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Contribution of motor representations to action verb processing

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ABSTRACT

Electrophysiological and brain imaging studies show a somatotopic activation of the premotor 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 representations. However, discrepancies in the literature led to the alternative hypothesis that motor representations are activated during the course of a mental imagery process emerging 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 evidence 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 somatotopically 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

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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 movements 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 generation 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 during 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). However, 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 provides 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 during 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 mapping 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 concrete 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 presence or absence of a time cost in sound judgment thus indicates whether the processes at work during verb judgment 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) advantage 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 imageable than abstract ones (Paivio, 1986). Finally, and crucially, 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 compatibility effect. A compatibility effect emerging during the central stage would indicate that the motor representations 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 emerging during the motor stage would indicate that the motor representations associated with action verbs are activated