

Body-specific representations of action verbs: Evidence from fMRI in right- and left-handers

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Abstract

According to theories of embodied cognition, understanding a verb like throw involves unconsciously simulating the action throwing, using areas of the brain that support motor planning. If understanding action words involves mentally simulating our own actions, then the neurocognitive representation of word meanings should differ for people with different kinds of bodies, who perform actions in systematically different ways. In a test of the body-specificity hypothesis (Casasanto, 2009), we used fMRI to compare premotor activity correlated with action verb understanding in right- and left-handers. Right-handers preferentially activated left premotor cortex during lexical decision on manual action verbs (compared with non-manual action verbs), whereas left-handers preferentially activated right premotor areas. This finding helps refine theories of embodied semantics, suggesting that implicit mental simulation during language processing is body-specific: Right and left-handers, who perform actions differently, use correspondingly different areas of the brain for representing action verb meanings.

Keywords: Action; Body-specificity; Embodied cognition; fMRI; Handedness; Semantics

Introduction

Theories of embodied cognition propose an intimate link between language and bodily experience. In this framework, to understand a word is to create an implicit mental simulation of its referent, using regions of the brain that support perception and action (e.g. Anderson, 2003; Barsalou, 2008; Zwaan, 2004). Consistent with this view, studies show that when participants read action-related verbs like ‘kick’, ‘pick’ and ‘lick’ they activate effector-specific regions of premotor cortex, as when they move the effector most associated with these verbs (i.e. their foot, hand, or tongue) (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Hauk, Johnsrude, & Pulvermuller, 2004; Tettamanti et al., 2005).

The goal of the present study was to refine the notion of implicit mental simulation during language processing, by framing experimental predictions in terms of the body-specificity hypothesis (Casasanto, 2009): If concepts and word meanings are constituted, in part, by implicit simulations of our own perceptions and actions, then their

neurocognitive representations should differ for people who perceive and act upon the environment in systematically different ways. We investigated whether activity in motor cortex during action verb processing reflects the way an individual language user typically performs the action that the verb refers to.

Across neuroimaging studies, activity in cortical motor areas associated with manual action verbs has been left-lateralized (Aziz-Zadeh et al., 2006; Hauk et al., 2004; Ruschemeyer, Brass, & Friederici, 2007; Tettamanti et al., 2005). This lateralization could be due to the general left-hemisphere dominance for language. Alternatively, it could be a consequence of testing only right-handed participants. We propose that if word meanings are implicit simulations, then understanding words for actions that people typically perform with their dominant hand should involve simulating these actions in contralateral premotor areas (i.e., areas that subserve planning of actions with the dominant hand).

To test this proposal, we used fMRI to compare premotor activation in right- and left-handers during a lexical decision task on manual action verbs (e.g., grasp, throw) and non-manual action verbs (e.g., kneel, giggle). If the motor component of an action verb’s meaning is a body-specific simulation of the action it refers to as the particular language user would be likely to perform it, then activity in premotor cortex during manual action verb processing should be differently lateralized in right- and left-handers. Each group should preferentially activate premotor areas contralateral to their dominant hand.¹

The non-manual action words served as a control. Finding the predicted difference between right- and left-handers for manual action words, alone, could be evidence for implicit body-specific simulation of manual actions during word reading. Alternatively, it could be an artifact of differences in language laterality between right- and left-handers, more generally. However, this alternative is ruled out by testing for the predicted interaction of Hemisphere (right premotor, left premotor) and Handedness (right-handed, left-handed) in voxels that are significantly more active during manual compared to non-manual action verbs (i.e., essentially, by testing for a particular three-way interaction of Hemisphere, Handedness, and Verb Type).

Methods

Participants

We tested thirty-two healthy participants 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 of whom gave informed consent. Half of the participants were left-handed ($N=16$, 12 female, mean age 23.4 years, range 19-32 years, adapted Dutch version of Edinburgh Handedness Inventory (EHI) score (Oldfield, 1971; Van Strien, 1992): mean=-94.3, s.d.=8.7, range -82 - -100, mode=-100), and half were right-handed ($N=16$, 10 female, mean age 23.2, range 20-29 years, EHI score: mean=96.6, s.d.=7.3, range 82 - 100, mode=100). The groups did not differ in age ($t(30)<1$), or in absolute EHI value ($t(30)<1$). The local ethics committee approved the study.

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 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). MAN words were significantly more associated with hand actions than NONMAN words ($t(94)=23.60$, $p<0.001$, $prep=0.99$). 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; $t(94)<1$) and number of letters ($t(94)=1.51$, $p=0.13$, $prep=0.78$). 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'). A stimulus list of 128 stimuli (48 MAN + 48 NONMAN + 16 fillers + 16 nonwords) was created, and pseudo-randomised 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.

Procedures

Experimental procedure Participants performed a lexical decision experiment in the MRI scanner. Stimuli were presented using Presentation software (www.nbs.com, version 10.2) and were projected from outside of the scanner room onto a mirror attached to the head coil such that the participant could see them. Words appeared for 1500 ms in white font, in the middle of a black background. A fixation cross appeared for 500 ms before word presentation, to signal the start of a new trial. In 25% of the trials (i.e. filler and non-word trials), stimulus presentation was followed by a screen with the question whether the previous stimulus was an existing word or not. Participants were instructed to answer as quickly and accurately as possible by pressing a button with their left or right index

finger. No responses were made following critical stimuli (MAN and NONMAN verbs). Response side varied between filler trials, such that sometimes the left button indicated 'yes' and sometimes the right button indicated 'yes'. This was done to prevent biased motor preparation to one response side. Participants had 1500 ms to respond and got feedback on the screen when they were too slow. Participants were familiarised with the procedure by means of 10 practice trials before the start of the experiment, with stimuli not used in the remainder of the experiment. Trial onset was effectively jittered with respect to onset of volume acquisition by varying the intertrial interval between 2 and 6 seconds in steps of 250 msec (mean ITI=4 sec) (Dale, 1999).

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). 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, fillers words and non-words. Responses (button presses) were modelled separately. 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). Head motion never exceeded 3 mm or 0.05 degrees.

Given our a priori hypothesis, we created subject-specific 4mm spherical regions of interest with the maximally activated voxel to the MAN stimuli (mapwise thresholded at $p<0.001$) as the center coordinate, in cytoarchitectonically defined left and right Brodmann Area (BA) 6 (Eickhoff, Heim, Zilles, & Amunts, 2006). In this way we optimised our analysis for each subject individually, while controlling the location of the ROI by means of independent anatomical data (see also Aziz-Zadeh et al., 2006). We ensured that no voxels from the opposite hemisphere were taken into account (which could occur due to the spherical shape of the ROIs). A similar analysis was performed for primary motor cortex by using cytoarchitectonic maps of BA4 (combination of BA4a and BA4p, (Geyer et al., 1996)). For the BA4 analysis, in some participants no voxels responded to the MAN contrast, so we computed the mean response over BA4 instead of the maximally activated voxel accordingly. Mean contrast weights from the MAN>NONMAN, MAN>0 and NONMAN>0 contrasts were taken to a second level analysis involving repeated

measures ANOVA with HEMISPHERE (left, right) as a within-subjects factor and GROUP (left-handers, right-handers) as a between-subjects factor. Given our a priori hypothesis we tested a specific interaction direction (i.e. left hemisphere>right hemisphere in right-handers and right-hemisphere>left-hemisphere in left-handers).

To assess sensitivity of areas outside of pre- and primary motor cortex, we also conducted a whole brain analysis, testing for the interactions described above in a random effects group analysis. Correction for multiple comparisons was implemented by thresholding the group statistical maps at $p<0.001$ uncorrected and subsequently taking the cluster extent into account to correct maps at $p<0.05$ (Friston, Holmes, Poline, Price, & Frith, 1996).

Behavioral data analysis involved independent samples t -tests on percentage of correct trials and late responses.

Results

Behavioral results

The groups did not differ in percentage of correct responses on the lexical decision task (left-handers: 93.9% (s.d. 5.5); right-handers: 95.5% (s.d. 3.6); $t(30)<1$), or in the percentage of too-late responses (left-handers: 0.58% (s.d. 1.26); right-handers: 0.19% (s.d. 0.78); $t(30)=1.05$, $p=0.30$, $prep=0.64$).

Neural results

The main analysis tested for a 3-way interaction of Handedness, Hemisphere, and Verb Type during lexical decision on manual and nonmanual verbs, in subject-specific ROIs within BA6 (premotor cortex). Results showed a significant HEMISPHERE x GROUP interaction in the MAN>NONMAN contrast values from the subject-specific ROIs ($t(30)=2.14$, $d=0.64$, $p=0.04$, $prep=0.89$; Fig. 1a). For manual compared to non-manual action verbs, left-handers had consistently stronger activations in right BA6, whereas right-handers showed stronger activation in left BA6 for this contrast, consistent with predictions based on the body-specificity hypothesis. There were no main effects of Hemisphere or Group (all $F<1$).

To confirm that this 3-way interaction was driven by the predicted difference in MAN responses (rather than by incidental differences in NONMAN responses), we analyzed MAN and NONMAN responses separately. The predicted 2-way interaction was present in the premotor response to MAN stimuli alone, but not to NONMAN stimuli (MAN HEMISPHERE x GROUP interaction: $F(1,30)=5.71$, $\eta^2p=0.16$, $MSe=0.30$, $p=0.02$, $prep=0.95$; Main effect of HEMISPHERE: $F(1,30)=4.77$, $\eta^2p=0.14$; $MSe=0.30$, $p=0.04$; $prep=0.89$; Main effect of GROUP: $F<1$; NONMAN HEMISPHERE x GROUP interaction: $F(1,30)=1.78$, $\eta^2p=0.05$, $MSe=0.35$, $p=0.19$, $prep=0.73$; Main effect of HEMISPHERE: $F(1,30)=2.72$, $\eta^2p=0.08$; $MSe=0.35$, $p=0.11$, $prep=0.81$; Main effect of GROUP: $F<1$).

To corroborate the main subject-specific ROI analysis, we tested for the predicted interaction of Handedness,

Hemisphere, and Verb Type in all voxels that responded to the presentation of MAN words at $p<0.001$ within our anatomical search region (left/right BA6). A pattern similar to the results of the subject-specific ROI analysis was found (Fig. 1b), although the interaction did not reach statistical significance using the more coarsely-defined ROI (MAN>NONMAN: Interaction HEMISPHERE x GROUP: $t(30)=1.59$, $d=0.41$, $p=0.12$, $prep=0.80$; Main effect of HEMISPHERE: $F<1$; Main effect of GROUP: $F<1$).

Interestingly, there was considerable variation in the location of the subject-specific ROIs within our anatomical search region, BA6. Whereas the majority of ROIs were relatively lateral in premotor cortex, the ROIs in a few participants were more medial, in pre-supplementary motor area (pre-SMA), another part of BA6 also involved in motor planning (Nachev, Kennard, & Husain, 2008) (see Table 1 and Fig. 2). Importantly, a similar association between handedness and hemisphere was found in pre-SMA as in lateral premotor cortex.

No effects of hemisphere or group were observed in BA4 (primary motor cortex), attesting to the specificity of this finding for premotor cortex (MAN>NONMAN: Interaction HEMISPHERE x GROUP: $t(30)<1$, Main effect of HEMISPHERE: $F(1,30)<1$; Main effect of GROUP: $F(1,30)<1$; MAN words only: Interaction HEMISPHERE x GROUP: $F(1,30)<1$; Main effect of Hemisphere: $F(1,30)=6.95$, $\eta^2p=0.19$; $MSe=0.75$, $p=0.01$, $prep=0.94$; Main effect of GROUP: $F<1$; NONMAN words only: Interaction HEMISPHERE x GROUP: $F(1,30)<1$; Main effect of HEMISPHERE: $F(1,30)=6.25$, $\eta^2p=0.17$; $MSe=0.67$, $p=0.02$, $prep=0.93$; Main effect of GROUP: $F<1$). Similar effects were obtained when taking all responsive voxels in BA4 into account. Likewise in a whole brain analysis, no areas were significantly activated by the directional Group x Verb Type interactions.

Discussion

This study investigated whether the meanings of action verbs are grounded in the ways that particular language users perform the actions they refer to. During a lexical decision task, right- and left-handers showed contrasting patterns of activity in brain regions responsible for planning manual actions when reading manual action verbs like *grasp* and *throw*, as compared to reading non-manual action verbs. Each group preferentially activated premotor areas in the hemisphere contralateral to their dominant hand, suggesting that the motor component of manual action verb semantics is body-specific (Casasanto, 2009). People with different bodies, who perform actions in systematically different ways, use correspondingly different neural tissues for representing action verb meanings.

Is it possible that these results reveal activation due to conscious mental imagery of actions, which could have been induced inadvertently by the lexical decision task? We conducted a control task to evaluate this possibility. After completing the lexical decision task, participants performed a mental imagery task in which they saw all of the manual

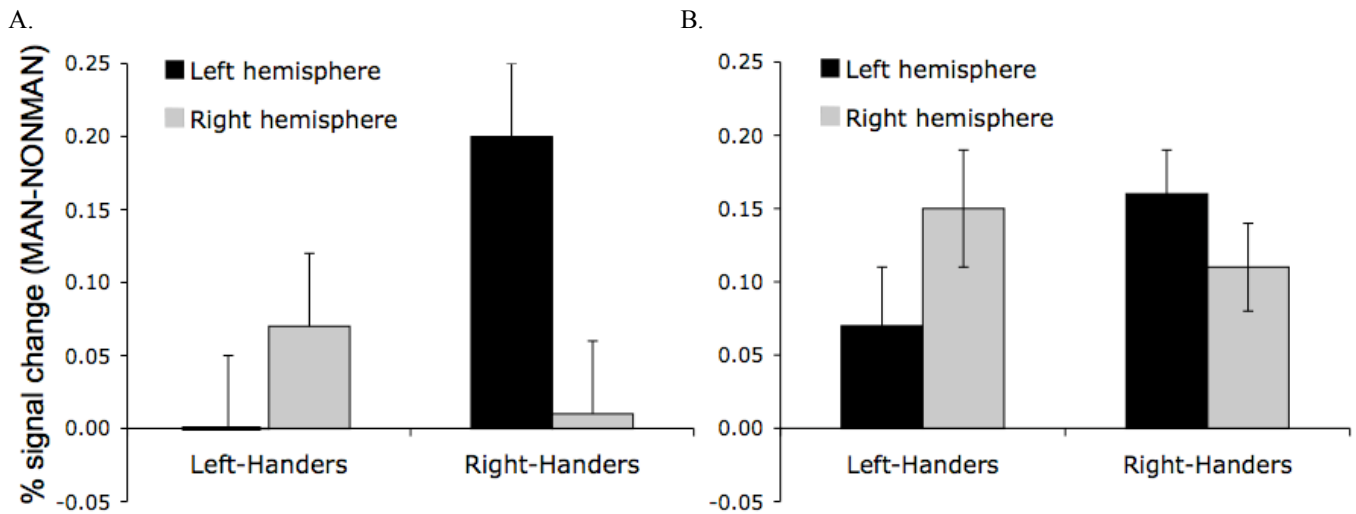


Figure 1. Results of the functionally-defined ROI analyses. Panel A: Results from a spherical ROI around the BA6 voxel maximally activated during MAN words. Panel B: Results from all BA6 voxels responsive to MAN words, thresholded at $p < 0.001$. Error bars indicate s.e.m.

Table 1 Mean coordinates and standard deviations for subject-specific ROIs in left and right BA6 (in MNI space).

Group	Hemisphere	Mean (s.d.)		
		x	y	z
Left-Handers	Left	-39 (20)	-3 (4)	44 (18)
	Right	32 (24)	0 (9)	50 (19)
Right-Handers	Left	-35 (20)	-1 (8)	53 (8)
	Right	32 (25)	0 (10)	50 (17)

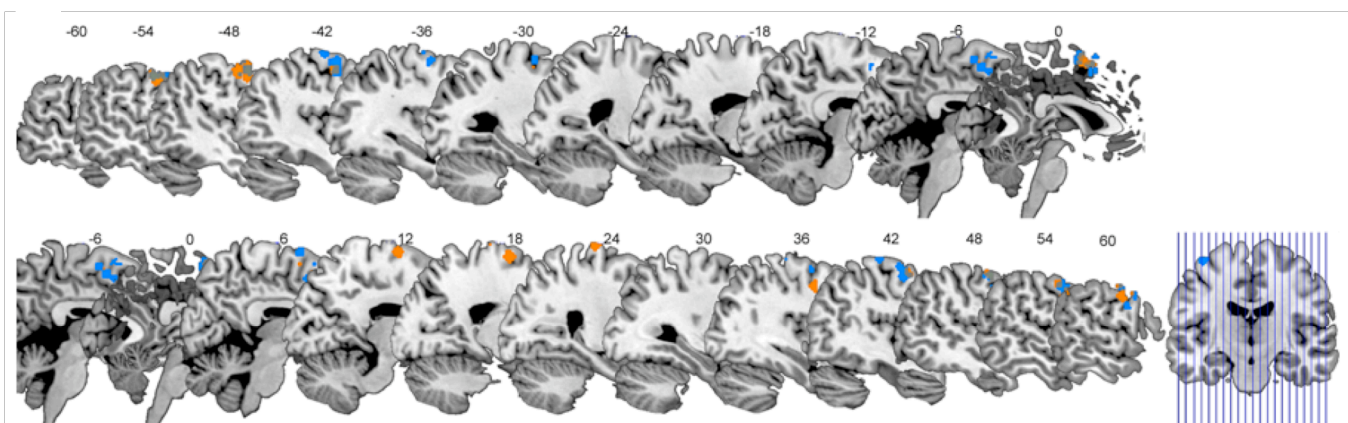


Figure 2. Locations of the subject-specific regions of interest in BA6 for left-handers (orange) and right-handers (blue) on multiple sagittal slices (x-coordinate is indicated).

and non-manual action verbs again, and were asked to consciously imagine performing the actions they referred to.

Space precludes reporting the details of the mental imagery data here. Importantly, however, when activity during lexical decision for manual action verbs and conscious imagery of manual actions was compared directly, we found no significant overlap between tasks in either primary or premotor areas, and no correlation between activity during the two tasks in subject-specific premotor ROIs. We can therefore conclude with high confidence that premotor activity during the lexical decision task was not due to conscious mental imagery, but rather to lexical processes, *per se* (see also Tettamanti, et al., 2005; Tomasino, et al., 2007).

Mental simulation during language processing

These findings suggest two refinements to the notion of implicit mental simulation during language processing. First, embodied cognition researchers sometimes suggest that unconscious simulation and conscious imagery are identical processes (e.g., Gallese & Lakoff, 2005). Indeed, some careful researchers have stated that they use the terms ‘mental simulation’ and ‘mental imagery’ synonymously (e.g., Bergen, et al., 2007 pg. 735). Yet, the present data urge caution in equating the notions of implicit simulation during language processing and explicit mental imagery.

Both implicit (unconscious) simulation and explicit (conscious) imagery engage body-specific representations in premotor cortex, but these representations may be different in character. When we read the verb *throw*, the corresponding premotor activity may constitute a far less elaborated action plan than when we consciously imagine throwing. Understanding *throw* apparently involves an action representation that is specified with respect to which arm we would use. But at least by default, the motor plan activated by a clause like *throw the ball* may lack the kinds of further specification that would be needed if we were to imagine this action explicitly (e.g., Is it an underhand or overhand throw? Is it a baseball or a basketball?) At minimum, premotor representations underlying implicit simulation and explicit imagery must differ quantitatively, in terms the detail with which action plans are specified. The finding of distinct premotor representations for these processes raises the possibility that they differ qualitatively, as well.

A second refinement these data suggest concerns the perspective that readers adopt when understanding action words. Based on previous studies (e.g. Aziz-Zadeh et al., 2006; Hauk et al., 2004; Tettamanti et al., 2005), it was not clear to what extent the motor component of action word meanings reflects actions we have observed others performing (*allocentric simulation*) or actions we have performed ourselves (*egocentric simulation*). The allocentric possibility predicts that neurocognitive representations of manual action word meanings should be similar in right- and left-handers, since presumably

everyone observes about the same proportion of right- and left-handed actions by other people. The discovery that motor activity associated with manual action words is body-specific supports the egocentric possibility, and suggests that people implicitly simulate their own prior or potential actions when understanding action words.

Is the perspective that people adopt when understanding action words fixed? We suggest that the egocentric simulations participants appear to have created during this lexical decision task reflect a default interpretation of the words’ meanings, but not the only possible interpretation. Furthermore, these results do not imply that people can only understand language about actions they have performed themselves. We propose, for example, that someone who has never used chopsticks could still understand the sentence *He picked up the dumpling with chopsticks* by creating a motor simulation based on visual experiences of other people using chopsticks, and on extrapolation from familiar motor actions (eating with a fork, holding a pencil between the fingertips, etc.) (see Anderson, 2003). It remains an open question whether people can understand words referring to actions they have never performed as completely as words for actions they have, and whether implicit simulations of actions they have never performed are body-specific (see Aglioti, Cesari, Romani, & Urgesi, 2008; Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006).

The functional significance of premotor activity for language understanding also remains a question for ongoing research. Due to the correlational nature of fMRI data, it is not possible to infer whether the premotor activity reported here is a necessary part of action verb semantics (see Willems & Hagoort, 2007 for discussion). Although some constituents of word meaning may be abstracted away from our physical experiences (Mahon & Caramazza, 2008), the present results suggest that at least part of action word meaning consists in implicit mental simulations of actions as we would perform them with our particular bodies.

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Notes

1. This ‘differential lateralisation logic’ is supported by previous literature. For instance, Longcamp and colleagues showed that observation of letters leads to motor resonance in left ventral premotor cortex in right-handers (Longcamp, Anton, Roth, & Velay, 2003), and in right ventral premotor cortex in left-handers (Longcamp, Anton, Roth, & Velay, 2005) (see also Lewis, Phinney, Brefczynski-Lewis, & DeYoe, 2006). This ‘differential lateralisation logic’ is supported by previous literature. For instance, Longcamp and colleagues showed that observation of letters leads to

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