

**Neural dissociations between action verb understanding  
and motor imagery**

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10 **Neural dissociations between action verb**  
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13 **understanding and motor imagery**  
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57 **Keywords:** Semantics; Embodied cognition; Imagery; Simulation; fMRI  
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## Abstract

According to embodied theories of language, people understand a verb like *throw*, at least in part, by mentally simulating *throwing*. This implicit simulation is often assumed to be similar or identical to motor imagery. Here we used fMRI to test whether implicit simulations of actions during language understanding involve the same cortical motor regions as explicit motor imagery. Healthy participants were presented with verbs related to hand actions (e.g. *to throw*) and non-manual actions (e.g. *to kneel*). They either read these verbs (lexical decision task) or actively imagined performing the actions named by the verbs (imagery task). Primary motor cortex showed effector-specific activation during imagery, but not during lexical decision. Parts of premotor cortex distinguished manual from non-manual actions during both lexical decision and imagery, but there was no overlap or correlation between regions activated during the two tasks. These dissociations suggest that implicit simulation and explicit imagery cued by action verbs may involve different types of motor representations, and that the construct of ‘mental simulation’ should be distinguished from ‘mental imagery’ in embodied theories of language.

## Introduction

According to embodied theories of semantics, we use our motor system to understand language about actions. For instance, upon reading *'he throws the ball'*, embodied accounts postulate that the reader mentally simulates this action, using some of the same motor areas that are activated when executing actual throwing (e.g. Pulvermuller, 2005). Implicit simulation during language understanding is often assumed to be the same as explicitly imagining linguistic content. As Gallese and Lakoff put forward, "the same neural substrate used in imagining is used in understanding" (Gallese & Lakoff, 2005, p. 456). They argue that imagination is necessary to understand action-related sentences such as "Harry picked up the glass," and write that "if you can't imagine picking up a glass or seeing someone picking up a glass, then you can't understand that sentence" (ibid, p. 456). Here we aim to directly test and refine the relationship between imagining actions and understanding action language.

Several neuroimaging studies support the conjecture that motor areas play some role in understanding action verbs. For instance, Hauk and colleagues found overlap in premotor cortex between movement of foot and fingers and during reading of foot- or hand-related action verbs (e.g. 'kick', 'pick') (Hauk, Johnsrude, & Pulvermuller, 2004). Likewise, areas in premotor cortex activated during observation of actions done with different effectors, are also activated upon reading of sentences describing these actions (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; see also Boulenger, Hauk, & Pulvermuller, 2008; Raposo, Moss, Stamatakis, & Tyler, 2009; Tettamanti et al., 2005, but see Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008; Sato, Mengarelli, Riggio, Gallese, & Buccino, 2008). From these and other findings it has been concluded that understanding action language involves activating parts of premotor cortex in a somatotopic way, as is also observed during motor

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3 control (e.g. Woolsey, 1963). This is to be expected if understanding action language  
4 involves implicitly simulating an action (see Aziz-Zadeh & Damasio, 2008;  
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6 Kemmerer & Gonzalez-Castillo, 2008; Mahon & Caramazza, 2008; Pulvermuller,  
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8 2005; Willems & Hagoort, 2007 for reviews).

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12 **In addition to supporting action word understanding, a host of studies**  
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14 implicate premotor cortex in supporting motor imagery of hand movements (e.g.  
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16 Bonda, Petrides, Frey, & Evans, 1995; Cisek & Kalaska, 2004; de Lange, Hagoort, &  
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18 Toni, 2005; de Lange, Helmich, & Toni, 2006; Gerardin et al., 2000; Helmich, de  
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20 Lange, Bloem, & Toni, 2007; Johnson et al., 2002). Yet, the relationship between the  
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22 premotor cortex correlates of motor imagery and action language understanding is not  
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24 well understood.  
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29 In this study we aimed to elucidate the relationship between motor imagery  
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31 and action semantics by directly comparing neural activity during action verb  
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33 understanding with activity during explicit mental imagery of actions cued by the  
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35 same verbs. In one fMRI run, participants performed a lexical decision task on action  
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37 verbs, and in a second run they actively imagined performing the actions described by  
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39 these verbs. To gain specificity of neural responses and for reasons of experimental  
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41 control (see methods), we contrasted action verbs related to hand actions (e.g. *to*  
42  
43 *throw*) with non-manual action verbs (e.g. *to kneel*).  
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49 Gallese and Lakoff's (2005) conjecture makes the clear prediction that  
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51 understanding an action verb and imagining performing that same action should rely  
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53 on the same neural tissue, most notably premotor cortex. This finding would be in line  
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55 with the idea that through Hebbian learning, cell assemblies of neurons firing together  
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57 during execution and observation of actions come to constitute the semantic  
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59 representation of an action verb (Pulvermuller, 2005). Alternatively, it is possible that  
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non-overlapping parts of motor areas are activated both when we read action verbs

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3 and during explicit motor imagery. This finding would require a refinement to  
4 theories of embodied semantics, suggesting that activation of the motor system during  
5 action verb understanding should be distinguished from motor imagery.  
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10 **Before we move on to describing the experiment we will first clarify what**  
11 **we mean by simulation and by imagery. Implicit motor simulations are often**  
12 **characterized as partial re-enactments of prior actions (e.g., Barsalou, 1999;**  
13 **2009). However, the computational function that such re-enactments could serve**  
14 **is not clear. When we use the term simulation in this paper, we do not refer to a**  
15 **re-enactment of prior experiences, which seem functionally unmotivated. Rather,**  
16 **we posit that motor simulations are *pre-enactments* of potential future**  
17 **experiences. A word like *grasp* can serve as a cue to activate neural circuits**  
18 **involved in partial preparation for *grasping* (see Barsalou, 2009; Zwaan, 2004 for**  
19 **compatible proposals). This schematic, unconscious, prospective activation of**  
20 **effector-specific regions in premotor cortex presumably facilitates further action**  
21 **planning if subsequent cues call for *grasping* to be executed, or to be imagined**  
22 **explicitly.**  
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41 **Motor imagery, by contrast, can be understood as covert enactment of an**  
42 **action. Like overt motor execution, motor imagery may entail the generation of**  
43 **an action plan (inverse model) as well as a prediction of the action' sensory**  
44 **consequences (forward model) (e.g. Grush, 2004; Wolpert & Ghahramani, 2000).**  
45 **The generation of the forward model can be described as a kind of simulation**  
46 **but this is not the way we use the term here.**  
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## 57 **Methods**

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59 *Subjects* We tested twenty healthy participants (14 female; mean age 22.7 y, range 19-  
60 28) with no known history of neurological problems, dyslexia or other language-

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3 related problems, or hearing complaints, and with normal or corrected-to-normal  
4 vision. All participants were right-handed (Oldfield, 1971; mean EHI: 97, range 82 -  
5 100) and gave written informed consent in accordance with the declaration of  
6 Helsinki. The study was approved by the local ethics committee.  
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15 *Materials* Stimuli were 96 Dutch verbs expressing concrete actions. Half of these  
16 were related to manual actions (MAN), half of them were not related to manual  
17 actions (NONMAN). This distinction was pretested with a larger number of verbs, in  
18 a group of raters who did not participate in the fMRI experiment (N=16), who scored  
19 for each verb how much they associated that action with their hand(s), and, if  
20 applicable whether they preferred to act out the action with their left, right or with  
21 both hands. MAN words were significantly more associated with hand actions than  
22 NONMAN words ( $t(94)=23.60$ ,  $p<0.001$ ). On average 79% of raters indicated that  
23 they tend to perform the action with their dominant hand (s.d.=11.8%, median=81%;  
24 mode=88%), that is, unimanually. MAN and NONMAN word lists did not differ in  
25 imageability (assessed by the same group of raters) ( $t(94)<1$ ), number of phonemes  
26 ( $t(94)<1$ ), lexical frequency (taken from the CELEX database (Baayen, Piepenbrock,  
27 & Rijn, 1993);  $t(94)<1$ ) and number of letters ( $t(94)=1.51$ ,  $p=0.13$ ). From the  
28 materials that were rejected on the basis of the pretest, 16 filler items were created.  
29 Additionally, 16 phonotactically legal non-words were created, all with the suffix  
30 typical of the regular infinitive form in Dutch ('-en').  
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55 *Experimental procedure* Stimuli were presented using Presentation software  
56 (www.nbs.com, version 10.2) through a projector from outside of the scanner room  
57 onto a screen at the back of the scanner bore and were visible to the participants  
58 through a mirror attached to the head coil. There were two separate task runs: Lexical  
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3 Decision (LD) and Imagery (IM) (Fig. 1). In the LD run participants were instructed  
4 to indicate as quickly and accurately as possible whether a word was an existing word  
5 or not **on** 25% of the trials (fillers and non-words). After presentation of fillers and  
6 non-words, participants saw a response screen with the question whether the previous  
7 word was an existing word with answer options ‘yes’ and ‘no’ on the left or right side  
8 of the screen, which could be indicated by pressing a button with the left or right  
9 index finger. Response side was non-predictably balanced across trials to prevent a  
10 biased motor response to the left or right hand. Participants had 1500 ms to respond  
11 and got feedback on the screen when they were too slow. A stimulus list of 128  
12 stimuli (48 MAN + 48 NONMAN + 16 fillers + 16 nonwords) was created, and  
13 pseudo-randomized with the constraint that the same condition was not repeated more  
14 than three times in a row. A mirrored version of this list was presented to half of the  
15 participants. Participants were familiarized with the procedure by means of 10  
16 practice items containing different words than used in the remainder of the  
17 experiment.

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20 In the IM run, the same words (except for filler and non-words, which means  
21 that there were 96 trials) were presented and participants were instructed to read the  
22 word, close their eyes, imagine performing the action and open their eyes to indicate  
23 that they had finished motor imagery. Closing and opening of the eyes was monitored  
24 by an infrared IviewX eyetracker ([www.smi.de](http://www.smi.de)) with custom-built shielding, and  
25 coded on-line by one of the experimenters. **We used opening and closing of the eyes**  
26 **to be able to measure imaging time on each trial while at the same time avoiding**  
27 **hand action interference from button presses. Performing motor imagery with**  
28 **eyes closed probably entails similar processes as motor imagery with eyes open**  
29 **(Heremans, Helsen, & Feys, 2008) and has been successfully used before in**  
30 **neuroimaging studies (Szameitat, Shen, & Sterr, 2007a, 2007b; Bakker et al.,**



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3 **2008**). A stimulus list of 96 stimuli (MAN and NONMAN words) was created,  
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5 pseudo-randomized with the constraint that the same condition was not repeated more  
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7 than three times in a row. A mirrored version of this list was presented to half of the  
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9 participants. Participants were familiarized with the procedure by means of 10  
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11 practice items containing different words than used in the remainder of the  
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13 experiment.  
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17 Stimuli were presented for 1500 msec and stimulus onset was effectively jittered  
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19 with respect to onset of volume acquisition by varying the intertrial interval between 2  
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21 and 6 seconds (mean=4 sec.) in steps of 250 ms (Dale, 1999) in both runs. A fixation  
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23 cross (250 ms) indicated the start of a new trial. The LD run always preceded the IM  
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25 run, to prevent a bias for participants to engage in motor imagery during the LD run.  
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29 **Finally at the end of the session participants engaged in an action execution**  
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31 **localizer in which they performed simple hand movements (opening and closing**  
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33 **of the hand) with either the left or the right hand. The localizer was a blocked**  
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35 **design and participants were cued to perform actions with the left or the right**  
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37 **hand by means of the words 'left' or 'right' presented on the screen. Each block**  
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39 **lasted 15 seconds and there were 8 blocks per condition. These action execution**  
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41 **blocks were intermingled with five rest blocks of the same duration in which**  
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43 **participants did not execute hand actions. Compliance with the task was checked**  
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45 **visually from outside of the scanner room.**  
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52 *Data acquisition and analysis* Echo-Planar Images (EPI) covering the whole brain  
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54 were acquired with a 8 channel head coil on a Siemens MR system with 3T magnetic  
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56 field strength (TR=2060 ms; TE=30 ms; flip angle 85°, 31 transversal slices; voxel  
57  
58 size 3.5x3.5x3 mm, 0.5 mm gap between slices). Data analysis was done using SPM5  
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60 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm5/>). Preprocessing involved

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3 realignment through rigid body registration to correct for head motion, slice timing  
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5 correction to the onset of the first slice, normalization to Montreal Neurological  
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7 Institute (MNI) space, interpolation of voxel sizes to 2x2x2 mm, and spatial  
8  
9 smoothing (8 mm FWHM kernel). First-level analysis involved a multiple regression  
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11 analysis with regressors describing the expected hemodynamic responses during  
12  
13 observation of MAN words, NONMAN words as well as fillers words and non-words  
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15 (fillers and non-words in the LD run only). Responses (button presses) were modeled  
16  
17 separately as stick functions. Stimuli in the LD run were modeled with 1500 ms  
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19 duration, in the IM run the actual imagining times were used. MR disturbances due to  
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21 small head movements were accounted for by a series of nuisance regressors, namely  
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23 the linear and exponential changes in the scan-by-scan estimated head motion, scan-  
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25 by-scan average signals from outside the brain, white matter, and cerebro-spinal fluid  
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27 (Verhagen, Grol, Dijkerman, & Toni, 2006). **Stimuli in the action execution**  
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29 **localizer were modeled as blocks of 15 seconds. The same nuisance regressors as**  
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31 **described above were included.**  
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39 A second-level whole brain group analysis with subjects as a random factor  
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41 ('random effects analysis') was carried out. First, we tested which regions were  
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43 activated by MAN as well as NONMAN words during each task in isolation. This  
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45 was done by means of conjunction analyses testing the conjunction null as defined by  
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47 Nichols and colleagues (Nichols, Brett, Andersson, Wager, & Poline, 2005), testing  
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49 for  $LD_{MAN} > 0 \cap LD_{NONMAN} > 0$  and for  $IM_{MAN} > 0 \cap IM_{NONMAN} > 0$ . Second, we looked  
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51 for regions which were more strongly activated to the MAN > NONMAN comparison  
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53 in either task (i.e.  $LD_{MAN > NONMAN} / IM_{MAN > NONMAN}$ ). This is a much more specific  
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55 analysis which asks whether there are areas during LD or IM, which are sensitive to  
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57 the effector with which an action is typically associated. Finally, the crucial analysis  
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59 involved looking for regions sensitive to MAN > NONMAN comparison in both tasks  
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3 by doing a conjunction analysis ( $LD_{MAN>NONMAN} \cap IM_{MAN>NONMAN}$ ), again testing the  
4 conjunction null hypothesis (Nichols et al., 2005). Correction for multiple  
5 comparisons was applied by thresholding group maps at  $p < 0.005$  uncorrected and  
6 subsequently taking the cluster extent into account by using the theory of Gaussian  
7 Random Fields (Friston, Holmes, Poline, Price, & Frith, 1996) to correct maps at  
8  $p < 0.05$  corrected for multiple comparisons (Poline, Worsley, Evans, & Friston, 1997).  
9  
10 Subsequently, in regions activated in the whole brain analysis to  $MAN > NONMAN$  in  
11 the one task, it was tested whether a comparable effect was present in the other task.  
12 We took the mean parameter estimates from areas activated to  $LD_{MAN>NONMAN}$  in the  
13 whole brain analysis and tested whether there was an  $IM_{MAN>NONMAN}$  effect in these  
14 areas, and vice versa.  
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29 For the main analysis, we created subject-specific regions of interest (ROIs) in  
30 which we selected voxels from cytoarchitecturally defined left Brodmann Area  
31 (BA) 6 (i.e. premotor cortex) (Eickhoff et al., 2005) and left BA4 (primary motor  
32 cortex, combining maps 4a and 4p (Geyer et al., 1996)). We choose BA6 and BA4  
33 since these have been implicated in action verb reading as well as in motor imagery  
34 (see Munzert, Lorey, & Zentgraf, 2009; Willems & Hagoort, 2007 for reviews). For  
35 each participant, voxels that were sensitive to the  $MAN > NONMAN$  contrast ( $p < 0.05$   
36 uncorrected) separately for the IM run and for the LD run were selected using the  
37 Marsbar toolbox (Brett, Anton, Valabregue, & Poline, 2002). Subsequently, we tested  
38 whether a  $MAN > NONMAN$  effect was also present in the data from the other run.  
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40 The rationale for this analysis was that we selected for every subject the voxels that  
41 were most sensitive to the  $MAN > NONMAN$  contrast in one task and subsequently  
42 tested whether there was a similar effect in the other task. **This is to be expected if**  
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60 **LD and IM lead to overlapping neural correlates.**

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In another subject-specific ROI analysis we tested for a MAN>NONMAN effect in left BA6/BA4 for the LD and IM run separately. **For this analysis we used a split-half approach, splitting the data in odd- and even-numbered trials<sup>1</sup>. First we created subject-specific 4mm spherical regions of interest around the maximally activated voxel in left BA6/BA4 in response to MAN words (thresholded at  $p < 0.001$ ). This ROI creation was based on half of the data (odd trials). Second we extracted contrast values for the MAN>NONMAN contrast from these ROIs, using the other half of the data (even trials)<sup>2</sup>. MAN>NONMAN contrast values were extracted for each participant and group statistics were performed by means of one-sample t-test on these contrast values. With this analysis it was ensured that ROI creation involved different data than the data in which we subsequently tested for a MAN>NONMAN effect. This procedure was repeated for the LD and IM runs separately.** The rationale for this analysis was to test whether BA6 and BA4 were sensitive to the MAN>NONMAN comparison in each run in isolation. We have employed this subject-specific ROIs procedure before (Willems, Hagoort, & Casasanto, in press), and found it to be more sensitive as compared to standard whole brain analysis (see also Aziz-Zadeh et al., 2006).

Finally, we performed multi-voxel pattern analysis (Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Peelen, Wiggett, & Downing, 2006) on the voxels from left BA6 and from left BA4 separately. In multi-voxel pattern analysis, the pattern of responses across voxels in a given area is taken into account instead of statistically thresholding voxels. **The rationale of this analysis is that if two conditions lead to a similar spatial pattern of responses in a given region, the activations across voxels in that region should be correlated between the two conditions. Imagine all voxels from left BA6 as a vector in which each value represent one voxel's contrast value on the MAN>NONMAN contrast. What we did is construct two**

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3 such vectors, one for  $LD_{MAN>NONMAN}$  and one for  $IM_{MAN>NONMAN}$ . Subsequently  
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5 the correlation coefficient between these two vectors was computed for each  
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7 participant separately. The correlation coefficients were converted to Fisher's  $z$   
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9 to comply with the normality assumption (Kleinbaum, Kupper, Muller, &  
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11 Nizam, 1998), and tested for a difference from mean zero in a one-sample  $t$ -test  
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13 (see Downing et al., 2006; Peelen et al., 2006 for a comparable approach). If  
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15  $MAN>NONMAN$  during LD and during IM lead to similar response patterns in  
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17 BA6/BA4, we expect to find high correlations in this analysis.

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22 Multi-voxel pattern analysis also allowed us to investigate the internal  
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24 consistency of patterns of activation *within* one run. Using a split half approach  
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26 we investigated whether the pattern of response in BA6/BA4 for  
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28  $MAN>NONMAN$  was the same for each half of the data in each task setting.  
29  
30 Thus we correlated patterns of voxels in BA6/BA4  $LD_{MAN>NONMAN}$  from odd-  
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32 numbered trials with the activation pattern during  $LD_{MAN>NONMAN}$  from even-  
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34 numbered trials. This was similarly done for the IM data. If the pattern of  
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36 responses in BA6/BA4 is robust and stable, we expect high correlations between  
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38 the  $MAN>NONMAN$  contrast values from the one half of the data as compared  
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40 to the other half of the data. We choose to not perform pattern correlation  
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42 analysis on unsmoothed data because of the spatial normalization procedure  
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44 which is inherently imperfect across sessions. The danger with unsmoothed data  
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46 is that correlations are artificially lower in across-session comparisons as  
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48 compared to within-session comparisons due to imperfect normalization. Spatial  
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50 smoothing essentially eliminates that problem and we therefore conducted the  
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52 correlation analysis on spatially smoothed data.  
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We never compared a single condition directly between the two tasks (e.g.  
 $LD_{MAN>IM_{MAN}}$ ), given the interpretational problems arising from a direct comparison

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3 between tasks with different trial durations and occurring in different scanning runs  
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5 (McGonigle et al., 2000). **Furthermore, given the heterogeneity of effectors**  
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7 **involved in the NONMAN trials, we did not contrast NONMAN>MAN.**  
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10 **The results from the action execution localizer task were used to**  
11 **investigate whether ROIs defined in the LD or IM data, were also activated**  
12 **during actual hand action execution. For this end we extracted contrast values to**  
13 **the Right hand>Rest comparison from the ROIs described above and**  
14 **statistically tested them in a one-sample one-sided t-test against mean zero.**  
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## 25 **Results**

### 26 Behavioral

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28 *Lexical decision* Participants answered correctly to the lexical decision catch trials in  
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30 the large majority of trials (mean=95.8%, s.d.=3.5%; range 87.5%-100%). There were  
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32 few incorrect responses (mean=3.9%, s.d.=3.64, range 0%-9.4%) and misses  
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34 (mean=0.3%, s.d.=0.99%, range 0%-3.1%)  
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41 *Imagery* Participants on average took 5.6 seconds (s.d.=1.79) to imagine doing the  
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43 MAN actions, compared to 5.5 seconds (s.d.=1.67) to imagine the NONMAN actions.  
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45 This difference was not statistically significant ( $t(19) < 1$ ).  
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### 50 Neural

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52 **For technical reasons in one subject no action execution localizer was measured.**  
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54 **Moreover, because of excessive head motion the action execution data from one**  
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56 **other participant were not analyzed. This means that 18 data sets entered the**  
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58 **analysis for the action execution localizer. The analysis of LD and IM data**  
59  
60 **involved data from all 20 participants. Head movement never exceeded 2mm or**

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3 **2 degrees in any rotation or translation in any of the runs which were included in**  
4 **the analysis.**  
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10 *Whole brain analysis* We performed exploratory whole-brain analysis, testing for  
11 task-specific activations as well as for overlap in response patterns between the lexical  
12 decision and imagery tasks. First, activations to reading of MAN and NONMAN  
13 words was compared to baseline in the LD run ( $LD_{MAN>0} \cap LD_{NONMAN>0}$ ). This  
14 comparison led to wide-spread overlapping activations in bilateral precentral sulci and  
15 inferior frontal gyri, bilateral superior and inferior parietal sulci, **bilateral superior**  
16 **and middle temporal sulci**, bilateral inferior occipital and calcarine sulci and left  
17 anterior cingulate sulcus and left hippocampus (Fig. 2A; Table 1). A similar activation  
18 pattern was observed for this analysis in the IM data ( $IM_{MAN>0} \cap IM_{NONMAN>0}$ ),  
19 encompassing bilateral inferior frontal gyri, bilateral precentral sulci, bilateral central  
20 sulci, bilateral anterior cingulate sulci, bilateral calcarine / inferior occipital sulci,  
21 bilateral middle and superior temporal gyri and bilateral cerebellum (Fig. 2B; Table  
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41 Second, comparing the MAN>NONMAN conditions in the LD task  
42 ( $LD_{MAN>NONMAN}$ ) led to increased activation in left superior frontal sulcus (Fig. 3;  
43 Table 2). The same comparison in the IM task ( $IM_{MAN>NONMAN}$ ) revealed increased  
44 activation levels in left dorsal precentral sulcus stretching into middle frontal sulcus,  
45 left central and postcentral sulcus, and left inferior temporal sulcus (Fig. 3; Table 2).  
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51 To confirm the specificity of the response in each of these areas, we computed the  
52 MAN>NONMAN contrast **for the other task in the areas activated in the whole**  
53 **brain analysis to MAN>NONMAN either in the LD task or in the IM task. Put**  
54 **differently in the areas showing  $IM_{MAN>NONMAN}$  in the whole brain analysis we**  
55 **tested whether a  $LD_{MAN>NONMAN}$  effect was similarly present. Similarly, in the**  
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3 one area showing an  $LD_{MAN>NONMAN}$  effect in the whole brain analysis we tested  
4 whether a  $MAN>NONMAN$  effect was also present during the IM task. The  
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6 results confirm that these areas are not sensitive to the  $MAN>NONMAN$   
7  
8 contrast from the other task (see parameter estimates in Fig. 3). That is, if an  
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10 area was sensitive to  $MAN>NONMAN$  in the IM task, it did not show a  
11  
12  $MAN>NONMAN$  effect in the LD task (Fig. 3). Of the areas showing a  
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14  $MAN>NONMAN$  effect in the whole brain analysis (Fig. 3), all but the left  
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16 superior frontal sulcus activation cluster were significantly activated during  
17  
18 action execution (LD area superior frontal sulcus:  $t(17)=-1.89$ ,  $p=0.074$ ; IM area  
19  
20 dorsal precentral sulcus:  $t(17)=2.39$ ,  $p=0.028$ ; IM area left central / postcentral  
21  
22 sulcus:  $t(17)=6.85$ ,  $p<0.001$ ; IM area left inferior temporal sulcus:  $t(17)=2.86$ ,  
23  
24  $p=0.010$ ).

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26  
27 Finally, there were no clusters showing overlapping responses across the two  
28  
29 tasks ( $LD_{MAN>NONMAN} \cap IM_{MAN>NONMAN}$ ), even at a very lenient statistical threshold  
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31 ( $p<0.01$  uncorrected).

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34 *Subject-specific regions of interest analysis* Our main analyses compared effector-  
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36 specific activation during the two tasks (i.e.  $LD_{MAN>NONMAN}$  and  $IM_{MAN>NONMAN}$ ) in  
37  
38 subject-specific regions of interest in left BA6 and left BA4. Consistent with the  
39  
40 whole-brain analysis, these ROI analyses also showed no overlap in effector-specific  
41  
42 response patterns across the two tasks. **In this analysis subject-specific ROIs**  
43  
44 **consisted of voxels sensitive to  $MAN>NONMAN$  in the one task session and we**  
45  
46 **subsequently tested for a  $MAN>NONMAN$  effect in the other task session.**  
47  
48 **Voxels were thresholded at  $p<0.05$  uncorrected to increase chances of finding**  
49  
50 **overlap between  $LD_{MAN>NONMAN}$  and  $IM_{MAN>NONMAN}$ . If IM and LD lead to**  
51  
52 **overlapping neural correlates, we should observe  $IM_{MAN>NONMAN}$  effects in ROIs**  
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3 based upon  $LD_{MAN>NONMAN}$  and vice versa. Note that creating ROIs based upon  
4  
5  $IM_{MAN>NONMAN}$  and subsequently testing for this same effect ( $IM_{MAN>NONMAN}$ ) is a  
6  
7  
8 biased measure leading to significant but uninformative results due to  
9  
10  
11 'overfitting' (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009). We hence do  
12  
13 not report the results of such comparisons.

14  
15 The left BA6 ROIs taken from the IM task (subject-specific voxels sensitive to  
16  
17  $IM_{MAN>NONMAN}$  at  $p < 0.05$  uncorrected) were not sensitive to the  $LD_{MAN>NONMAN}$   
18  
19 contrast ( $t(19) = -1.83$ ,  $p = 0.082$ , note negative t-value). Conversely, taking the BA6  
20  
21 ROIs from the voxels activated to the  $LD_{MAN>NONMAN}$  contrast revealed that there was  
22  
23 no such effect for  $IM_{MAN>NONMAN}$  ( $t < 1$ ). A similar pattern of responses was observed  
24  
25 in subject-specific ROIs in left BA4. The ROIs taken from the  $IM_{MAN>NONMAN}$   
26  
27 contrast showed no  $LD_{MAN>NONMAN}$  effect ( $t(19) = -1.62$ ,  $p = 0.12$ , note negative t-  
28  
29 value). The ROIs taken from the  $LD_{MAN>NONMAN}$  contrast revealed no  $IM_{MAN>NONMAN}$   
30  
31 effect ( $t(19) < 1$ ).  
32  
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36 To gain better insight into the differential localization of parts of left BA6 and  
37  
38 left BA4 sensitive to  $LD_{MAN>NONMAN}$  and  $IM_{MAN>NONMAN}$ , we extracted the  
39  
40 coordinates of the maximally activated voxel from each subject-specific ROI (Fig. 4).  
41  
42 The mean coordinates for the BA6 LD ROIs were (MNI [-22 -5 56], s.d. [19 16 13]),  
43  
44 and for the BA6 IM ROIs ([-34 -5 52], s.d. [17 10 16]). For the BA4 LD ROIs ([-20 -  
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46 29 58, s.d.: [17 13 14]), and for the BA4 IM ROIs ([-30 -23 50, s.d. [18 17 16]). In  
47  
48 both BA6 and BA4, the LD maxima tended to be located more medially than the IM  
49  
50 maxima, though there was considerable variability in the locations of maxima across  
51  
52 subjects (see also Aziz-Zadeh et al., 2006; Fernandino & Iacoboni, 2009; Kemmerer  
53  
54 & Gonzalez-Castillo, 2008). We also computed the percentage overlap between  
55  
56  $LD_{MAN>NONMAN}$  and  $IM_{MAN>NONMAN}$  ROIs. We took the voxels for each subject at  
57  
58 a threshold of  $p < 0.05$  uncorrected for  $LD_{MAN>NONMAN}$  and for  $IM_{MAN>NONMAN}$  and  
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computed the percentage of voxels represented in both ROIs. The results show that overlap was nearly absent: For left BA6 the mean percentage of voxels overlapping in a given participant was 1.26% (s.d. 3.3%, median 0%, range 0-13.4%). For left BA4 the mean percentage of overlapping voxels was 1.13% (s.d. 3.8%, median 0%, range 0-16.5%).

We also tested whether there were MAN>NONMAN effects within each task in left BA6/4. We did by means of subject-specific ROIs defined as spherical 4mm ROIs around the maximally activated voxel to MAN words (thresholded at  $p < 0.001$ ). **Recall that ROI construction was based upon one half of the data and subsequent testing was done on the other half of the data (see Methods section).** This analysis was included to determine whether there were MAN>NONMAN effect in BA6/4 in the two runs separately. That is, now we do not look at overlapping neural correlates, but we ask whether there is an  $LD_{MAN>NONMAN}$  or  $IM_{MAN>NONMAN}$  effect in BA6/4 at all. We have observed before that testing this in subject-specific ROIs is much more sensitive than in whole brain analysis, given the relatively large spread of activations across participants (Willems et al., in press; see also Aziz-Zadeh et al., 2006). The results show that there is an  $LD_{MAN>NONMAN}$  effect in the subject-specific ROIs based upon one half of the data from the LD run in BA6 ( $t(19)=2.80$ ,  $p=0.011$ ). **There was no  $IM_{MAN>NONMAN}$  effect in these ROIs ( $t(19)<1$ ).** Similarly, **there was an  $IM_{MAN>NONMAN}$  effect in BA6 in the ROIs based upon one half of the data from the IM run ( $t(19)=2.38$ ,  $p=0.028$ ), but there was no  $LD_{MAN>NONMAN}$  effect in these ROIs ( $t(19)=1.023$ ,  $p=0.319$ ).** In BA4 there was an  $IM_{MAN>NONMAN}$  effect in the subject-specific IM ROIs ( $t(19)=2.97$ ,  $p=0.008$ ), but there was no  $LD_{MAN>NONMAN}$  effect in these ROIs ( $t < 1$ ). **There was no  $LD_{MAN>NONMAN}$  effect in the BA4 ROIs from the LD run ( $t(19)<1$ ), and a marginally significant negative effect for  $IM_{MAN>NONMAN}$  ( $t(19)=-1.89$ ,  $p=0.073$ ).** This is in line with previous

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3 studies showing premotor but not primary motor activation during action  
4  
5 language understanding (Tettamanti, et al., 2005; Tomasino et al., 2007).  
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8 All the subject-specific ROIs described above were also activated above  
9  
10 baseline during action execution (LD ROIs BA4:  $t(17)=2.04$ ,  $p=0.026$ ; LD ROIs  
11  
12 BA6:  $t(17)=3.03$ ,  $p=0.004$ ; IM ROIs BA4:  $t(17)=1.75$ ,  $p=0.048$ ; IM ROIs BA6:  
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15  $t(17)=1.83$ ,  $p=0.042$ ).  
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20 *Multi-voxel pattern analysis* To test for overlap in the pattern of response in  
21  
22 BA6/BA4 using a technique that is not susceptible to statistical thresholding effects,  
23  
24 we performed multi-voxel pattern analysis. **In this analysis, the MAN>NONMAN**  
25  
26 **contrast values for each voxel from a given area (left BA6 / left BA4) during LD**  
27  
28 **and during IM were taken and a correlation coefficient was computed between**  
29  
30 **them. That is, we took two vectors representing contrast values from voxels from**  
31  
32 **BA6 or BA4 and correlated for each voxel the value during  $LD_{MAN>NONMAN}$  with**  
33  
34 **the value during  $IM_{MAN>NONMAN}$ . This was done for each participant separately,**  
35  
36 **yielding twenty correlation coefficients, which were converted to Fisher's z and**  
37  
38 **tested in a one-sample t-test against mean zero.** There was no correlation between  
39  
40 patterns of activation to the MAN>NONMAN contrast in the LD and the IM tasks,  
41  
42 neither in left BA6 ( $t(19)<1$ ), nor in left BA4 ( $t(19)<1$ ). **This type of analysis also**  
43  
44 **allowed us to do an additional check upon the stability of MAN>NONMAN**  
45  
46 **differences within each session separately. We correlated the MAN>NONMAN**  
47  
48 **contrast values from the one half of the LD session with those of the other half of**  
49  
50 **the LD session. The same was done for the IM data ( $IM_{odd_{MAN>NONMAN}}$  was**  
51  
52 **correlated with  $IM_{even_{MAN>NONMAN}}$ ). These correlations were significant in BA6**  
53  
54 **(LD:  $t(19)=2.61$ ,  $p=0.017$ ; IM:  $t(19)=3.15$ ,  $p=0.005$ ), as well as for IM in BA4**  
55  
56 **( $t(19)=2.73$ ,  $p=0.01$ ), and marginally so for LD in BA4 ( $t(19)=1.96$ ,  $p=0.065$ ). The**  
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3 latter may come as a surprise given that in the subject-specific ROI analysis we  
4 did not observe a MAN>NONMAN effect in the LD run. However, we want to  
5 stress that these within-session correlations might be inflated because of the high  
6 temporal correlation in the data and we therefore refrain from drawing strong  
7 conclusions based upon them.  
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18 In summary, we observed that reading of action verbs as well as explicit imagination  
19 led to activation in motor areas compared to baseline. However, the parts of both  
20 primary motor and premotor cortex that distinguished manual from non-manual action  
21 verbs during one task were not activated during the other, even in subject-specific  
22 ROIs that were constructed to maximize potential overlap between tasks. In unbiased  
23 subject-specific ROIs, primary motor cortex showed effector-specific activation  
24 during imagery, but not during lexical decision. Premotor cortex showed effector-  
25 specific activation during both tasks, but the areas activated during lexical decision  
26 did not overlap with areas activated during imagery. No overlap was observed even  
27 when we employed MVPA, which is not susceptible to artifacts due to statistical  
28 thresholding. The more exploratory whole-brain analysis also showed no overlap  
29 between MAN>NONMAN in the two tasks. We found left dorsal premotor cortex,  
30 left primary motor cortex and left inferior temporal cortex to be sensitive to  
31  $IM_{MAN>NONMAN}$  (but not to  $LD_{MAN>NONMAN}$ ), whereas an area in left superior frontal  
32 sulcus was sensitive to  $LD_{MAN>NONMAN}$  (but not  $IM_{MAN>NONMAN}$ ).  
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## 55 Discussion

56 In this study, we investigated whether understanding action verbs involves the same  
57 tissues in cortical motor regions as explicit motor imagery. Left premotor cortex  
58 (BA6) showed effector-specific activation (i.e., stronger responses to manual  
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3 compared to non-manual verbs), during both the lexical decision and imagery tasks.  
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5 Crucially, there was no overlap in the effector-specific response patterns in subject-  
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7 specific ROIs in premotor cortex across the two tasks. More precisely, portions of  
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9 BA6 and BA4 that were defined based on effector-specific activity during the imagery  
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11 task showed no such activity during lexical decision. Conversely, BA6/BA4 ROIs  
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13 based on effector-specific activity during the lexical decision task showed no effector-  
14  
15 specific activity during imagery. This lack of overlap cannot be attributed to  
16  
17 thresholding effects, since multi-voxel pattern analysis on un-thresholded t-maps  
18  
19 showed that there was no correlation between effector-specific responses across tasks  
20  
21 in BA4/6. Rather, these double-dissociations show that implicit motor simulation and  
22  
23 explicit motor imagery do not necessarily engage the same neural tissues in premotor  
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25 and primary motor cortices, and by inference, may not involve the same cognitive  
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27 processes.  
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33  
34 A double-dissociation between action verb understanding and mental imagery  
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36 of actions was also found in the exploratory whole-brain analysis. There were no  
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38 regions that showed effector-specific activation in both tasks. That is, there was no  
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40 overlap between regions activated significantly in the MAN>NONMAN contrast  
41  
42 during both lexical decision and imagery. Rather, a region of left dorsal premotor  
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44 cortex distinguished between manual and non-manual verbs during motor imagery,  
45  
46 but not during lexical decision. Conversely, an area in left superior frontal sulcus  
47  
48 distinguished manual and non-manual verbs during lexical decision, but not during  
49  
50 motor imagery (Fig. 3). It is not clear why this region of superior frontal sulcus should  
51  
52 show effector-specific activation during lexical decision<sup>3</sup>. For the present purposes,  
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54 the findings from the whole-brain analysis underscore the dissociation between the  
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56 neural substrates of action verb understanding and mental imagery of actions.  
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4       **Is it possible that the lexical decision task only evoked processing of the**  
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6 **verbs at a pre-semantic level, and hence did not activate representations of**  
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8 **action verb meaning in the lexical decision task? We cannot definitely rule out**  
9  
10 **this possibility, but it is unlikely to be an adequate alternative explanation of**  
11  
12 **these data for several reasons. First, previous research indicates that lexical**  
13  
14 **decision leads to processing up to the semantic level, as indexed by modulations**  
15  
16 **of the N400 component (e.g. Chwilla, Brown, & Hagoort, 1995; Relander, Rama,**  
17  
18 **& Kujala, 2009), reaction time studies (see Neely, 1991) and overlapping neural**  
19  
20 **correlates between more explicit semantic tasks and lexical decision task (Ruff,**  
21  
22 **Blumstein, Myers, & Hutchison, 2008). Second, the non-words were all phono-**  
23  
24 **tactically legal and all ended in the suffix indicating the infinitive in Dutch,**  
25  
26 **which necessitates full reading of the verb in order to be able to perform the**  
27  
28 **task. Finally, it would be hard to explain the effector-specific activations we**  
29  
30 **observed in premotor cortex if the action verbs were not processed beyond a pre-**  
31  
32 **semantic level.**  
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39       According to the version of embodied semantics proposed by Gallese and  
40  
41 Lakoff (2005), the neural correlates of motor imagery and action semantics should be  
42  
43 identical, or at least overlapping (see also Pulvermuller, 2005). Yet, the present data  
44  
45 provide no support for this proposal, despite showing that both motor imagery and  
46  
47 action verb semantics engage premotor cortex. Some researchers have stated that they  
48  
49 use the terms ‘mental simulation’ and ‘mental imagery’ synonymously (e.g., Bergen,  
50  
51 et al., 2007 p. 735). But our results urge caution in equating these constructs, and  
52  
53 suggest that theories of embodied semantics should distinguish *implicit mental*  
54  
55 *simulation* during language processing from *explicit mental imagery*.  
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### *Possible relationships between simulation and imagery*

How does implicit simulation differ from explicit imagery? Here we explore three possibilities. First, simulation could simply be an unconscious version of mental imagery. Whereas language understanding is usually fast and effortless, constructing conscious mental images is comparatively slow and effortful (Farah, 1989; Kosslyn & Ochsner, 1994). Hence, perhaps implicit simulation comprises a subset of the neurocognitive processes involved in explicit imagery (i.e., imagery = simulation + consciousness)? In principle, this view could be easily reconciled with Gallese & Lakoff's (2005) proposal. When they wrote that the neural substrates of language understanding and imagination were "the same," (2005, p. 456), presumably they were referring to the motor correlates of these processes. Yet, this possibility is difficult to reconcile with the present data. If simulation were a proper subset of imagery, we would expect to see overlapping activation in motor areas during the lexical decision and imagery tasks. In fact, we found that the parts of premotor cortex activated during lexical decision and imagery were mutually exclusive.

On a second possibility, perhaps implicit simulation and explicit imagery are at opposite ends of a continuum of richness or detail? In order for mental simulations to occur rapidly enough to support online language processing, they must be highly schematic. Details can be filled in if the context encourages elaborating on the initial simulation, and if time permits. On this account, motor representations that constitute simulation and imagery differ in amount of detail, but not in kind. Yet, this is also inconsistent with the present data. The neural correlates of two processes that only differ in amount should be partially overlapping, or at least correlated, contrary to our findings. Although simulations and images may, indeed, differ in richness or detail, this difference cannot account for the double-dissociation between their neural substrates (*N.B.*, The present data should not be interpreted as suggesting that the



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3 neural substrates of simulation and imagery can never be overlapping, a point we  
4  
5 return to below).

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8         On a third possibility, perhaps implicit simulation during language  
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10 understanding and explicit imagery rely on different cerebral structures because they  
11  
12 serve different functions at a computational level (Marr, 1982). A core component of  
13  
14 implicit simulation during language processing is *prediction*. Myriad studies using  
15  
16 behavioral and neural measures have demonstrated language users' forward-looking  
17  
18 orientation. Comprehenders use incoming linguistic and extra-linguistic information,  
19  
20 rapidly and often unconsciously, to anticipate words, sounds, semantic associates,  
21  
22 syntactic structures, discourse referents, and changes in the extra-linguistic  
23  
24 environment that are likely to be relevant (e.g. DeLong, Urbach, & Kutas, 2005; Van  
25  
26 Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005; for review see Van  
27  
28 Berkum, in press). Presumably, prediction during language comprehension is not  
29  
30 motivated solely by the need to comprehend language, per se. Rather, language is a  
31  
32 tool that helps its users to interact with their physical and social environments. As  
33  
34 such, implicit motor simulation during action verb understanding (termed  
35  
36 'presonance' by Zwaan & Kaschack, 2008) may serve predictive functions: preparing  
37  
38 the language user for likely actions, linguistic or extra-linguistic, on a brief timescale  
39  
40 that is relevant for using language and planning bodily actions (see Zwaan, 2004;  
41  
42 Zwaan & Kaschak, 2008 for discussion).

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45         By contrast with implicit simulation during language processing, explicit  
46  
47 mental imagery is fundamentally *reflective*. Explicit imagery cued by words  
48  
49 necessarily occurs after a word has been at least partially understood; we must know  
50  
51 what to imagine before we can start imagining it consciously. The computational  
52  
53 functions of imagery that have been proposed emphasize its utility for retrospective  
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55 tasks (Pinker, 1984), such as recovering information learned implicitly via perception  
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3 (e.g., you may not know how many windows your house has, but you can recover this  
4 information from your perceptual experiences by mentally scanning its exterior) or  
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8 confirming initial perceptual guesses during motor imagery (e.g. de Lange et al.,  
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10  
11 2005; Parsons, 1994). Of course mental imagery can be used prospectively, as when  
12  
13 an athlete mentally rehearses a sequence of movements before executing them, but  
14  
15 even in such examples the imager prepares for a future event via gradual, effortful  
16  
17 mental re-enactment of past experiences.  
18

19  
20 **If implicit motor simulation is predictive, then understanding action**  
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22 **words should preferentially engage regions involved in motor planning. If**  
23  
24 **conscious motor imagery is reflective (i.e., a covert re-enactment of prior**  
25  
26 **actions), then imagining actions should engage not only regions involved in**  
27  
28 **motor planning but also regions involved in motor execution. Consistent with**  
29  
30 **these proposals, we find effector-specific activation during lexical decision in**  
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32 **premotor cortex but not primary motor cortex (see also Aziz-Zadeh, et al., 2006;**  
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34 **Tettamanti, et al., 2005; but see Pulvermuller, 2005). By contrast, we find**  
35  
36 **effector-specific activation during imagery in both premotor and primary motor**  
37  
38 **cortices (Tomasino, et al., 2007; 2008; see also Papeo, Vallesi, Isaja, & Rumiati,**  
39  
40 **2009)<sup>4</sup>.**  
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46 **The proposal that simulation and imagery are partially distinct processes**  
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48 **with different computational goals predicts a dissociation in the motor system,**  
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50 **and it is the only proposal we are aware of that can predict the double-**  
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52 **dissociation we observe in premotor cortex. But it does not necessarily entail a**  
53  
54 **double-dissociation. Why might simulations and images cued by the same verbs**  
55  
56 **have different premotor representations? Assuming that participants had to**  
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58 **understand each word before they could begin to imagine the action it referred**  
59  
60 **to, the words presented in the ‘imagery’ condition may have first cued implicit**

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3 simulations (partly constitutive of understanding), followed by explicit images.  
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5 Initial premotor activation in the imagery condition may have corresponded  
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7 closely to the activation observed for lexical decision. Although this prospective  
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9 activation is specified at the level of the effector, it is likely to be highly  
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11 schematic. This schematicity is important for two reasons. First, simulation must  
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13 be fast enough to support online language processing. Second, simulations cued  
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15 by language must be underspecified enough to flexibly accommodate an  
16  
17 incoming message: very different action plans would be necessary if the word  
18  
19 *grasp* were followed by “...*the barbell*” as opposed to “...*the needle*”.

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21  
22 A different level of specification is necessary in order to create a mental  
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24 image cued by language. If we vividly imagine the action corresponding to the  
25  
26 verb *throw*, it is necessary to decide whether to imagine throwing a baseball or a  
27  
28 frisbee, since these require different grips and different arm motions. As  
29  
30 simulation ends and imagery begins, the premotor representation cued by the  
31  
32 appearance of the word *throw* is changed, perhaps due to the specification of  
33  
34 action plans within premotor cortex. Such a change should be observable given  
35  
36 neuroimaging methods with sufficient spatiotemporal resolution. Given the  
37  
38 temporal resolution of fMRI, however, any transient activation corresponding to  
39  
40 implicit simulation at the beginning of an ‘imagery’ trial is obscured by  
41  
42 activation corresponding to the more sustained process of creating and  
43  
44 monitoring an explicit mental image.

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46  
47 As should now be clear, our proposal does not imply that simulation during  
48  
49 understanding language precludes explicit imagery. On the contrary, at times  
50  
51 language encourages explicit imagery, as when we appreciate a vivid description of  
52  
53 scenery, or reflect on poetry (e.g. Just, Newman, Keller, McEleney, & Carpenter,  
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55 2004). We may engage mental imagery more in these contexts than during mundane  
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3 language understanding, or when reading isolated verbs in a lexical decision task.

4  
5 Again, we emphasize that nothing we propose here implies that the neural correlates  
6  
7 of language understanding and explicit motor imagery can never be overlapping.

8  
9 Rather, our data show that they do not necessarily overlap, contrary to the predictions  
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11 derived from some theories of embodied language understanding.  
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### 15 16 17 *Constraining interpretation of previous experimental results*

18  
19 The present study addressed two concerns raised by Postle, et al. (2008), which have  
20  
21 complicated interpretation of previous experimental results. First, on a skeptical  
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23 interpretation of the original studies to show effector-specific activation of motor  
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25 areas during verb processing (e.g., Hauk, et al., 2004; Tettamanti, et al., 2005), it is  
26  
27 possible that observed activation was due to explicit imagery, rather than action verb  
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29 semantics, per se (see also Willems & Hagoort, 2007). Although participants in these  
30  
31 studies were not instructed to form explicit mental images in response to the stimuli,  
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33 they were not prevented from forming them (perhaps to pass the time between stimuli  
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35 in the scanner). By comparing effector-specific activation across tasks (lexical  
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37 decision versus imagery), we explicitly controlled for spurious activation due to  
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39 explicit imagery during lexical decision.  
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46 Second, Postle, et al. (2008), did not find effector-specific activation in  
47  
48 premotor cortex during action verb processing, in contrast to earlier studies. They  
49  
50 suggested that perhaps earlier positive results were artifacts of differences in  
51  
52 imageability between critical and control stimuli. Indeed, some previous studies  
53  
54 compared action verbs to abstract language as a high-level control (Tettamanti et al.,  
55  
56 2005) or to hash-marks as a lower-level control (Hauk et al., 2004). Given that  
57  
58 concrete action verbs are arguably more imageable than abstract words and that this is  
59  
60 known to affect activations in (among other regions) premotor cortex (e.g. D'Esposito

1  
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3 et al., 1997), it is possible that effects in earlier studies were mainly driven by  
4  
5 increased imagery to concrete action language as compared to more abstract language.  
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8 Yet, in the present study we find effects in the premotor ROI during lexical decision  
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10 on MAN>NONMAN words, despite having equated the different verb types for  
11  
12 imageability, among other standard psycholinguistic variables.  
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15  
16 Finally, whereas Postle and colleagues defined their ROIs based on previous  
17  
18 studies, we used subject-specific ROIs, which may have enhanced our ability to detect  
19  
20 effector-specific activation in primary motor and premotor cortices (see also Aziz-  
21  
22 Zadeh et al., 2006).  
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## 27 **Conclusion**

28  
29 Understanding manual action verbs and forming mental images of the actions they  
30  
31 name both produce effector-specific activation in regions of premotor cortex. Yet,  
32  
33 parts of premotor cortex involved in these processes were found to be mutually  
34  
35 exclusive: activation in the two tasks was neither overlapping nor correlated. These  
36  
37 dissociations are inconsistent with the proposal that the neural substrates of implicit  
38  
39 mental simulation during language processing and explicit mental imagery are the  
40  
41 same, and also inconsistent with the possibility that simulation and imagery merely  
42  
43 differ in degree of conscious awareness or level of detail. Rather, these data are most  
44  
45 consistent with the possibility that simulation and imagery serve different functions at  
46  
47 a computational level, simulation being strongly *predictive* and imagery being largely  
48  
49 *reflective*. Given the observed neural dissociations and the proposed computational-  
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51 level distinctions, the constructs of *mental simulation* and *mental imagery* should be  
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53 distinguished in theories of embodied semantics.  
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## Notes

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1) As a control analysis we also split the data in four bins of 12 trials each, comparing data from bin 1 and 3 with data from bin 2 and 4. The results confirm the odd-even split-half analysis and we do not report the results of the four-bins analysis.

2) The same results were obtained when ROIs were based upon the even-numbered trials and testing was done on the odd-numbered trials.

3) This area of superior frontal sulcus has been implicated previously in working memory maintenance (Passingham & Rowe, 2002; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000). Notably, Hauk and colleagues observed activation in middle frontal gyrus to reading of hand action verbs compared to abstract verbs (Hauk et al., 2004). This activation was more lateral but in the same vicinity as activation found here in the  $LD_{MAN>NONMAN}$  comparison. More research is needed to reveal what underlies these activations. **It is interesting to note that this was the only region from the whole-brain analysis which was not activated during the action execution localizer.**

4) Potentially, this distinction could help to explain conflicting findings of primary motor cortex involvement during motor imagery (see de Lange, Roelofs, & Toni, 2008; Jeannerod, 2006; Munzert, Lorey, & Zentgraf, 2009), an issue which is beyond the scope of the present paper.

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6  
7 assistance and two anonymous reviewers for their helpful comments.  
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### Figure captions

**Fig. 1** Example of a trial in the lexical decision (LD) task (A) and in the imagery (IM) task (B). A) In the LD run, words were presented for 1500 ms, followed by a variable intertrial interval (between 2-6 sec, mean=4sec). On 25% of the trials, a lexical decision response screen was shown and the participants had to indicate whether the immediately preceding word was an existing word or not by pressing the left or the right button. Response side was unpredictably balanced between left and right so that no response could be prepared. A fixation cross indicated start of a new trial. B) In the imagery run, MAN and NONMAN words were presented for 1500 ms. After reading the word, participants closed their eyes and imagined performing the action and opened their eyes to indicate that they were ready. Opening and closing of the eyes was monitored with an infrared eye-tracker. After a variable ITI (2-6 sec, mean=4sec), a fixation cross indicated start of a new trial. All materials were in Dutch. In Dutch the infinitive form is indicated by a non-separable suffix ('-en'), which means that only one word was presented per trial (and not two as in the English example).

**Fig. 2** Overlapping activation to MAN and NONMAN words during lexical decision (A) and motor imagery (B). Displayed are the conjunction analyses (Nichols et al., 2005)  $LD_{MAN>0} \cap LD_{NONMAN>0}$  (in red, A) and  $IM_{MAN>0} \cap IM_{NONMAN>0}$  (in green, B). Reading of all word types led to strong bilateral occipital cortex activation as well as bilateral (but more left-lateralized) primary and premotor cortex activation. Moreover, for all conditions inferior frontal cortex was activated bilaterally.

**Fig. 3** Results of whole brain analysis. Results are displayed on a rendered image. Displayed are the  $LD_{MAN>NONMAN}$  (in yellow) and the  $IM_{MAN>NONMAN}$  (in blue)

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3 contrasts. As can be seen in the figure there were no overlapping areas in both  
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5 contrast maps. This was confirmed by a conjunction analysis as well as by informal  
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7 inspection of both contrast maps at  $p < 0.01$  uncorrected. The bar graphs show mean  
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9 responses (beta weights expressed as percent signal change) for the  $LD_{MAN>NONMAN}$   
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11 (white bars) and the  $IM_{MAN>NONMAN}$  (black bars) contrasts in each of the areas  
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13 activated in the whole brain analysis. An asterisk indicates a difference between  
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15 conditions at the  $p < 0.05$  significance level. Note that we only tested  
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18  $MAN > NONMAN$  in the task in which the activation cluster was not activated to  
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20 avoid circularity. **That is, if an area shows an  $IM_{MAN>NONMAN}$  effect in the whole**  
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22 **brain analysis, we only tested whether there was a similar  $MAN > NONMAN$**   
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24 **effect in the LD task and vice versa. We do display the parameter estimates from**  
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26 **both task runs for the sake of clarity and ease of reading.** Error bars represent  
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28 standard error of the mean (s.e.m.).  
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36 **Fig. 4** Local maxima for subject-specific ROIs in left BA4 (upper panel) and in left  
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38 BA6 (lower panel). Displayed is the maximally activated voxel for each participant to  
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40 the  $LD_{MAN>NONMAN}$  comparison (white circles) and to the  $IM_{MAN>NONMAN}$  comparison  
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42 (filled circles). **The local maxima for each participant are connected with a line.**  
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44 **Participants that did not have a local maximum for the  $LD_{MAN>NONMAN}$  or for the**  
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46  **$IM_{MAN>NONMAN}$  comparison are represented as isolated (non-connected dots).**  
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48 **This was the case for two participants ( $IM_{MAN>NONMAN}$ ) and four**  
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50 **( $LD_{MAN>NONMAN}$ ) in BA4 and for two ( $LD_{MAN>NONMAN}$ ) and one ( $IM_{MAN>NONMAN}$ )**  
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52 **participants in BA6.** The mean coordinates are indicated by the bigger circles. The  
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54 LD maximally activated voxels were more medial than the IM maximally activated  
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56 voxels, but note the large spread around the mean coordinates. Axes represent x-  
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58 coordinate (x-axis) and z-coordinates (y-axis) in MNI space. Mean coordinates in  
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3 BA6: LD ([-22 -5 56, s.d. [19 16 13]), IM ([-34 -5 52, s.d.: [17 10 16]), mean  
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6 coordinates BA4: LD: ([-20 -29 58, s.d. 17 13 14]), IM: ([-30 -23 50, s.d. [18 17 16]).  
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Comparison	Region	x	y	z	Tmax	nr voxels	
$LD_{MAN>0} \cap LD_{NONMAN>0}$	L precentral sulcus / inferior frontal gyrus	-52	-6	48	7.11	3708	
	L insula	-36	-2	60	5.64		
	R precentral sulcus / inferior frontal gyrus		-30	24	0	6.04	977
			44	0	56	5.19	
	L superior / inferior parietal sulcus		36	0	48	4.79	1989
			46	8	32	4.73	
			-28	-68	30	6.59	
	R superior / inferior parietal sulcus		-34	-56	52	6.11	1114
			-42	-32	44	5.39	
	R superior temporal gyrus		30	-60	44	6.45	717
			30	-64	32	6.29	
	L inferior occipital / fusiform gyrus / middle temporal sulcus		46	-32	4	6.02	5153
			-22	-96	-8	16.93	
	L calcarine sulcus		-40	-72	-14	16.59	4170
			-36	-88	-12	14.64	
	R inferior occipital / fusiform gyrus		-18	-72	10	4.42	4170
			30	-90	-12	19.28	
	R calcarine sulcus		44	-72	-14	12.06	2713
			46	-58	-16	10.76	
	L anterior cingulate sulcus		20	-68	12	3.81	2713
		-6	2	60	7.48		
L hippocampus		-4	10	54	7.45	446	
		-8	28	34	4.57		
$IM_{MAN>0} \cap IM_{NONMAN>0}$	L inferior frontal gyrus / precentral sulcus	-18	-28	-2	7.35	23650	
	R inferior frontal gyrus / precentral sulcus	-28	-12	-4	3.03		
	L central sulcus		-50	16	-4	8.81	3256
			-44	-8	56	7.28	
	R central sulcus		50	16	-2	7.33	1881
			54	-2	48	6.85	
	R anterior cingulate sulcus		-44	-36	58	4.78	1881
			46	-30	56	2.90	
	L anterior cingulate sulcus		4	2	66	10.22	1881
			-4	-4	70	11.87	
	R calcarine sulcus		24	-58	4	9.22	1881
			20	-66	12	8.38	
	L calcarine sulcus		54	-56	6	4.74	1881
			-22	-62	4	9.10	
	L middle temporal gyrus		-10	-72	18	6.01	1881
			-52	-62	8	4.22	
Right cerebellum		26	-62	-22	5.59		
Left cerebellum		-22	-60	-20	3.1		

**Table 1** Overlapping regions activated to presentation of MAN as well as to

NONMAN words in the LD run (upper part) and in the IM run (lower part). Reported

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3 are a description of the activated region, the coordinates of the local maxima in MNI  
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5 space, the T-value of the maximally activated voxel in a cluster and the number of  
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8 2x2x2 mm voxels of the activated cluster. Results are corrected for multiple  
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10 comparisons at  $p < 0.05$ . Only a limited amount of peak voxels per cluster are reported  
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12 (e.g. in occipital cortex). See Fig. 2.  
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	<b>Region</b>	<b>x y z</b>	<b>T(max)</b>	<b>nr voxels</b>
<b>LD</b> <sub>MAN&gt;NONMAN</sub>	Left superior frontal sulcus	-18 16 50	4.12	624
		-8 40 50		
		-14 34 54		
<b>IM</b> <sub>MAN&gt;NONMAN</sub>	Left dorsal precentral sulcus	-26 -8 54	4.77	922
		-26 -8 68		
	Left central sulcus / postcentral sulcus	-52 -26 38	4.37	2169
		-16 -72 54		
		-32 -32 40		
	Left inferior / middle temporal sulcus	-48 -64 2	4.96	1467
		-42 -50 -16		
		-32 -62 18		

**Table 2** Results from whole brain analysis showing areas more strongly activated to manual (MAN) as compared to non-manual (NONMAN) action verbs, in the lexical decision task (LD) or in the motor imagery task (IM). Reported are a description of the activated region, the coordinates of the local maxima in MNI space, the T-value of the maximally activated voxel in a cluster and the number of 2x2x2 mm voxels of the activated cluster. Maximal 3 local maxima are reported which are more than 8mm apart. Results are corrected for multiple comparisons at  $p < 0.05$ .

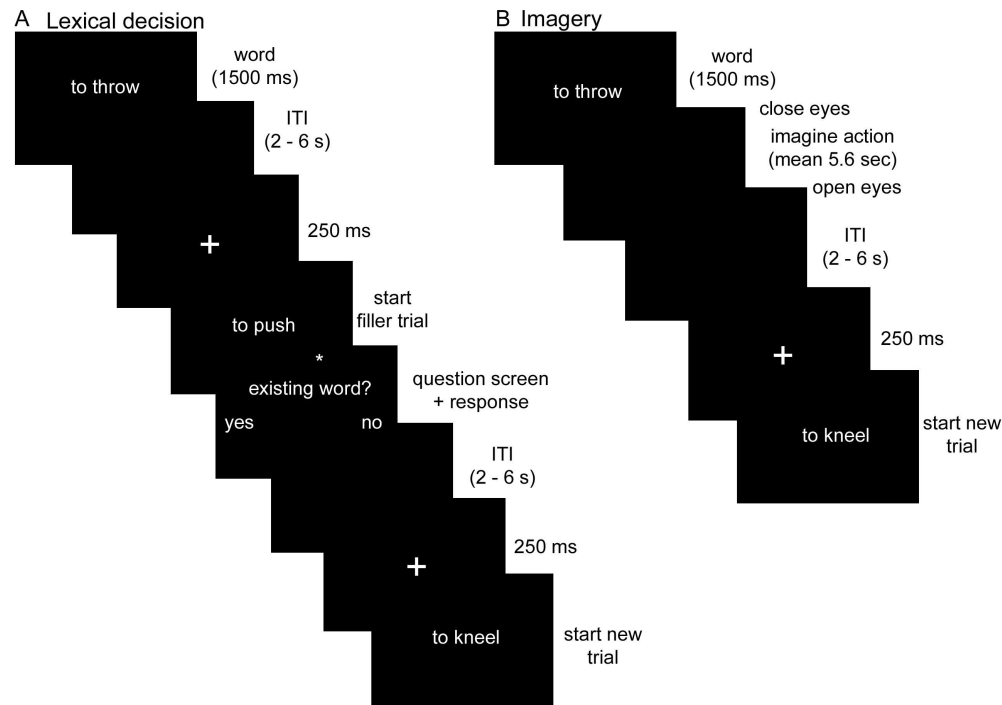


Fig. 1 Example of a trial in the lexical decision (LD) task (A) and in the imagery (IM) task (B). A) In the LD run, words were presented for 1500 ms, followed by a variable intertrial interval (between 2-6 sec, mean=4sec). After 25% of the trials, a lexical decision response screen was shown and the participants had to indicate whether the immediately preceding word was an existing word or not by pressing the left or the right button. Response side was unpredictably balanced between left and right so that no response could be prepared. A fixation cross indicated start of a new trial. B) In the imagery run, MAN and NONMAN words were presented for 1500 ms. After reading the word, participants closed their eyes and imagined performing the action and opened their eyes to indicate that they were ready. Opening and closing of the eyes was monitored with an infrared eye-tracker.

After a variable ITI (2-6 sec, mean=4sec), a fixation cross indicated start of a new trial. All materials were in Dutch. In Dutch the infinitive form is indicated by a non-separable suffix ('-en'), which means that only one word was presented per trial (and not two as in the English example).

219x170mm (300 x 300 DPI)



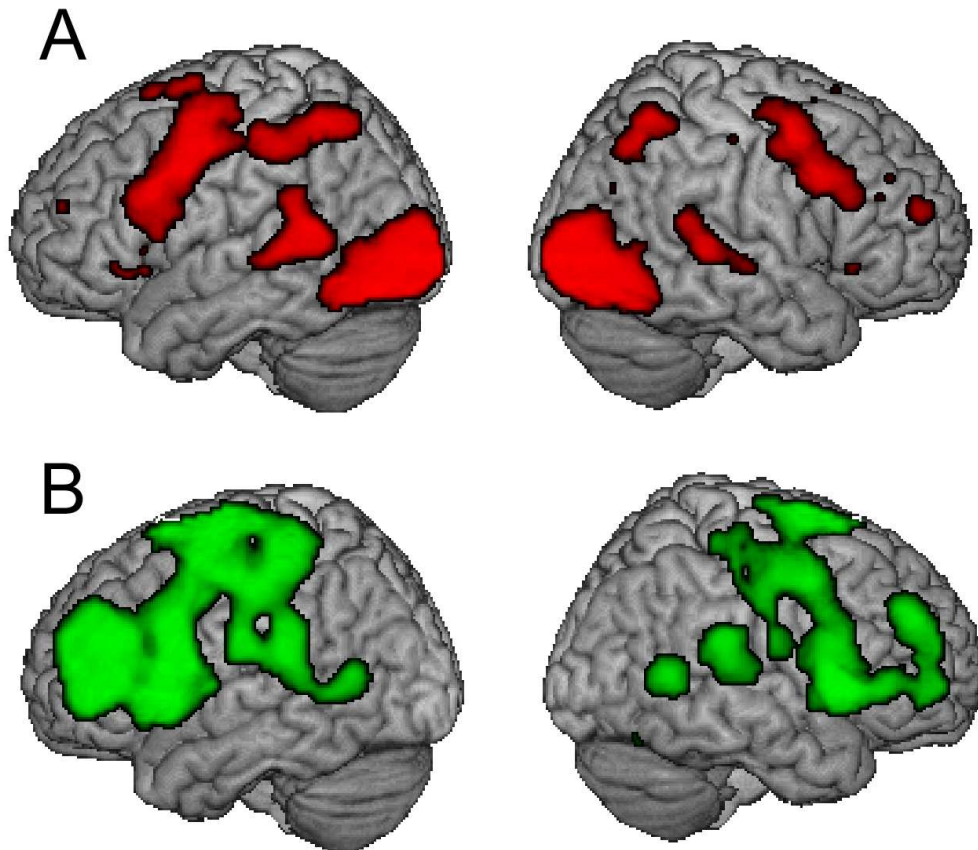


Fig. 2 Overlapping activation to MAN and NONMAN words during lexical decision (A) and motor imagery (B). Displayed are the conjunction analyses (Nichols et al., 2005)  $LD_{MAN>0} \cap LD_{NONMAN>0}$  (in red, A) and  $IM_{MAN>0} \cap IM_{NONMAN>0}$  (in green, B). Reading of all word types led to strong bilateral occipital cortex activation as well as bilateral (but more left-lateralized) primary and premotor cortex activation. Moreover, for all conditions inferior frontal cortex was activated bilaterally.  
450x450mm (72 x 72 DPI)

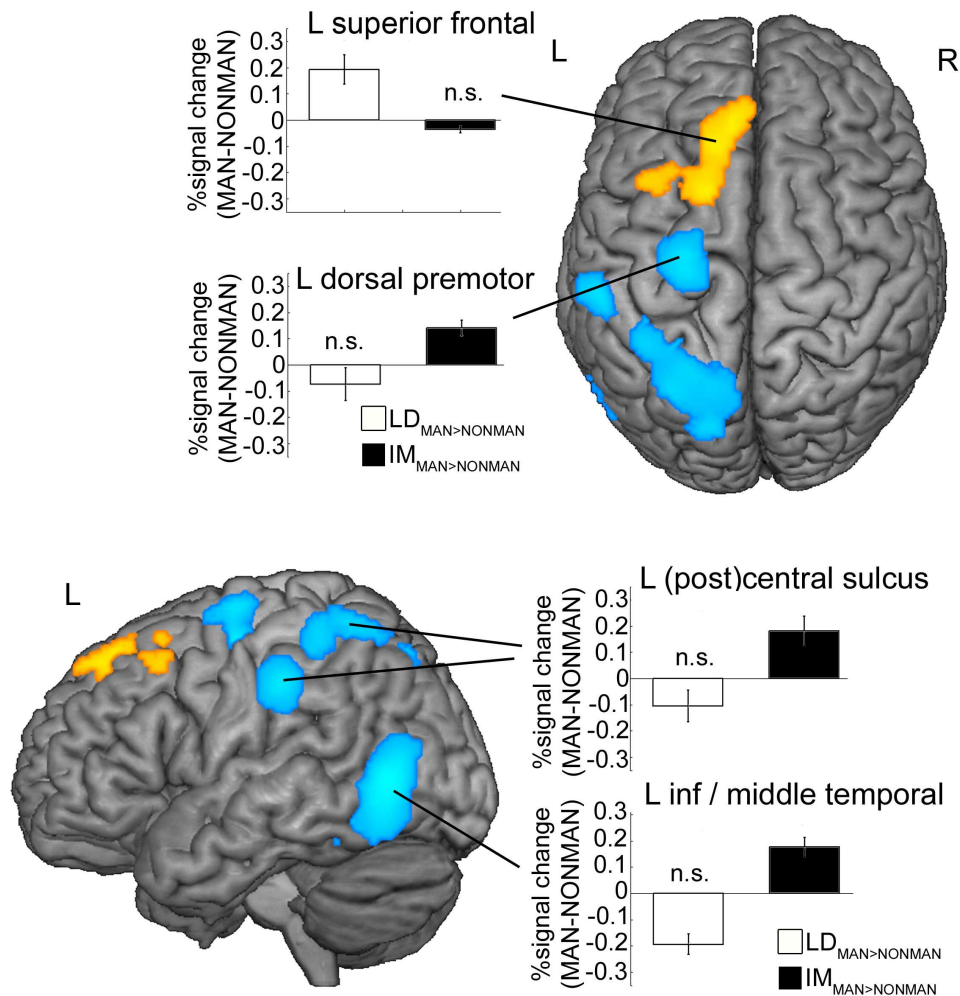


Fig. 3 Results of whole brain analysis. Results are displayed on a rendered image. Displayed are the LDMAN>NONMAN (in yellow) and the IMMAN>NONMAN (in blue) contrasts. As can be seen in the figure there were no overlapping areas in both contrast maps. This was confirmed by a conjunction analysis as well as by informal inspection of both contrast maps at  $p < 0.01$  uncorrected. The bar graphs show mean responses (beta weights expressed as percent signal change) for the LDMAN>NONMAN (white bars) and the IMMAN>NONMAN (black bars) contrasts in each of the areas activated in the whole brain analysis. An asterisk indicates a difference between conditions at the  $p < 0.05$  significance level. Note that we only tested MAN>NONMAN in the task in which the activation cluster was not activated to avoid circularity. That is, if an area shows an IMMAN>NONMAN effect in the whole brain analysis, we only tested whether there was a similar MAN>NONMAN effect in the LD task and vice versa. We do display the parameter estimates from both task runs for the sake of clarity and ease of reading. Error bars represent standard error of the mean (s.e.m.).

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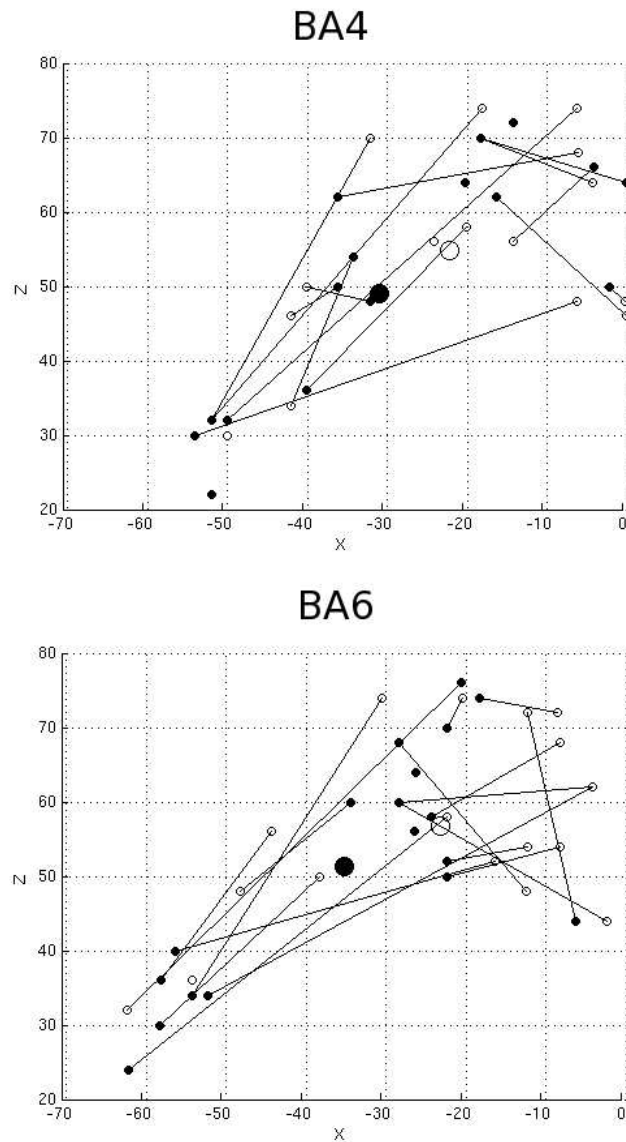


Fig. 4 Local maxima for subject-specific ROIs in left BA4 (upper panel) and in left BA6 (lower panel). Displayed is the maximally activated voxel for each participant to the LDMAN>NONMAN comparison (white circles) and to the IMMAN>NONMAN comparison (filled circles). The local maxima for each participant are connected with a line. Participants that did not have a local maximum for the LDMAN>NONMAN or for the IMMAN>NONMAN comparison are represented as isolated (non-connected dots). This was the case for two participants (IMMAN>NONMAN) and four (LDMAN>NONMAN) in BA4 and for two (LDMAN>NONMAN) and one (IMMAN>NONMAN) participants in BA6. The mean coordinates are indicated by the bigger circles. The LD maximally activated voxels were more medial than the IM maximally activated voxels, but note the large spread around the mean coordinates. Axes represent x-coordinate (x-axis) and z-coordinates (y-axis) in MNI space. Mean coordinates in BA6: LD ([-22 -5 56, s.d. [19 16 13]], IM ([-34 -5 52, s.d.: [17 10 16]], mean coordinates BA4: LD: ([-20 -29 58, s.d. 17 13 14]), IM: ([-30 -23 50, s.d. [18 17 16]).

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