound task (ranked dRTs)
Verb task (ranked dRTs)

Fig. 4. Relationship between the same effects measured in the two tasks in an interference (SOA 150 ms, left panel) or a non-interference regime (SOA 900 ms, right panel) for each participant. RT differences (dRTs) were computed individually to estimate the effect of case (uppercase vs. lowercase), imageability (abstract vs. concrete), verb meaning-response compatibility (incompatible vs. compatible), and response (pedal vs. button). In each graph, participants (N = 14) were ranked according to the size of their dRTS in verb judgments (X axis) and sound judgments (Y axis).

part. This verb meaning-response compatibility effect appeared slightly more pronounced for foot than hand responses (but only in the verb task and not in the sound task). The finding that action verb processing interacted more strongly with activation of foot than hand motor responses might indicate that sensorimotor experience is particularly important for understanding foot-related verbs. Pulvermüller, Hauk, et al. (2005) suggested that foot-related verbs are more dependent on motor represen- tations than other body-related verbs because lower-limb actions tend to be more similar to each other (e.g., walk, run and jog involve many of the same movements). Alternatively, our result might more simply reflect a floor effect in the quick hand response pattern.

In the secondary task, we found that sounds presented 150 ms after the verb display took more time to be dis- criminated than sounds presented 900 ms later. This delay reflects the PRP induced by the concurrent processing of verbs in the short SOA condition. In this condition, responses to the sounds were slower after abstract than concrete verb judgments, suggesting that sound discrimi- nation could not be initiated before a decision was reached about the semantic status of the verb. These results corrob- orate the idea that, during verb judgments, lexico-semantic processing constitutes a bottleneck that prevents the per- formance of the other task. Regarding the influence of the response effect in the secondary task, sounds were answered faster when they followed a verb that required a hand response rather than a foot response. However, this advantage was observed not only in the dual-task condi- tion but also in the control condition when the sound was presented 900 ms after the verb. Therefore, the propagation of this response effect is unlikely to reflect attentional limitations at the level of the bottleneck. The absence of interaction between response and SOA confirms that this effect arises outside the PRP, presumably at the level of motor execution. In line with recent electrophysi- ological results (Hauk & Pulvermüller, 2004; Hauk et al., 2008; Pulvermüller, 2005; Pulvermüller, Shtyrov, & Ilmoniemi, 2005; Pulvermüller et al., 2001; Shtyrov et al., 2004), it is possible that the frequent association of hand and mouth movements in speech facilitated the co-activa- tion of their motor programs, allowing faster vocal responses (required for sound judgments) after hand than foot movements (required for verb judgments), irrespec- tive of the SOA. The co-activation of hand and mouth movements is further corroborated by the spatial proxim- ity of their brain representation (Matelli & Luppino, 2001; Rizzolatti, Luppino & Matelli, 1988) and by the finding that CS excitability increases in hand – but not leg – muscles while reading aloud (Meister et al., 2003).

The crucial issue, in the present study, was whether the

verb meaning-response compatibility effect would propa- gate from the primary to the secondary task in dual-task trials. Under the assumption that motor activation accom- panies the lexico-semantic processes leading to response selection, the verb-response compatibility effect should affect sound judgments because the PRP predicts that the central response selection stage must be completed before another task can be initiated. Alternatively, if the verb- response compatibility effect is a by-product of an explicit mental imagery process emerging only at the response execution stage, then sound judgments should reveal equal RTs after compatible and incompatible trials because the conflict between the verb meaning and the response effector occurs outside the time window concerned by the PRP. The three-way interaction between verb meaning, response and SOA provides positive evidence for the assumption of verb meaning interference at the central response selection stage. When the verb meaning was incompatible with the effector selected to perform verb judgments, a delay was observed for sounds played imme- diately after the verb display, whereas this effect was absent at a larger SOA. This pattern of results clearly indi- cates that the verb-response compatibility effect propa- gates from the primary task to the secondary task, supporting the view that interference from verb meaning emerges at the central stage and can thus not be ascribed to a mental imagery process taking place at the response execution stage after the action concept has been identified. In order to strengthen our conclusions, we investigated whether propagation to the dual task was proportional to the effect size in the primary task. This analysis indicated that, in the short SOA condition, partic- ipants showing the largest effects of perceptual and semantic factors in the verb task were also the ones show- ing the largest effects in the sound task; in the long SOA condition, no correlation was observed, as predicted by the absence of interference between the two tasks. It is worth noting that, in the present paradigm, the effect of verb case was also expected to influence the discrimination of the forthcoming sound because word recognition is nec- essary for lexico-semantic processing. Although this effect was too small to reach significance in the ANOVA, its influ- ence on verb judgments was sufficient to be tracked in the sound task using correlation methods.

It could be argued that the time interval defined by the RT difference between sound judgments performed after a short (150 ms) and a long SOA (900 ms), which can be con- sidered as an estimate of the PRP duration, is sufficiently long to allow post-lexical imagery processes to take place during word judgment. However, in the present study, the PRP duration is not exclusively related to the central stage of the primary task: it may be shorter or longer, depending upon the relative duration of the perceptual stages of the two tasks. Thus, our paradigm does not allow to precisely defining the duration of the different process- ing stages. Independently from the exact temporal dura- tion of the PRP, the critical contribution of our paradigm comes from the fact that we can functionally separate cen- tral decision making from post-decision making stages of information processing. Our results show that motor inter- ference from verb meaning occurs during the central stage of lexical decision making, thereby excluding a mental imagery process that would take place during response execution after a decision has been made about the con- crete status of the verbs.

We cannot exclude that action verbs primed motor representations during the central response selection stage because of the task requirements but we believe that the experimental manipulation of the response effector was required to reveal such a subtle interaction between lan- guage and action at the behavioral level. The present study demonstrates a minima that, in the context of semantic judgments, action verbs activate motor representations during response selection and not as a consequence of response selection. Our results also converge with other results suggesting that motor activation induced by action verbs is an early and automatic process that cannot be explained by conscious processing of task requirements. Previous electrophysiological results showed that the motor content of action verbs influences frontal activity as early as 200 ms post-stimulus onset (Hauk & Pulvermüller, 2004; Hauk et al., 2008; Pulvermüller, 2005; Pulvermüller, Shtyrov et al., 2005, 2004). Kinematic studies showed a timely effect of action verbs on the prep- aration (Boulenger et al., 2006; Dalla Volta, Gianelli, Campione, & Gentilucci, 2009; Mirabella, Iaconelli, Spadacenta, Federico, & Gallese, 2012) or execution of reaching movements (Dalla Volta et al., 2009; Nazir et al., 2008), even when verbs were displayed subliminally (Boulenger, Silber, et al., 2008), evidencing a continuous and automatic crosstalk between language and action. Other chronometric studies used a go – no go paradigm to show that action verbs interfere with manual responses when they are processed in close temporal proximity with response production but these studies provided scarce evi- dence for a somatotopic activation given that only manual responses were tested (Marino, Gough, Gallese, Riggio, & Buccino, 2013; Sato, Mengarelli, Riggio, Gallese, & Buccino, 2008). More importantly, we knew there was an early activation of motor representations by action verbs in these studies but the functional locus of their interaction was unknown. The present study showed a crossed interaction between verb meaning (hand-related vs. foot- related) and response effector (hand vs. foot), providing indubitable evidence that the motor interference of action verbs follows the somatotopic organization of motor repre- sentations. Moreover, the use of the dual task allowed us to track the functional locus of this interference at the central response selection stage, thereby excluding a mental imag- ery process that would deploy during response execution after decision making.

Altogether, the present results rather suggest that motor activation induced by action verbs accompanies the lexico-semantic processes that lead to response selec- tion. At the brain level, such an account of the verb-effector compatibility effect implies that hand and foot motor rep- resentations should be distinctively activated while read- ing action verbs. As mentioned in the Introduction, several studies showed that the frontal activation induced by foot, hand or mouth-related verbs follows a medial-to- lateral gradient reminiscent of the motor homunculus (Aziz-Zadeh et al., 2006; Boulenger et al., 2009; Hauk et al., 2004; Pulvermüller et al., 2001; Tettamanti et al., 2005). However, a recent study showed that these activa- tions lie mainly in higher-order premotor areas that repre- sent information in a more abstract format than the primary motor areas (Postle et al., 2008). This was taken as evidence that the resources shared by motor control and verb processing are unrelated to bodily experience (Bedny & Caramazza, 2011). Whatever the exact neural substrate of the reported sensorimotor compatibility effect, the present study demonstrates that the motor knowledge involved in action verb processing includes some information about the body part associated with the action. A speculative account for the inconsistencies across the different published fMRI studies is that action verb reading could be accompanied by an inhibition of the motor cortex to prevent action execution, making motor activity more difficult to detect with conventional fMRI analysis methods. This view fits with the repetitive involvement of the pre-supplementary motor area (SMA) while deciphering the meaning of action verbs (Postle et al., 2008; Willems et al., 2010). Indeed, this area is known to play a role in controlling the release of an action by the primary motor cortex (Forstmann et al., 2008; Neubert, Mars, Buch, Olivier, & Rushworth, 2010).

A review of fMRI studies suggests that somatotopic acti- vation is more obvious during sentence comprehension (Aziz-Zadeh et al., 2006) than during word comprehension (Postle et al., 2008). This observation has led to the assumption that motor representations may contribute to the building of detailed situation models rather than verb comprehension itself (Bedny & Caramazza, 2011). Our results go against this idea because the verb-response compatibility effect was observed in semantic judgments that do not require a contextualized representation of the action. The compatibility effect reported here rather evi- dences fast and automatic interactions between lexical entries and motor representations. It should be noted, however, that our results do not imply that the semantic content of action verbs is solely dependent on motor repre- sentations. Other non-motor knowledge is also activated as part of the semantic representation of action verbs because it has been shown that lesions of the motor system only have moderate effects on lexico-semantic processing of action verbs (Arévalo, Baldo, & Dronkers, 2010; Boulenger, Mechtouff, et al., 2008; Papeo, Negri, Zadini, & Rumiati, 2010).

5. Conclusion

We used the PRP as a tool to parcel out perceptual, cen- tral and motor stages in verb judgments. Participants were asked to judge hand- and foot-related verbs in a dual-task context. Results provided unambiguous evidence for a verb meaning – response effector compatibility effect while judging action verbs. As predicted by the PRP, we found that lexico-semantic processing, but not response execu- tion, influenced the initiation of sound judgments per- formed as a dual task. The verb-response compatibility effect also affected the initiation of the dual task, indicating that the motor interference of verb meaning cannot be ascribed to a mental imagery process taking place at the response execution stage after the action concept has been identified.

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