# Neural dissociations between action verb understanding and motor imagery

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Neural dissociations between action verb understanding and motor imagery

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

In addition to supporting action word understanding, a host of studies implicate premotor cortex in supporting motor imagery of hand movements (e.g. Bonda, Petrides, Frey, & Evans, 1995; Cisek & Kalaska, 2004; de Lange, Hagoort, & Toni, 2005; de Lange, Helmich, & Toni, 2006; Gerardin et al., 2000; Helmich, de Lange, Bloem, & Toni, 2007; Johnson et al., 2002). Yet, the relationship between the premotor cortex correlates of motor imagery and action language understanding is not well understood.

In this study we aimed to elucidate the relationship between motor imagery and action semantics by directly comparing neural activity during action verb understanding with activity during explicit mental imagery of actions cued by the same verbs. In one fMRI run, participants performed a lexical decision task on action verbs, and in a second run they actively imagined performing the actions described by these verbs. To gain specificity of neural responses and for reasons of experimental control (see methods), we contrasted action verbs related to hand actions (e.g. to throw) with non-manual action verbs (e.g. to kneel).

Gallese and Lakoff’s (2005) conjecture makes the clear prediction that understanding an action verb and imagining performing that same action should rely on the same neural tissue, most notably premotor cortex. This finding would be in line with the idea that through Hebbian learning, cell assemblies of neurons firing together during execution and observation of actions come to constitute the semantic representation of an action verb (Pulvermüller, 2005). Alternatively, it is possible that non-overlapping parts of motor areas are activated both when we read action verbs
and during explicit motor imagery. This finding would require a refinement to theories of embodied semantics, suggesting that activation of the motor system during action verb understanding should be distinguished from motor imagery.

Before we move on to describing the experiment we will first clarify what we mean by simulation and by imagery. Implicit motor simulations are often characterized as partial re-enactments of prior actions (e.g., Barsalou, 1999; 2009). However, the computational function that such re-enactments could serve is not clear. When we use the term simulation in this paper, we do not refer to a re-enactment of prior experiences, which seem functionally unmotivated. Rather, we posit that motor simulations are pre-enactments of potential future experiences. A word like grasp can serve as a cue to activate neural circuits involved in partial preparation for grasping (see Barsalou, 2009; Zwaan, 2004 for compatible proposals). This schematic, unconscious, prospective activation of effector-specific regions in premotor cortex presumably facilitates further action planning if subsequent cues call for grasping to be executed, or to be imagined explicitly.

Motor imagery, by contrast, can be understood as covert enactment of an action. Like overt motor execution, motor imagery may entail the generation of an action plan (inverse model) as well as a prediction of the action' sensory consequences (forward model) (e.g. Grush, 2004; Wolpert & Ghahramani, 2000). The generation of the forward model can be described as a kind of simulation but this is not the way we use the term here.

Methods

Subjects We tested twenty healthy participants (14 female; mean age 22.7 y, range 19-28) with no known history of neurological problems, dyslexia or other language-
related problems, or hearing complaints, and with normal or corrected-to-normal vision. All participants were right-handed (Oldfield, 1971; mean EHI: 97, range 82 - 100) and gave written informed consent in accordance with the declaration of Helsinki. The study was approved by the local ethics committee.

Materials Stimuli were 96 Dutch verbs expressing concrete actions. Half of these were related to manual actions (MAN), half of them were not related to manual actions (NONMAN). This distinction was pretested with a larger number of verbs, in a group of raters who did not participate in the fMRI experiment (N=16), who scored for each verb how much they associated that action with their hand(s), and, if applicable whether they preferred to act out the action with their left, right or with both hands. MAN words were significantly more associated with hand actions than NONMAN words (t(94)=23.60, p<0.001). On average 79% of raters indicated that they tend to perform the action with their dominant hand (s.d.=11.8%, median=81%; mode=88%), that is, unimanually. MAN and NONMAN word lists did not differ in imageability (assessed by the same group of raters) (t(94)<1), number of phonemes (t(94)<1), lexical frequency (taken from the CELEX database (Baayen, Piepenbrock, & Rijn, 1993); (t(94)<1)) and number of letters (t(94)=1.51, p=0.13). From the materials that were rejected on the basis of the pretest, 16 filler items were created. Additionally, 16 phonotactically legal non-words were created, all with the suffix typical of the regular infinitive form in Dutch (‘-en’).

Experimental procedure Stimuli were presented using Presentation software (www.nbs.com, version 10.2) through a projector from outside of the scanner room onto a screen at the back of the scanner bore and were visible to the participants through a mirror attached to the head coil. There were two separate task runs: Lexical
Decision (LD) and Imagery (IM) (Fig. 1). In the LD run participants were instructed to indicate as quickly and accurately as possible whether a word was an existing word or not on 25% of the trials (fillers and non-words). After presentation of fillers and non-words, participants saw a response screen with the question whether the previous word was an existing word with answer options ‘yes’ and ‘no’ on the left or right side of the screen, which could be indicated by pressing a button with the left or right index finger. Response side was non-predictably balanced across trials to prevent a biased motor response to the left or right hand. Participants had 1500 ms to respond and got feedback on the screen when they were too slow. A stimulus list of 128 stimuli (48 MAN + 48 NONMAN + 16 fillers + 16 nonwords) was created, and pseudo-randomized with the constraint that the same condition was not repeated more than three times in a row. A mirrored version of this list was presented to half of the participants. Participants were familiarized with the procedure by means of 10 practice items containing different words than used in the remainder of the experiment.

In the IM run, the same words (except for filler and non-words, which means that there were 96 trials) were presented and participants were instructed to read the word, close their eyes, imagine performing the action and open their eyes to indicate that they had finished motor imagery. Closing and opening of the eyes was monitored by an infrared IviewX eyetracker (www.smi.de) with custom-built shielding, and coded on-line by one of the experimenters. We used opening and closing of the eyes to be able to measure imaging time on each trial while at the same time avoiding hand action interference from button presses. Performing motor imagery with eyes closed probably entails similar processes as motor imagery with eyes open (Heremans, Helsen, & Feys, 2008) and has been successfully used before in neuroimaging studies (Szameitat, Shen, & Sterr, 2007a, 2007b; Bakker et al.,
A stimulus list of 96 stimuli (MAN and NONMAN words) was created, pseudo-randomized with the constraint that the same condition was not repeated more than three times in a row. A mirrored version of this list was presented to half of the participants. Participants were familiarized with the procedure by means of 10 practice items containing different words than used in the remainder of the experiment.

Stimuli were presented for 1500 msec and stimulus onset was effectively jittered with respect to onset of volume acquisition by varying the intertrial interval between 2 and 6 seconds (mean=4 sec.) in steps of 250 ms (Dale, 1999) in both runs. A fixation cross (250 ms) indicated the start of a new trial. The LD run always preceded the IM run, to prevent a bias for participants to engage in motor imagery during the LD run.

Finally at the end of the session participants engaged in an action execution localizer in which they performed simple hand movements (opening and closing of the hand) with either the left or the right hand. The localizer was a blocked design and participants were cued to perform actions with the left or the right hand by means of the words 'left' or 'right' presented on the screen. Each block lasted 15 seconds and there were 8 blocks per condition. These action execution blocks were intermingled with five rest blocks of the same duration in which participants did not execute hand actions. Compliance with the task was checked visually from outside of the scanner room.

Data acquisition and analysis Echo-Planar Images (EPI) covering the whole brain were acquired with a 8 channel head coil on a Siemens MR system with 3T magnetic field strength (TR=2060 ms; TE=30 ms; flip angle 85°, 31 transversal slices; voxel size 3.5x3.5x3 mm, 0.5 mm gap between slices). Data analysis was done using SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/spm5/). Preprocessing involved
realignment through rigid body registration to correct for head motion, slice timing
correction to the onset of the first slice, normalization to Montreal Neurological
Institute (MNI) space, interpolation of voxel sizes to 2x2x2 mm, and spatial
smoothing (8 mm FWHM kernel). First-level analysis involved a multiple regression
analysis with regressors describing the expected hemodynamic responses during
observation of MAN words, NONMAN words as well as fillers words and non-words
(fillers and non-words in the LD run only). Responses (button presses) were modeled
separately as stick functions. Stimuli in the LD run were modeled with 1500 ms
duration, in the IM run the actual imagining times were used. MR disturbances due to
small head movements were accounted for by a series of nuisance regressors, namely
the linear and exponential changes in the scan-by-scan estimated head motion, scan-
by-scan average signals from outside the brain, white matter, and cerebro-spinal fluid
(Verhagen, Grol, Dijkerman, & Toni, 2006). **Stimuli in the action execution**
localizer were modeled as blocks of 15 seconds. The same nuisance regressors as
described above were included.

A second-level whole brain group analysis with subjects as a random factor
(‘random effects analysis’) was carried out. First, we tested which regions were
activated by MAN as well as NONMAN words during each task in isolation. This
was done by means of conjunction analyses testing the conjunction null as defined by
Nichols and colleagues (Nichols, Brett, Andersson, Wager, & Poline, 2005), testing
for $LD_{MAN}>0 \cap LD_{NONMAN}>0$ and for $IM_{MAN}>0 \cap IM_{NONMAN}>0$. Second, we looked
for regions which were more strongly activated to the MAN>NONMAN comparison
in either task (i.e. $LD_{MAN>NONMAN} / IM_{MAN>NONMAN}$). This is a much more specific
analysis which asks whether there are areas during LD or IM, which are sensitive to
the effector with which an action is typically associated. Finally, the crucial analysis
involved looking for regions sensitive to MAN>NONMAN comparison in both tasks
by doing a conjunction analysis (LD_{MAN>NONMAN} \cap IM_{MAN>NONMAN}), again testing the conjunction null hypothesis (Nichols et al., 2005). Correction for multiple comparisons was applied by thresholding group maps at \( p<0.005 \) uncorrected and subsequently taking the cluster extent into account by using the theory of Gaussian Random Fields (Friston, Holmes, Poline, Price, & Frith, 1996) to correct maps at \( p<0.05 \) corrected for multiple comparisons (Poline, Worsley, Evans, & Friston, 1997). Subsequently, in regions activated in the whole brain analysis to MAN>NONMAN in the one task, it was tested whether a comparable effect was present in the other task. We took the mean parameter estimates from areas activated to LD_{MAN>NONMAN} in the whole brain analysis and tested whether there was an IM_{MAN>NONMAN} effect in these areas, and vice versa.

For the main analysis, we created subject-specific regions of interest (ROIs) in which we selected voxels from cytoarchitectonically defined left Brodmann Area (BA) 6 (i.e. premotor cortex) (Eickhoff et al., 2005) and left BA4 (primary motor cortex, combining maps 4a and 4p (Geyer et al., 1996)). We choose BA6 and BA4 since these have been implicated in action verb reading as well as in motor imagery (see Munzert, Lorey, & Zentgraf, 2009; Willems & Hagoort, 2007 for reviews). For each participant, voxels that were sensitive to the MAN>NONMAN contrast (\( p<0.05 \) uncorrected) separately for the IM run and for the LD run were selected using the Marsbar toolbox (Brett, Anton, Valabregue, & Poline, 2002). Subsequently, we tested whether a MAN>NONMAN effect was also present in the data from the other run. The rationale for this analysis was that we selected for every subject the voxels that were most sensitive to the MAN>NONMAN contrast in one task and subsequently tested whether there was a similar effect in the other task. This is to be expected if LD and IM lead to overlapping neural correlates.
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. 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). 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
such vectors, one for LD\textsubscript{MAN>NONMAN} and one for IM\textsubscript{MAN>NONMAN}. Subsequently the correlation coefficient between these two vectors was computed for each participant separately. The correlation coefficients were converted to Fisher’s $z$ to comply with the normality assumption (Kleinbaum, Kupper, Muller, & Nizam, 1998), and tested for a difference from mean zero in a one-sample t-test (see Downing et al., 2006; Peelen et al., 2006 for a comparable approach). If MAN>NONMAN during LD and during IM lead to similar response patterns in BA6/BA4, we expect to find high correlations in this analysis.

Multi-voxel pattern analysis also allowed us to investigate the internal consistency of patterns of activation within one run. Using a split half approach we investigated whether the pattern of response in BA6/BA4 for MAN>NONMAN was the same for each half of the data in each task setting. Thus we correlated patterns of voxels in BA6/BA4 LD\textsubscript{MAN>NONMAN} from odd-numbered trials with the activation pattern during LD\textsubscript{MAN>NONMAN} from even-numbered trials. This was similarly done for the IM data. If the pattern of responses in BA6/BA4 is robust and stable, we expect high correlations between the MAN>NONMAN contrast values from the one half of the data as compared to the other half of the data. We choose to not perform pattern correlation analysis on unsmoothed data because of the spatial normalization procedure which is inherently imperfect across sessions. The danger with unsmoothed data is that correlations are artificially lower in across-session comparisons as compared to within-session comparisons due to imperfect normalization. Spatial smoothing essentially eliminates that problem and we therefore conducted the correlation analysis on spatially smoothed data.

We never compared a single condition directly between the two tasks (e.g. LD\textsubscript{MAN}>IM\textsubscript{MAN}), given the interpretational problems arising from a direct comparison
between tasks with different trial durations and occurring in different scanning runs (McGonigle et al., 2000). Furthermore, given the heterogeneity of effectors involved in the NONMAN trials, we did not contrast NONMAN>MAN.

The results from the action execution localizer task were used to investigate whether ROIs defined in the LD or IM data, were also activated during actual hand action execution. For this end we extracted contrast values to the Right hand>Rest comparison from the ROIs described above and statistically tested them in a one-sample one-sided t-test against mean zero.

Results

Behavioral

Lexical decision Participants answered correctly to the lexical decision catch trials in the large majority of trials (mean=95.8%, s.d.=3.5%; range 87.5%-100%). There were few incorrect responses (mean=3.9%, s.d.=3.64, range 0%-9.4%) and misses (mean=0.3%, s.d.=0.99%, range 0%-3.1%)

Imagery Participants on average took 5.6 seconds (s.d.=1.79) to imagine doing the MAN actions, compared to 5.5 seconds (s.d.=1.67) to imagine the NONMAN actions. This difference was not statistically significant (t(19)<1).

Neural

For technical reasons in one subject no action execution localizer was measured. Moreover, because of excessive head motion the action execution data from one other participant were not analyzed. This means that 18 data sets entered the analysis for the action execution localizer. The analysis of LD and IM data involved data from all 20 participants. Head movement never exceeded 2mm or
2 degrees in any rotation or translation in any of the runs which were included in the analysis.

Whole brain analysis We performed exploratory whole-brain analysis, testing for task-specific activations as well as for overlap in response patterns between the lexical decision and imagery tasks. First, activations to reading of MAN and NONMAN words was compared to baseline in the LD run (LD\textit{MAN}>0 \cap LD\textit{NONMAN}>0). This comparison led to wide-spread overlapping activations in bilateral precentral sulci and inferior frontal gyri, bilateral superior and inferior parietal sulci, \textbf{bilateral superior and middle temporal sulci}, bilateral inferior occipital and calcarine sulci and left anterior cingulate sulcus and left hippocampus (Fig. 2A; Table 1). A similar activation pattern was observed for this analysis in the IM data (IM\textit{MAN}>0 \cap IM\textit{NONMAN}>0), encompassing bilateral inferior frontal gyri, bilateral precentral sulci, bilateral central sulci, bilateral anterior cingulate sulci, bilateral calcarine / inferior occipital sulci, bilateral middle and superior temporal gyri and bilateral cerebellum (Fig. 2B; Table 1).

Second, comparing the MAN>NONMAN conditions in the LD task (LD\textit{MAN>NONMAN}) led to increased activation in left superior frontal sulcus (Fig. 3; Table 2). The same comparison in the IM task (IM\textit{MAN>NONMAN}) revealed increased activation levels in left dorsal precentral sulcus stretching into middle frontal sulcus, left central and postcentral sulcus, and left inferior temporal sulcus (Fig. 3; Table 2). To confirm the specificity of the response in each of these areas, we computed the MAN>NONMAN contrast for the other task in the areas activated in the whole brain analysis to MAN>NONMAN either in the LD task or in the IM task. Put differently in the areas showing IM\textit{MAN>NONMAN} in the whole brain analysis we tested whether a LD\textit{MAN>NONMAN} effect was similarly present. Similarly, in the
one area showing an \( \text{LD}_{\text{MAN}} > \text{NONMAN} \) effect in the whole brain analysis we tested whether a \( \text{MAN} > \text{NONMAN} \) effect was also present during the IM task. The results confirm that these areas are not sensitive to the \( \text{MAN} > \text{NONMAN} \) contrast from the other task (see parameter estimates in Fig. 3). That is, if an area was sensitive to \( \text{MAN} > \text{NONMAN} \) in the IM task, it did not show a \( \text{MAN} > \text{NONMAN} \) effect in the LD task (Fig. 3). Of the areas showing a \( \text{MAN} > \text{NONMAN} \) effect in the whole brain analysis (Fig. 3), all but the left superior frontal sulcus activation cluster were significantly activated during action execution (LD area superior frontal sulcus: \( t(17) = -1.89, p = 0.074 \); IM area dorsal precentral sulcus: \( t(17) = 2.39, p = 0.028 \); IM area left central / postcentral sulcus: \( t(17) = 6.85, p < 0.001 \); IM area left inferior temporal sulcus: \( t(17) = 2.86, p = 0.010 \)).

Finally, there were no clusters showing overlapping responses across the two tasks (\( \text{LD}_{\text{MAN}} > \text{NONMAN} \cap \text{IM}_{\text{MAN}} > \text{NONMAN} \)), even at a very lenient statistical threshold (\( p < 0.01 \) uncorrected).

*Subject-specific regions of interest analysis* Our main analyses compared effector-specific activation during the two tasks (i.e. \( \text{LD}_{\text{MAN}} > \text{NONMAN} \) and \( \text{IM}_{\text{MAN}} > \text{NONMAN} \)) in subject-specific regions of interest in left BA6 and left BA4. Consistent with the whole-brain analysis, these ROI analyses also showed no overlap in effector-specific response patterns across the two tasks. In this analysis subject-specific ROIs consisted of voxels sensitive to \( \text{MAN} > \text{NONMAN} \) in the one task session and we subsequently tested for a \( \text{MAN} > \text{NONMAN} \) effect in the other task session. Voxels were thresholded at \( p < 0.05 \) uncorrected to increase chances of finding overlap between \( \text{LD}_{\text{MAN}} > \text{NONMAN} \) and \( \text{IM}_{\text{MAN}} > \text{NONMAN} \). If IM and LD lead to overlapping neural correlates, we should observe \( \text{IM}_{\text{MAN}} > \text{NONMAN} \) effects in ROIs
based upon $L_{D{\text{MAN} > \text{NONMAN}}}$ and vice versa. Note that creating ROIs based upon $I_{M{\text{MAN} > \text{NONMAN}}}$ and subsequently testing for this same effect ($I_{M{\text{MAN} > \text{NONMAN}}}$) is a biased measure leading to significant but uninformative results due to ‘overfitting’ (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009). We hence do not report the results of such comparisons.

The left BA6 ROIs taken from the IM task (subject-specific voxels sensitive to $I_{M{\text{MAN} > \text{NONMAN}}}$ at $p<0.05$ uncorrected) were not sensitive to the $L_{D{\text{MAN} > \text{NONMAN}}}$ contrast ($t(19)=-1.83$, $p=0.082$, note negative $t$-value). Conversely, taking the BA6 ROIs from the voxels activated to the $L_{D{\text{MAN} > \text{NONMAN}}}$ contrast revealed that there was no such effect for $I_{M{\text{MAN} > \text{NONMAN}}}$ ($t<1$). A similar pattern of responses was observed in subject-specific ROIs in left BA4. The ROIs taken from the $I_{M{\text{MAN} > \text{NONMAN}}}$ contrast showed no $L_{D{\text{MAN} > \text{NONMAN}}}$ effect ($t(19)=-1.62$, $p=0.12$, note negative $t$-value). The ROIs taken from the $L_{D{\text{MAN} > \text{NONMAN}}}$ contrast revealed no $I_{M{\text{MAN} > \text{NONMAN}}}$ effect ($t(19)<1$).

To gain better insight into the differential localization of parts of left BA6 and left BA4 sensitive to $L_{D{\text{MAN} > \text{NONMAN}}}$ and $I_{M{\text{MAN} > \text{NONMAN}}}$, we extracted the coordinates of the maximally activated voxel from each subject-specific ROI (Fig. 4). The mean coordinates for the BA6 LD ROIs were (MNI [-22 -5 56], s.d. [19 16 13]), and for the BA6 IM ROIs ([34 -5 52], s.d. [17 10 16]). For the BA4 LD ROIs ([20 -29 58], s.d.: [17 13 14]), and for the BA4 IM ROIs ([30 -23 50], s.d. [18 17 16]). In both BA6 and BA4, the LD maxima tended to be located more medially than the IM maxima, though there was considerable variability in the locations of maxima across subjects (see also Aziz-Zadeh et al., 2006; Fernandino & Iacoboni, 2009; Kemmerer & Gonzalez-Castillo, 2008). We also computed the percentage overlap between $L_{D{\text{MAN} > \text{NONMAN}}}$ and $I_{M{\text{MAN} > \text{NONMAN}}}$ ROIs. We took the voxels for each subject at a threshold of $p<0.05$ uncorrected for $L_{D{\text{MAN} > \text{NONMAN}}}$ and for $I_{M{\text{MAN} > \text{NONMAN}}}$ and
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\textsubscript{MAN>NONMAN} or IM\textsubscript{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\textsubscript{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\textsubscript{MAN>NONMAN} effect in these ROIs (t(19)<1). Similarly,
there was an IM\textsubscript{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\textsubscript{MAN>NONMAN}
effect in these ROIs (t(19)=1.023, p=0.319). In BA4 there was an IM\textsubscript{MAN>NONMAN}
effect in the subject-specific IM ROIs (t(19)=2.97, p=0.008), but there was no
LD\textsubscript{MAN>NONMAN} effect in these ROIs (t<1). There was no LD\textsubscript{MAN>NONMAN} effect in
the BA4 ROIs from the LD run (t(19)<1), and a marginally significant negative
effect for IM\textsubscript{MAN>NONMAN} (t(19)=-1.89, p=0.073). This is in line with previous
studies showing premotor but not primary motor activation during action language understanding (Tettamanti, et al., 2005; Tomasino et al., 2007).

All the subject-specific ROIs described above were also activated above baseline during action execution (LD ROIs BA4: t(17)=2.04, p=0.026; LD ROIs BA6: t(17)=3.03, p=0.004; IM ROIs BA4: t(17)=1.75, p=0.048; IM ROIs BA6: t(17)=1.83, p=0.042).

*Multi-voxel pattern analysis* To test for overlap in the pattern of response in BA6/BA4 using a technique that is not susceptible to statistical thresholding effects, we performed multi-voxel pattern analysis. In this analysis, the MAN>NONMAN contrast values for each voxel from a given area (left BA6 / left BA4) during LD and during IM were taken and a correlation coefficient was computed between them. That is, we took two vectors representing contrast values from voxels from BA6 or BA4 and correlated for each voxel the value during LD \text{MAN>NONMAN} with the value during IM \text{MAN>NONMAN}. This was done for each participant separately, yielding twenty correlation coefficients, which were converted to Fisher's z and tested in a one-sample t-test against mean zero. There was no correlation between patterns of activation to the MAN>NONMAN contrast in the LD and the IM tasks, neither in left BA6 (t(19)<1), nor in left BA4 (t(19)<1). This type of analysis also allowed us to do an additional check upon the stability of MAN>NONMAN differences within each session separately. We correlated the MAN>NONMAN contrast values from the one half of the LD session with those of the other half of the LD session. The same was done for the IM data (IM_\text{oddMAN>NONMAN} was correlated with IM_\text{evenMAN>NONMAN}). These correlations were significant in BA6 (LD: t(19)=2.61, p=0.017; IM: t(19)=3.15, p=0.005), as well as for IM in BA4 (t(19)=2.73, p=0.01), and marginally so for LD in BA4 (t(19)=1.96, p=0.065). The
latter may come as a surprise given that in the subject-specific ROI analysis we did not observe a MAN>NONMAN effect in the LD run. However, we want to stress that these within-session correlations might be inflated because of the high temporal correlation in the data and we therefore refrain from drawing strong conclusions based upon them.

In summary, we observed that reading of action verbs as well as explicit imagination led to activation in motor areas compared to baseline. However, the parts of both primary motor and premotor cortex that distinguished manual from non-manual action verbs during one task were not activated during the other, even in subject-specific ROIs that were constructed to maximize potential overlap between tasks. In unbiased subject-specific ROIs, primary motor cortex showed effector-specific activation during imagery, but not during lexical decision. Premotor cortex showed effector-specific activation during both tasks, but the areas activated during lexical decision did not overlap with areas activated during imagery. No overlap was observed even when we employed MVPA, which is not susceptible to artifacts due to statistical thresholding. The more exploratory whole-brain analysis also showed no overlap between MAN>NONMAN in the two tasks. We found left dorsal premotor cortex, left primary motor cortex and left inferior temporal cortex to be sensitive to IM\textsubscript{MAN>NONMAN} (but not to LD\textsubscript{MAN>NONMAN}), whereas an area in left superior frontal sulcus was sensitive to LD\textsubscript{MAN>NONMAN} (but not IM\textsubscript{MAN>NONMAN}).

**Discussion**

In this study, we investigated whether understanding action verbs involves the same tissues in cortical motor regions as explicit motor imagery. Left premotor cortex (BA6) showed effector-specific activation (i.e., stronger responses to manual
compared to non-manual verbs), during both the lexical decision and imagery tasks. Crucially, there was no overlap in the effector-specific response patterns in subject-specific ROIs in premotor cortex across the two tasks. More precisely, portions of BA6 and BA4 that were defined based on effector-specific activity during the imagery task showed no such activity during lexical decision. Conversely, BA6/BA4 ROIs based on effector-specific activity during the lexical decision task showed no effector-specific activity during imagery. This lack of overlap cannot be attributed to thresholding effects, since multi-voxel pattern analysis on un-thresholded t-maps showed that there was no correlation between effector-specific responses across tasks in BA4/6. Rather, these double-dissociations show that implicit motor simulation and explicit motor imagery do not necessarily engage the same neural tissues in premotor and primary motor cortices, and by inference, may not involve the same cognitive processes.

A double-dissociation between action verb understanding and mental imagery of actions was also found in the exploratory whole-brain analysis. There were no regions that showed effector-specific activation in both tasks. That is, there was no overlap between regions activated significantly in the MAN>NONMAN contrast during both lexical decision and imagery. Rather, a region of left dorsal premotor cortex distinguished between manual and non-manual verbs during motor imagery, but not during lexical decision. Conversely, an area in left superior frontal sulcus distinguished manual and non-manual verbs during lexical decision, but not during motor imagery (Fig. 3). It is not clear why this region of superior frontal sulcus should show effector-specific activation during lexical decision. For the present purposes, the findings from the whole-brain analysis underscore the dissociation between the neural substrates of action verb understanding and mental imagery of actions.
Is it possible that the lexical decision task only evoked processing of the verbs at a pre-semantic level, and hence did not activate representations of action verb meaning in the lexical decision task? We cannot definitely rule out this possibility, but it is unlikely to be an adequate alternative explanation of these data for several reasons. First, previous research indicates that lexical decision leads to processing up to the semantic level, as indexed by modulations of the N400 component (e.g. Chwilla, Brown, & Hagoort, 1995; Relander, Rama, & Kujala, 2009), reaction time studies (see Neely, 1991) and overlapping neural correlates between more explicit semantic tasks and lexical decision task (Ruff, Blumstein, Myers, & Hutchison, 2008). Second, the non-words were all phono-tactically legal and all ended in the suffix indicating the infinitive in Dutch, which necessitates full reading of the verb in order to be able to perform the task. Finally, it would be hard to explain the effector-specific activations we observed in premotor cortex if the action verbs were not processed beyond a pre-semantic level.

According to the version of embodied semantics proposed by Gallese and Lakoff (2005), the neural correlates of motor imagery and action semantics should be identical, or at least overlapping (see also Pulvermuller, 2005). Yet, the present data provide no support for this proposal, despite showing that both motor imagery and action verb semantics engage premotor cortex. Some researchers have stated that they use the terms ‘mental simulation’ and ‘mental imagery’ synonymously (e.g., Bergen, et al., 2007 p. 735). But our results urge caution in equating these constructs, and suggest that theories of embodied semantics should distinguish implicit mental simulation during language processing from explicit mental imagery.


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

On a third possibility, perhaps implicit simulation during language understanding and explicit imagery rely on different cerebral structures because they serve different functions at a computational level (Marr, 1982). A core component of implicit simulation during language processing is prediction. Myriad studies using behavioral and neural measures have demonstrated language users’ forward-looking orientation. Comprehenders use incoming linguistic and extra-linguistic information, rapidly and often unconsciously, to anticipate words, sounds, semantic associates, syntactic structures, discourse referents, and changes in the extra-linguistic environment that are likely to be relevant (e.g. DeLong, Urbach, & Kutas, 2005; Van Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005; for review see Van Berkum, in press). Presumably, prediction during language comprehension is not motivated solely by the need to comprehend language, per se. Rather, language is a tool that helps its users to interact with their physical and social environments. As such, implicit motor simulation during action verb understanding (termed ‘presonance’ by Zwaan & Kaschack, 2008) may serve predictive functions: preparing the language user for likely actions, linguistic or extra-linguistic, on a brief timescale that is relevant for using language and planning bodily actions (see Zwaan, 2004; Zwaan & Kaschak, 2008 for discussion).

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

If implicit motor simulation is predictive, then understanding action words should preferentially engage regions involved in motor planning. If conscious motor imagery is reflective (i.e., a covert re-enactment of prior actions), then imagining actions should engage not only regions involved in motor planning but also regions involved in motor execution. Consistent with these proposals, we find effector-specific activation during lexical decision in premotor cortex but not primary motor cortex (see also Aziz-Zadeh, et al., 2006; Tettamanti, et al., 2005; but see Pulvermüller, 2005). By contrast, we find effector-specific activation during imagery in both premotor and primary motor cortices (Tomasino, et al., 2007; 2008; see also Papeo, Vallesi, Isaja, & Rumiati, 2009).

The proposal that simulation and imagery are partially distinct processes with different computational goals predicts a dissociation in the motor system, and it is the only proposal we are aware of that can predict the double-dissociation we observe in premotor cortex. But it does not necessarily entail a double-dissociation. Why might simulations and images cued by the same verbs have different premotor representations? Assuming that participants had to understand each word before they could begin to imagine the action it referred to, the words presented in the ‘imagery’ condition may have first cued implicit
simulations (partly constitutive of understanding), followed by explicit images. Initial premotor activation in the imagery condition may have corresponded closely to the activation observed for lexical decision. Although this prospective activation is specified at the level of the effector, it is likely to be highly schematic. This schematicity is important for two reasons. First, simulation must be fast enough to support online language processing. Second, simulations cued by language must be underspecified enough to flexibly accommodate an incoming message; very different action plans would be necessary if the word grasp were followed by “…the barbell” as opposed to “…the needle”.

A different level of specification is necessary in order to create a mental image cued by language. If we vividly imagine the action corresponding to the verb throw, it is necessary to decide whether to imagine throwing a baseball or a frisbee, since these require different grips and different arm motions. As simulation ends and imagery begins, the premotor representation cued by the appearance of the word throw is changed, perhaps due to the specification of action plans within premotor cortex. Such a change should be observable given neuroimaging methods with sufficient spatiotemporal resolution. Given the temporal resolution of fMRI, however, any transient activation corresponding to implicit simulation at the beginning of an ‘imagery’ trial is obscured by activation corresponding to the more sustained process of creating and monitoring an explicit mental image.

As should now be clear, our proposal does not imply that simulation during understanding language precludes explicit imagery. On the contrary, at times language encourages explicit imagery, as when we appreciate a vivid description of scenery, or reflect on poetry (e.g. Just, Newman, Keller, McEleney, & Carpenter, 2004). We may engage mental imagery more in these contexts than during mundane
language understanding, or when reading isolated verbs in a lexical decision task. Again, we emphasize that nothing we propose here implies that the neural correlates of language understanding and explicit motor imagery can never be overlapping. Rather, our data show that they do not necessarily overlap, contrary to the predictions derived from some theories of embodied language understanding.

**Constraining interpretation of previous experimental results**

The present study addressed two concerns raised by Postle, et al. (2008), which have complicated interpretation of previous experimental results. First, on a skeptical interpretation of the original studies to show effector-specific activation of motor areas during verb processing (e.g., Hauk, et al., 2004; Tettamanti, et al., 2005), it is possible that observed activation was due to explicit imagery, rather than action verb semantics, per se (see also Willems & Hagoort, 2007). Although participants in these studies were not instructed to form explicit mental images in response to the stimuli, they were not prevented from forming them (perhaps to pass the time between stimuli in the scanner). By comparing effector-specific activation across tasks (lexical decision versus imagery), we explicitly controlled for spurious activation due to explicit imagery during lexical decision.

Second, Postle, et al. (2008), did not find effector-specific activation in premotor cortex during action verb processing, in contrast to earlier studies. They suggested that perhaps earlier positive results were artifacts of differences in imageability between critical and control stimuli. Indeed, some previous studies compared action verbs to abstract language as a high-level control (Tettamanti et al., 2005) or to hash-marks as a lower-level control (Hauk et al., 2004). Given that concrete action verbs are arguably more imageable than abstract words and that this is known to affect activations in (among other regions) premotor cortex (e.g. D'Esposito...
et al., 1997), it is possible that effects in earlier studies were mainly driven by increased imagery to concrete action language as compared to more abstract language. Yet, in the present study we find effects in the premotor ROI during lexical decision on MAN>NONMAN words, despite having equated the different verb types for imageability, among other standard psycholinguistic variables.

Finally, whereas Postle and colleagues defined their ROIs based on previous studies, we used subject-specific ROIs, which may have enhanced our ability to detect effector-specific activation in primary motor and premotor cortices (see also Aziz-Zadeh et al., 2006).

**Conclusion**

Understanding manual action verbs and forming mental images of the actions they name both produce effector-specific activation in regions of premotor cortex. Yet, parts of premotor cortex involved in these processes were found to be mutually exclusive: activation in the two tasks was neither overlapping nor correlated. These dissociations are inconsistent with the proposal that the neural substrates of implicit mental simulation during language processing and explicit mental imagery are the same, and also inconsistent with the possibility that simulation and imagery merely differ in degree of conscious awareness or level of detail. Rather, these data are most consistent with the possibility that simulation and imagery serve different functions at a computational level, simulation being strongly *predictive* and imagery being largely *reflective*. Given the observed neural dissociations and the proposed computational-level distinctions, the constructs of *mental simulation* and *mental imagery* should be distinguished in theories of embodied semantics.

**Notes**
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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References


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) $\text{LD}_{\text{MAN}} > 0 \cap \text{LD}_{\text{NONMAN}} > 0$ (in red, A) and $\text{IM}_{\text{MAN}} > 0 \cap \text{IM}_{\text{NONMAN}} > 0$ (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 $\text{LD}_{\text{MAN}} < \text{NONMAN}$ (in yellow) and the $\text{IM}_{\text{MAN}} < \text{NONMAN}$ (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 LD\textsubscript{MAN>NONMAN} (white bars) and the IM\textsubscript{MAN>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 IM\textsubscript{MAN>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.).

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 LD\textsubscript{MAN>NONMAN} comparison (white circles) and to the IM\textsubscript{MAN>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 LD\textsubscript{MAN>NONMAN} or for the IM\textsubscript{MAN>NONMAN} comparison are represented as isolated (non-connected dots). This was the case for two participants (IM\textsubscript{MAN>NONMAN}) and four (LD\textsubscript{MAN>NONMAN}) in BA4 and for two (LD\textsubscript{MAN>NONMAN}) and one (IM\textsubscript{MAN>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]).
| Comparison Region x y z Tmax nr voxels |
|--------------------------------------|-----------------|
| LD\(_{\text{MAN}>0}\) ∩ LD\(_{\text{NONMAN}>0}\) |
| L precentral sulcus / inferior frontal gyrus | -52 -6 48 | 7.11 | 3708 |
| L insula | -30 -2 60 | 5.64 |
| R precentral sulcus / inferior frontal gyrus | 46 8 32 | 4.73 |
| L superior / inferior parietal sulcus | -28 -68 30 | 6.59 | 1989 |
| R superior / inferior parietal sulcus | 30 -64 44 | 6.45 | 1114 |
| R superior temporal gyrus | 46 -32 -8 | 6.02 | 717 |
| L inferior occipital / fusiform gyrus / middle temporal sulcus | -40 -72 -14 | 16.59 |
| L calcarine sulcus | -18 -72 10 | 4.42 |
| R inferior occipital / fusiform gyrus | 46 -72 -16 | 10.76 |
| R calcarine sulcus | 20 -68 12 | 3.81 |
| L anterior cingulate sulcus | -6 2 60 | 7.48 | 2713 |
| L hippocampus | -18 -28 -2 | 7.35 | 446 |
| IM\(_{\text{MAN}>0}\) ∩ IM\(_{\text{NONMAN}>0}\) |
| L inferior frontal gyrus / precentral sulcus | 44 -8 56 | 7.28 |
| R inferior frontal gyrus / precentral sulcus | 50 16 -2 | 7.33 |
| L central sulcus | -44 -36 58 | 4.78 |
| R central sulcus | 46 -30 56 | 2.90 |
| R anterior cingulate sulcus | 4 2 66 | 10.22 |
| L anterior cingulate sulcus | -4 -4 70 | 11.87 |
| R calcarine sulcus | 24 -58 4 | 9.22 | 3256 |
| R middle temporal gyrus | 54 -56 6 | 4.74 |
| L calcarine sulcus | -22 -62 4 | 9.10 | 1881 |
| L middle temporal gyrus | -10 -72 18 | 6.01 |
| L middle temporal gyrus | -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
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. Results are corrected for multiple comparisons at p<0.05. Only a limited amount of peak voxels per cluster are reported (e.g. in occipital cortex). See Fig. 2.
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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=4 sec). 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=4 sec), 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) LDMAN>0 ∩ LDNONMAN>0 (in red, A) and IMMAN>0 ∩ IMNONMAN>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 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.).
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]).