Observing, Performing, and Understanding Actions: Revisiting the Role of Cortical Motor Areas in Processing of Action Words

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Abstract

■ Language content and action/perception have been shown to activate common brain areas in previous neuroimaging studies. However, it is unclear whether overlapping cortical activation reflects a common neural source or adjacent, but distinct, sources. We address this issue by using multivoxel pattern analysis on fMRI data. Specifically, participants were instructed to engage in five tasks: (1) execute hand actions (AE), (2) observe hand actions (AO), (3) observe nonbiological motion (MO), (4) read action verbs, and (5) read nonaction verbs. A classifier was trained to distinguish between data collected from neural motor areas during (1) AE versus MO and (2) AO versus MO. These two algorithms were then used to test for a distinction between data collected during the reading of action versus nonaction verbs. The results show that the algorithm trained to distinguish between AE and MO distinguishes between word categories using signal recorded from the left parietal cortex and pre-SMA, but not from ventrolateral premotor cortex. In contrast, the algorithm trained to distinguish between AO and MO discriminates between word categories using the activity pattern in the left premotor and left parietal cortex. This shows that the sensitivity of premotor areas to language content is more similar to the process of observing others acting than to acting oneself. Furthermore, those parts of the brain that show comparable neural pattern for action execution and action word comprehension are high-level integrative motor areas rather than low-level motor areas. ■

INTRODUCTION

In the past decade, many studies have shown that conceptual information activates perceptual and motor areas of the brain. For example, words denoting actions activate the neural motor system (Rueschemeyer, Rooij, Lindemann, Willems, & Bekkering, 2010; Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008; Rueschemeyer, Brass, & Friederici, 2007; Hauk, Johnsrude, & Pulvermueller, 2004), whereas language denoting motion ("the car approaches") activates parts of the visual processing stream responsive to visually perceived motion (Rueschemeyer, Glenberg, Kaschak, Mueller, & Friederici, 2010; Saygin, McCullough, Alac, & Emmorey, 2010). In the past decade, converging evidence from behavioral, neuroimaging, and patient data all point consistently to the idea that language comprehension involves sensory-motor areas in a content-specific manner (reviews by Binder, Desai, Graves, & Conant, 2009; Aziz-Zadeh & Damasio, 2008; Zwaan & Fischer, 2008).

It should be noted that the automaticity and consistency with which lexical forms activate sensory-motor areas remain a topic of open debate. Several studies have demonstrated that embodied language effects are highly sensitive to linguistic and pragmatic context as well as to task demands. For example, words with motor meaning used in idiomatic phrases or nonliteral sentences, which are largely devoid of motor content (e.g., "he kicked the bucket"), have been shown to elicit less or no activation in sensory-motor areas (Schuil, Smits, & Zwaan, 2013; Van Dam, van Dijk, Bekkering, & Rueschemeyer, 2012; Raposo, Moss, Stamatakis, & Tyler, 2009; Rueschemeyer et al., 2007; but see also Boulenger, Hauk, & Pulvermuller, 2009). Likewise, words with no motor meaning, which are used to imply a request for action (e.g., "it is hot in here" spoken in the context of a closed window), do activate sensory-motor areas reliably (Van Ackeren, Casasanto, Hagoort, Bekkering, & Rueschemeyer, 2012), suggesting that lexical forms are not necessary to elicit motor activation. Finally, words presented in the context of a motor task are more likely to elicit activation patterns consistent with an embodied framework of words presented in nonmotoric contexts (e.g., Tomasino & Rumiati, 2013; Papeo, Rumiati, Cecchetto, & Tomasino, 2012). Thus, the recruitment of sensory-motor areas appears to be a flexible enterprise that is affected by linguistic and pragmatic context as well as task demands.

A wide range of theoretical accounts are offered to explain the link between language and sensory-motor

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processing (for reviews, see Kiefer & Pulvermueller, 2012; Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012; Barsalou, 2008). On one side, sensory-motor involvement in language processing is thought to be epiphenomenal (e.g., Mahon & Caramazza, 2008; Patterson, Nestor, & Rogers, 2007). Such accounts argue that semantic information is instantiated in an abstract format distinct from modality-specific cortical areas. Any activation of sensory-motor areas during language processing tasks is thought to reflect late mental imagery, morphological, and/or ortho-phonological statistical properties of lexical items rather than the locus of semantic content (see also De Zubicaray, Arciuli, & McMahon, 2013; Papeo, Pascual-Leone, & Caramazza, 2013). On the other extreme are accounts proposing that semantic information is stored in sensory-motor code (Pulvermueller, 2005; Glenberg & Kaschak, 2002). This reenactment view proposes that modality-specific activations during language processing are representational in nature. Between the two extremes lie theories proposing that features of semantic content are represented in sensory-motor codes but that abstraction of these features and integration across multiple perceptual and cognitive domains are necessary during language comprehension (e.g., Kiefer & Pulvermueller, 2012; Barsalou, 2008; Vigliocco, Vinson, Lewis, & Garrett, 2004). This integrative view proposes that modality-specific areas reflect general representation of content; however, the temporal and spatial characteristics of modality-specific activations differ for language and action experiences.

In this experiment, we used a pattern classification approach to distinguish between these three accounts (Mur, Bandettini, & Kriegeskorte, 2009). Whereas previous neuroimaging studies have demonstrated that words with specific content modulate modality-specific brain areas, we aimed to assess whether cortical processes in motor areas share the same neural basis for motor experience and language comprehension. To this end, a classifier was trained to distinguish between neural activity associated with (1) action execution (AE) versus nonbiological motion and (2) action observation (AO) versus observation of nonbiological motion. The classifiers trained to make these two distinctions were then tested on patterns of neural activity elicited by words denoting actions versus words denoting nonbiological motion. If the classifier trained on neural activity elicited by actual action experience can distinguish between activity elicited by the comprehension of different word categories, this bolsters the claim that previously reported results indeed reflect a common neural mechanism for language and action (note that this stands in contrast to the prediction of integration theories). If the classifier fails to distinguish between activity elicited by the different word categories, this will show that the mechanisms underlying action and language processing are not the same (note: in contrast to the prediction of reenactment theories).

METHODS

Participants

Twenty-two participants (seven men, $M = 22.22$ years, $SD = 1.99$ years) took part in this study after giving informed consent. Participants were recruited through the Radboud University participant pool and were reimbursed financially or with course credit for their time. All participants were native speakers of Dutch, had no history of neurological disorder, and had normal or corrected-to-normal eyesight.

Stimuli

Participants were presented with stimuli in five conditions: AE, AO, nonbiological motion observation (MO), action words (AW), and nonaction words (NW). Word stimuli were matched across conditions with respect to word length ($t(118) = -1.61, p > .1$), frequency per million ($t(118) = 1.01, p > .1$), and motion imageability ($t(118) = .05, p > .1$; for means per condition, please see below). For a complete list of the word stimuli used, please see Appendix 1.

- AE: Participants watched a short film clip (2 sec) in which they saw a hand executing a simple intransitive action (e.g., extending and flexing the fingers). After 2 sec, the video disappeared completely. Participants then executed the instructed action continuously for 30 sec. Onset and offset of the participants movement were marked with a button press. Twelve different hand actions were executed. The AE condition is for all intents and purposes an action imitation condition, but critically, it involves explicit execution of a hand motor act.
- AO: Participants observed an intransitive hand action for 30 sec. In total, 12 video clips showing different hand actions were used.
- MO: Participants observed mechanical toys (i.e., nonbiological agents) in motion. Film clips lasted 30 sec. In total, 12 video clips showing three different mechanical toys were used.
- AW: Participants read 10 verbs depicting hand actions (e.g., "to grasp," "to pinch"); each word was presented for 3 sec. In total, 60 words were presented (mean length = 7.45, $SE = 0.19$; mean frequency = 36.57, $SE = 6.24$; mean motion imageability = 0.43, $SE = 0.02$).
- NW: Participants read 10 verbs depicting highly imageable but nonbiological events (e.g., "to snow," "to melt"); each word was presented for 3 sec. As in the case of the action verbs, 60 words were presented in total (mean length = 7.88, $SE = 0.19$; mean frequency = 24, $SE = 10.8$; mean motion imageability = 0.428, $SE = 0.03$; for a complete list of words, please see Appendix 1).

Task

Participants were asked to watch the stimuli carefully. Following the presentation of five experimental blocks

(e.g., one instance of each condition), participants were shown three stimuli (e.g., words or videos) and asked to indicate whether each stimulus had appeared in the previous set of stimuli. Participants responded via button press. The purpose of the task was (1) to ensure that participants attended to stimuli and (2) to provide an overt hand movement temporally independent from any experimental stimulus to use as a hand action localizer.
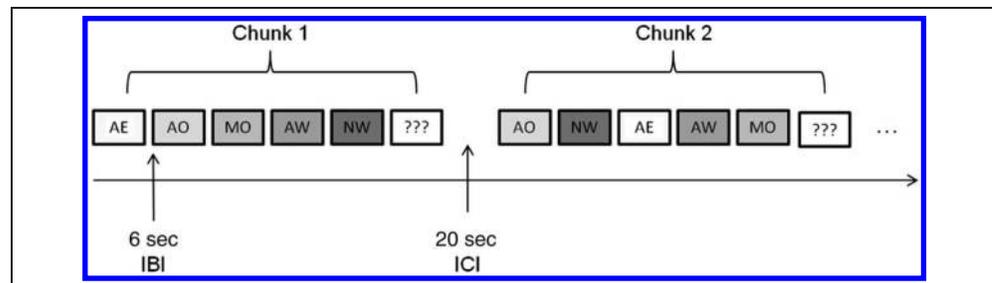
Stimulus Presentation

Stimuli were presented in 12 chunks, each consisting of five 30-sec blocks separated by a 6-sec interblock interval (see Figure 1). Chunks were made temporally independent from one another by including a 20-sec interchunk interval. Each block contained stimuli from one of each of the five conditions (AE, AO, MO, AW, NW). The order of blocks within each chunk was pseudorandomized, so that each chunk had a unique order of block presentation. Following each chunk, participants were presented with three stimuli (e.g., video clips, word stimuli) and asked to indicate whether the stimuli were included in the preceding chunk.

Data Acquisition

MRI data acquisition was performed on a Siemens Magnetom Trio scanner (Siemens Medical System, Erlangen, Germany) with a magnetic field strength of 3 T. The functional scans were acquired using a multiecho gradient pulse sequence (repetition time = 2390 msec; echo time = 9.4, 21.17, 32.94, 44.71, and 56.48 msec; flip angle = 90°). Each volume consisted of 31 transversal slices with a thickness of 3 mm. The voxel resolution was 3.5 mm × 3.5 mm × 3.5 mm. After the collection of functional data, a structural scan was performed for each individual participant. The image was a T1-weighted 3-D magnetization prepared rapid gradient echo sequence comprising 192 sagittal slices (repetition time = 2300 msec, echo time = 3.03 msec, slice thickness = 1 mm).

Data Analysis

fMRI Preprocessing

SPM8 was used to initially transform DICOM images into NIFTI images for further processing. Subsequently, six movement parameters (three translations and three rotations) were extracted from the first echo of each volume and subsequently used to correct for small head movements in all five echoes of each volume. All five echoes were then combined into a single volume using a weighted average (Poser, Versluis, Hoogduin, & Norris, 2006). Further preprocessing and data analysis were carried out using FMRIB's Software Library 4.1.9 (Smith, Jenkinson, Woolrich, Beckman, & Behrens, 2004). A high-pass temporal filter using a 100-sec cutoff was applied, and images were normalized into a 2-mm standard stereotaxic space (Montreal Neurological Institute). No spatial smoothing was performed to preserve local voxel information.

Functional Localizer

Motor areas were defined using a general linear model and carried out using fMRI Expert Analysis Tool 5.92. A canonical gamma function was used to model the BOLD response. The model contained six regressors, the button press plus five task conditions. The contrast was calculated as button press versus baseline. Statistical maps were computed using FMRIB's Local Analysis of Mixed Effects stage 1 (Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004) and thresholded with a z value of 2.56 and a corrected cluster significance threshold of $p < .05$ (Worsley, 2001).

Multivoxel Pattern Classification

Two types of pattern classification analyses were performed. First, the classifier was trained and tested on the same conditions, namely, (1) AE versus MO and (2) AO versus MO. This ensures that the classifier successfully learned to distinguish between task conditions. ROIs were only included in the second level of analysis if the classifier was successful in learning to distinguish between the initial task conditions. In ROIs in which the first level of pattern classification was successful, the trained classifiers

Figure 1. Stimulus presentation. Stimuli from the five experimental conditions (AE, AO, MO, AW, NW) were presented in random order in blocks of 30 sec each. Between each block of stimuli, a 6-sec interblock interval (IBI) was inserted. At the end of each chunk of five stimulus blocks, a short question block was presented, which gauged

participant's attention and required participants to make an overt button press. Between chunks, a 20-sec interchunk interval (ICI) was inserted to ensure the temporal independence of chunks.

Figure 2. (Top) Areas identified by the functional localizer (i.e., simple button press; cluster corrected threshold, $p < .05$). (Bottom) ROIs used for classification analysis (sphere with 9-mm radius surround peak activations in areas seen on top. L = left; R = right.
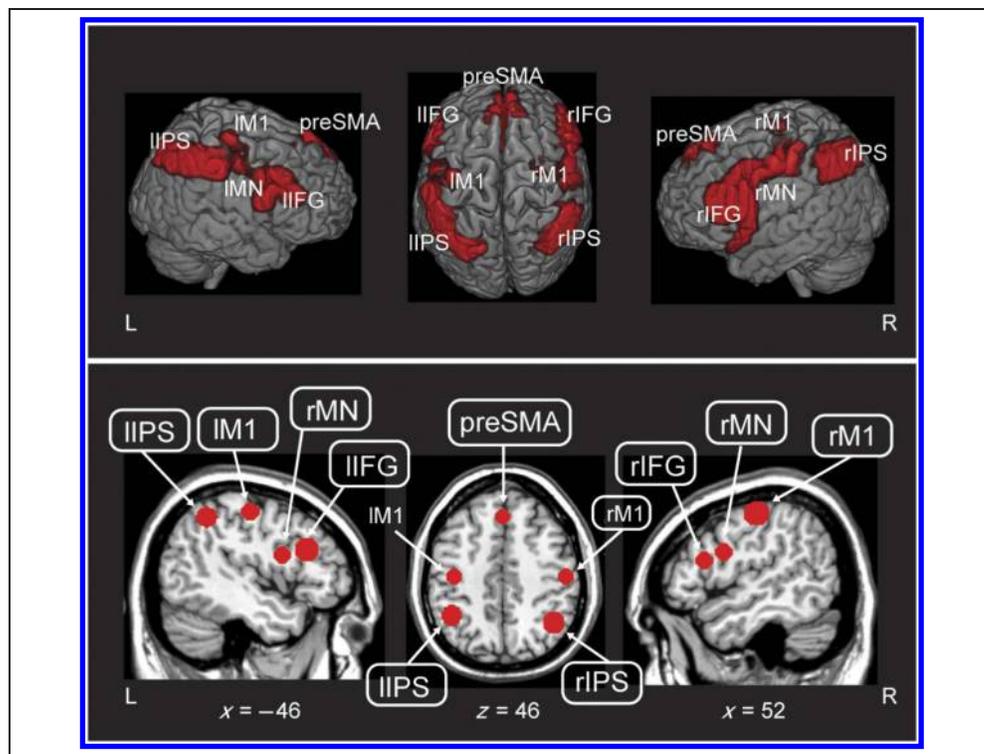
were used to test between the reading of action versus nonaction verbs (AW vs. NW). Importantly, this was done without any further training of the initial classifier.

Each task condition was modeled with a general linear model containing a separate regressor for every chunk. Note that the chunk for AE condition was the time between button presses, during which participants repeatedly executed the action they had been shown in the 2-sec video clip. Resulting beta estimates (12×5 per participant) were z scored to a mean of 0 and to a standard deviation of 1. In each fold, a linear support vector machine ($C = 1$) was trained on the extracted voxel pattern for all but one participant. The remaining participant was used as an independent test set. This procedure (leave-one-participant-out cross-validation with $n = 22$ folds; Clithero, Smith, Carter, & Huettel, 2011) was repeated until every participant was used in the test set once. The classification analysis was performed separately for seven ROIs identified by the functional localizer and two taken from the literature, which correspond to the putative location of mirror neurons in the lateral pFC (Oosterhof, Tipper, & Downing, 2012; Kilner, Neal, Wiskopf, Friston, & Frith, 2009). Note that the classification tests a common spatial pattern across participants as opposed to between trials.

A statistical test of the classification accuracy was performed using a nonparametric permutation analysis (Nichols & Holmes, 2002). To this end, we repeated each classification 10.000 times with shuffled task labels. The p value was calculated as the amount of times the permuted classification reached an accuracy level higher or equal to the original classification accuracy without permu-

tation, divided by the total number of permutations. All classification analyses were performed using the PyMVPA software package (Hanke et al., 2009).

RESULTS

Functional Localizer

The results of the functional localizer show brain areas that were activated when participants performed an action with their right hand (i.e., pushed a button). Importantly, this hand action was not performed in conjunction with any of the critical experimental conditions; thus, the data from this condition are temporally independent from the experimental data in this experiment. The results of the functional localizer show activation in conjunction with button presses in seven large regions. These included bilateral inferior frontal gyrus (part of the ventral premotor cortex; e.g., Binkofski & Buccino, 2006), bilateral inferior parietal cortex, bilateral primary motor cortex (M1), and the pre-SMAs (preSMAs). In addition, we included two additional ROIs in the bilateral ventral premotor cortex, which target specific areas in the premotor cortex that have been described previously as potential sites for mirror neurons in humans (Oosterhof et al., 2012; Kilner et al., 2009). We created a spherical ROI with radius = 9 mm (358 voxels) around the peak coordinates of the functional localizer map (see Figure 2). This results in nine, equally sized ROIs that were used for all subsequent analyses: (1) left inferior frontal gyrus (lIFG), (2) right IFG (rIFG), (3) the preSMA, (4) left intraparietal sulcus

Table 1. Classifier Performance Rates and Spatial Information for ROIs

| | Coordinates | Classification Performance | | | |
| | Spherical ROI Centers | Trained on AE versus MO | | Trained on AO versus MO | |
ROI	x, y, z	Test: AE versus MO	Test: AW versus NW	Test: AO versus MO	Test: AW versus NW
lIFG	−46, 24, 24	67.50**	54.54	85.00***	70.45***
rIFG	46, 20, 18	70.00**	50.12	67.50**	65.00**
preSMA	0, 32, 40	77.50***	75.00***	70.00**	50.00
lIPS	−42, −50, 48	70.00***	62.50**	80.84***	67.5***
rIPS	42, −56, 46	62.50**	72.50***	75.00**	52.50
lM1	−40, −18, 52	50.12	–	53.64	–
rM1	52, −18, 52	49.95	–	55.09	–
lMN	−53, 6, 21	50.12	–	47.87	–
rMN	57, 6, 24	55.09	–	52.91	–

Information about the center of each spherical ROI (Montreal Neurological Institute coordinates, size = 358 voxels) is provided in the second column. Performance rates for classifiers are provided for each ROI in the final four columns. The columns shaded in gray show the performance rates when the classifier was trained on AE versus MO and then tested on (1) AE versus MO and (2) AW versus NW. The final two columns show the performance rates when the classifier was trained on AO versus MO and then tested on (1) AO versus MO and (2) AW vs. NW. Performance rates are shown for each ROI individually. Asterisks represent significance level.

*$p < .05$.

**$p < .01$.

***$p < .005$.

(lIPS), (5) right IPS (rIPS), (6) left M1 (lM1), (7) right M1 (rM1), (8) left ventrolateral premotor cortex (lMN), and (9) right MN (rMN).

Pattern Classification

Using the pattern of activation identified in each of the nine ROIs, a classifier was trained to distinguish between neural activity associated with (1) AE in contrast to nonbiological motion (AE vs. MO) and (2) AO in contrast to observation of nonbiological motion (AO vs. MO). If the classifier was able to reliably distinguish between these categories (i.e., performance significantly above chance), it was subsequently tested on patterns of neural activity elicited by words denoting actions (e.g., "to grasp," "to pinch") in contrast to words denoting nonbiological motion (e.g., "to flow," "to melt"; AW vs. NW).

AE versus MO

In five of nine ROIs, the classifier trained to distinguish between AE and MO was able to distinguish between a test set of AE and MO stimuli, which were not included in the training session (all $ps < .001$; see Table 1 for exact performance rates and p values). This shows that the classifier successfully learned to discriminate between AE and MO. The signal from these five ROIs was thus reliable for training and testing between action conditions (i.e.,

train AE vs. MO, test AE vs. MO) and can therefore be used for training and then testing across word conditions (i.e., train AE vs. MO, test AW vs. NW). These ROIs were the bilateral IFG, the bilateral IPS, and the preSMA. The additional four ROIs were not tested further.

Without further training, the AE-versus-MO classifier was applied to distinguish between the word categories (AW vs. NW) in the five successful ROIs. The classifier successfully predicted word categories using information from the bilateral IPS and preSMA, but not using information from IFG (see Table 1, Figure 3).
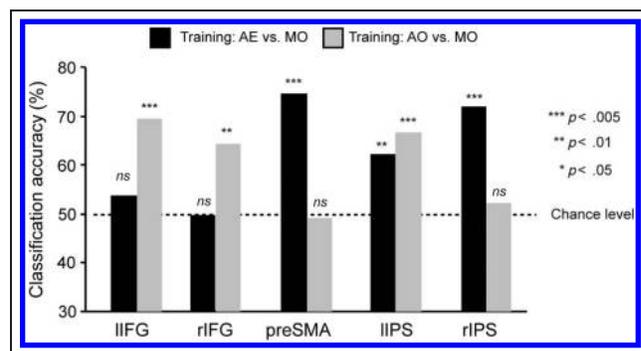

Figure 3. Classification accuracy for the prediction of reading AW versus NW. Accuracy for algorithm trained on AE versus MO is shown in black; accuracy for the algorithm trained on AO versus MO is shown in gray.

AO versus MO

The classifier trained to distinguish between AO and MO showed significant classification accuracy in five of the nine ROIs (all $ps < .001$; see Table 1). As explained above, this indicates that the pattern extracted from these five ROIs is reliable for training and testing between action conditions (i.e., train AO vs. MO, test AO vs. MO) and is therefore viable for use in training and testing across word conditions (i.e., train AO vs. MO, test AW vs. NW). Therefore, the AO-versus-MO classifier was used in these five ROIs to distinguish between AW and NW. Categorization was successful based on signal from lIPS and lIFG, but not using the signal from the preSMA nor either of the right hemisphere ROIs.

DISCUSSION

In the current study, we used a pattern classification method to investigate the spatial similarity of the signal elicited in motor areas by AE, AO, and the comprehension of AW. Our results show (1) that the pattern of activation elicited by AE and AW was comparable within the preSMA and bilateral IPS, but not within bilateral ventrolateral premotor cortex (vlPMC). Second, the pattern of activation elicited by AO and AW was comparable within lIFG and lIPS. The results of this study make two important contributions: (1) activation in the lateral frontoparietal motor areas, often reported previously for the comprehension of AW, is shown to be inconsistent with the pattern of activation elicited by the execution of actual motor movements. Second, the pattern of activation observed in lateral frontoparietal motor areas in conjunction with AW is consistent with the pattern of activation observed during AO. The implications of these findings are discussed further below.

Lateral PMC

The central claim of many embodied theories of language is that modality-specific brain areas are involved in the representation of conceptual information because words initiate a reenactment of actual experience. For example, action verbs such as "grasp" or "kick" activate the respective neural motor areas involved in actually planning and executing grasping or kicking actions (e.g., Pulvermueller, 2005). One popular proposal has been that, during development, the common co-occurrence of performing a given action and hearing the word denoting the action causes word form and the neural correlates of acting to become connected (Hebbian learning; Pulvermueller, 1999, 2005). Thus, premotor and even primary motor areas are assumed to play a crucial role in representing meaning of action verbs and concepts. The bulk of evidence in favor of this perspective shows selective activation of neural substrate close to or within primary motor and premotor areas (e.g., Aziz-Zadeh, Wilson,

Rizzolatti, & Iacoboni, 2006; Tettamanti et al., 2005; Hauk et al., 2004).

The current data show that the signal elicited in the ventral PMC by action verbs is not spatially comparable with that elicited by AE. On the other hand, the spatial parameter of activation within ventral PMC during the comprehension of AW is very similar to what is seen during AO. Intuitively, this finding is reasonable: Language stimuli may evoke an internal form of observation as we follow the verbal description of an unfolding event that is fundamentally different to the processes involved in preparing to act or imagining one's own movements. Although these results indicate that overlapping activation reported previously for AE and word comprehension (e.g., Rueschemeyer et al., 2007; Hauk et al., 2004) probably does not reflect a common neural substrate, shared activation reported in conjunction with AO and word comprehension indeed result from common neural resources (e.g., Aziz-Zadeh et al., 2006). Interestingly, a previous study has shown that action word comprehension activates neural resources distinct from those engaged by instructed motor imagery (Willems, Toni, Hagoort, & Casasanto, 2009); thus, the internal observation of actions suggested here contrasts with imagining what it would be like to perform an action oneself and is more comparable with the process of visually perceiving another acting.

It is worth noting that the involvement of the cortical motor areas in processing lexical-semantic meaning has been shown to be influenced by task demands (Tomasino & Rumiati, 2013; Papeo et al., 2012; Van Dam et al., 2012). Specifically, it has been argued that words elicit more reliable activation with cortical motor areas in language and situational contexts that highlight motor acts (e.g., performing mental rotation, thinking about actions vs. forms, etc.). In the current study, participants were arguably motivated to reflect on actions (e.g., they acted out and observed hand actions within each experimental chunk as well as processing word stimuli). Thus, based on previous literature, the current paradigm is one in which the link between AW and cortical motor areas should be strong. Nevertheless, under these optimized conditions, our results show that the pattern of activation across multiple voxels in the cortical motor network is different for the processing of AW and the execution of hand actions.

Medial PMC and Parietal Cortex

In this study, AE and action word comprehension do elicit similar patterns of activation in cortical regions outside lateral PMC. Good correspondence between the pattern of activation elicited by actions and words was observed in medial PMC (preSMA) and bilateral IPS. Both the preSMA and IPS are known to play key roles in the planning and execution of actions (e.g., Fogassi & Luppino, 2005; Picard & Strick, 2001), but both are involved in high-level integrative forms of action planning (e.g., adapting actions to a given context), rather than servicing the

control of individual muscles. This suggests that the parts of the network that are activated in a comparable manner across AE and language comprehension are high-level abstractions of motor movements and not low-level residual traces of actual movements.

To summarize the results thus far, ventrolateral PMC is not engaged in the same manner during AE and action word comprehension. On the one hand, this is unsurprising, as participants in the word condition are not engaged in any action, and brain activation should hopefully reflect that nontrivial distinction. On the other hand, this finding stands in contrast to the interpretation offered by the numerous studies, which have reported consistent overlapping activation in lateral premotor sites for AE and action word comprehension. The results of the current study suggest that the results of previous studies do not reflect a common neural mechanism, but rather either spatially or temporally different processes in nearby neural tissue. In contrast, activation in higher-level integrative motor areas (i.e., preSMA and IPS) is common to action word content and AE.

There are three conclusions that can be drawn from the current experiment. First, brain areas showing comparable activation across action and language processing are high-level multimodal areas (e.g., preSMA, IPS). The areas in question are undoubtedly also crucial components of the neural motor system, but they are not domain specific in the same manner that M1 is. Thus, action and language content share common representation, but the code in which lexical-semantic information is stored cannot be described as motor based. This finding stands in contrast to strongly embodied theories but is in general correspondence with more moderate and weakly embodied perspectives.

Second, the function of high-level multimodal areas is surprisingly consistent across participants. We trained our classifier to distinguish between AE and MO on the basis of signal generated from one participant (or multiple participants) but tested its performance on the signal generated in another participant. Therefore, we show not only that patterns of brain activation are common across cognitive tasks but also that there is a high degree of commonality across participants in the functional profile of high-level cognitive areas (preSMA, IPS).

Third, we contribute to the accumulating evidence suggesting different functional roles for lIFG/vlPMC engagement during AE and AO. Specifically, although evidence for the existence of small populations of neurons sensitive to both AE and AO exists (e.g., Kilner et al., 2009; for a review, see Rizzolatti & Craighero, 2004), the vast majority of neurons within PMC has been shown to exhibit different patterns of activation during execution and observation (e.g., Press, Weiskopf, & Kilner, 2012; Lingnau, Gesierich, & Caramazza, 2009). There are several points that make a distinction between execution and observation plausible. First, although it is likely that the posterior PMC is involved in forming predictions about the consequences of actions during both AE and AO (for a review, see Kilner, 2011),

the predicted consequences of acting and observing are often quite different (see, e.g., Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007). In line with this, Oosterhof et al. (2012) demonstrate that the pattern of activation in the posterior PMC elicited by AE and observation is similar if actions are presented from the first-person perspective but that this similarity does not hold if actions are presented from the third-person perspective. In the current study, we show that the pattern of activation in the lIFG/vPMC is similar for AO and word comprehension, but not for AE and lexical-semantic processing. We suggest above that words generate internal simulations of actions that are more similar to watching others act than to acting oneself. Thus, we show that action-word content does activate the lIFG/vPMC (i.e., does draw on resources of neural motor areas), but it does so in a manner akin to watching others act rather than to acting oneself.

Conclusion

In the current study, we used multivoxel pattern analysis to investigate whether overlapping cortical activation reported previously for AE and action-word comprehension reflects a common neural source or adjacent, but distinct, sources. The results demonstrate that overlapping activation in high-level multimodal areas (e.g., preSMA, IPS) reflects activation of a common source for AE and word comprehension. In contrast, activation in modality-specific areas (e.g., vlPMC) reflects activation of a common source for AO and word comprehension, but not for AE. The results of this study demonstrate that lexical-semantic meaning is derived from features that make use of neural substrate also involved in executing and observing actions in the real world but that the code in which action features are stored in the brain cannot be equated with motor content.

APPENDIX 1: DUTCH WORDS IN THE TWO-WORD CONDITIONS AND THEIR ENGLISH TRANSLATION EQUIVALENTS

Original Dutch Stimuli	English Translation Equivalents
Action Words	
aaien	stroke/caress
aansteken	use a lighter
aftasten	examine (with the hands)
bedekken	cover (with hands)
betalen	pay
bonken	bump
borstelen	brush

Original Dutch Stimuli	English Translation Equivalents
Action Words	
breken	break
buigen	bend/fold
deppen	blot/dab
dobbelen	throw a die
duwen	push
epileren	tweeze
fladderen	flutter
fotograferen	take a photograph
gooien	throw
grabbelen	grabble
grijpen	grasp
hameren	hammer
kerven	carve
knijpen	pinch
knutselen	fiddle
naaien	sew
noteren	write down
openen	open
ophangen	hang up
opnemen	take/pick up
optillen	lift
peuteren	pick
pinnen	pin
plukken	pluck
poetsen	clean
prakken	mash
prikken	prick
puzzelen	do jigsaw puzzles
reiken	hand over
salueren	salute
scheren	shave
scheuren	tear
schieten	shoot
schilderen	paint
schrapen	scratch
schroeven	screw
smeren	smear

Original Dutch Stimuli	English Translation Equivalents
Action Words	
smijten	throw
snijden	cut
steken	prick
stompen	punch
stoten	push
strelen	caress
strijken	iron
strooien	strew
tekenen	draw
uitgummen	erase
verkreukelen	crease
verspreiden	spread
verven	paint
wapperen	wave
werpen	throw
wrijven	rub
Non-action Words	
aanspoelen	wash ashore
barsten	burst
bestuiven	pollinate
bevriezen	freeze
blaken	scorch
blikkeren	flicker
bliksemen	blaze
blinken	glitter
bloezen	droop
blubberen	blubber
bollen	bulge
detoneren	detonate
dooien	melt
drogen	dry
druppelen	drip
fonkelen	sparkle
glippen	slide
gloeien	glow
golven	move in waves

Original Dutch Stimuli	English Translation Equivalents
Non-action Words	
kletteren	clang
lekken	leak
lubberen	bulge out
miezeren	rain
misten	fog up
ontkiemen	germinate
ontladen	explode
opladen	load
opzwellen	bulge
overspoelen	flood
ploffen	thud
plonzen	splash
rijpen	ripen
roesten	get rusty
roteren	rotate
schijnen	shine
sidderen	tremble
slieren	slither
sneeuwen	snow
spatten	splash
splijten	split
splinteren	splinter (v)
stijgen	sliver
stomen	steam
storten	fall
uitbarsten	erupt
uitdrogen	dry
verzachten	drain
vallen	fall
verbrokkelen	crumble
verdampen	evaporate
verdikken	thicken
vergaan	perish
vergroten	enlarge
verkolen	char
verlichten	light up
verzachten	attenuate

Original Dutch Stimuli	English Translation Equivalents
Non-action Words	
waaien	blow (wind)
wegebben	fade away
zinken	sink
zwellen	swell up

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