

# Putting an “End” to the Motor Cortex Representations of Action Words

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## Abstract

■ Language processing is an example of implicit learning of multiple statistical cues that provide probabilistic information regarding word structure and use. Much of the current debate about language embodiment is devoted to how action words are represented in the brain, with motor cortex activity evoked by these words assumed to selectively reflect conceptual content and/or its simulation. We investigated whether motor cortex activity evoked by manual action words (e.g., *caress*) might reflect sensitivity to probabilistic orthographic–phonological cues to grammatical category embedded within individual words. We first review neuroimaging data demonstrating that nonwords evoke activity much more reliably than action words along the entire motor strip, encompassing regions proposed to be action category specific. Using fMRI, we found that disyl-

labic words denoting manual actions evoked increased motor cortex activity compared with non-body-part-related words (e.g., *canyon*), activity which overlaps that evoked by observing and executing hand movements. This result is typically interpreted in support of language embodiment. Crucially, we also found that disyllabic nonwords containing endings with probabilistic cues predictive of verb status (e.g., *-eve*) evoked increased activity compared with nonwords with endings predictive of noun status (e.g., *-age*) in the identical motor area. Thus, motor cortex responses to action words cannot be assumed to selectively reflect conceptual content and/or its simulation. Our results clearly demonstrate motor cortex activity reflects implicit processing of ortho-phonological statistical regularities that help to distinguish a word’s grammatical class. ■

## INTRODUCTION

Language is represented in multiple, distributed areas of the human cortex. This representation has remarkable plasticity and may develop following reduction or removal of large portions of cortex because of genetic disorders or early injury and often in the absence of sight, hearing, or capacity to produce speech or lateralized body movements (e.g., Bedny, Caramazza, Pascual-Leone, & Saxe, 2011; Stiles, Reilly, Paul, & Moses, 2005; Bates, 2004; Bates et al., 2001). Precisely how the cortex permits word meaning to be represented remains controversial. For the aphasiologists of the late 19th century including Freud (1891) and Lichtheim (1885), the cortex played host to various distributed conceptual representations distinct from the localist representations then being assumed for motor articulation and speech perception (e.g., Ferrier, 1874; see Henderson, 1992). This perspective informed models of language comprehension for over a century. However, recent theories have proposed that encapsulation of conceptual information is achieved by “grounding” representations of action word meanings in the perceptual and motor systems responsible for per-

forming those actions, reflecting an “embodied” approach to language comprehension (e.g., Barsalou, 2008; Gallese & Lakoff, 2005; Pulvermüller, 2005; Glenberg & Kaschak, 2002).

Neuroimaging investigations have provided much of the impetus for embodied language theories. Some initial studies reported that semantic representations of action words such as *punch*, *lick*, and *kick* elicited activity corresponding to the somatotopic ventral-to-dorsal organization of mouth/face, hand/arm, and foot/leg effectors within primary (M1) and premotor (PM) cortices (e.g., Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Tettamanti et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004; cf. Perani et al., 1999). Although motor system activity elicited during language comprehension tasks is often interpreted as evidence for embodiment, it can also be interpreted as context-dependent or epiphenomenal, reflecting the flow of activation from conceptual to motor systems (e.g., Postle, Ashton, McFarland, & de Zubicaray, 2013; Willems & Casasanto, 2011; Mahon & Caramazza, 2008; Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008). Nonetheless, the reported somatotopic organization of the motor activity elicited by specific action words has been characterized by some authors as a “breakthrough in the study of category-specific brain processes” (e.g., Carota, Moseley, & Pulvermüller, 2012; p. 1503). This is despite the fact that similar motor responses have been reported for nonword

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and action word stimuli, suggesting that the activity is not category specific, that is, it cannot be attributed selectively to conceptual representations and/or their implicit motor simulation (see Tomasino, Weiss, & Fink, 2010; Postle et al., 2008).

### **Action Word and Nonword Representations in Motor Cortex**

Given the central importance of the motor somatotopy/category-specificity assumption for embodied theories of action meaning representation, we collated 53 activity peaks ascribed to PM and M1 regions from 15 neuroimaging studies (Table 1). In addition, we verified the location of each peak within the cytoarchitectonically defined PM or M1 cortex maps by determining the probabilities of their respective coordinates (Eickhoff et al., 2007; Eickhoff, Heim, Zilles, & Amunts, 2006), adopting a liberal 20% probability criterion for assignment. Defining PM cortex cytoarchitectonically is essential, as it has no macroanatomical landmark to distinguish it anteriorly from the pFC (Geyer, 2003; see Postle et al., 2008). Figure 1 shows the activity peaks rendered on a left hemisphere cortical surface similar to that depicted in earlier reviews (e.g., Carota et al., 2012; Kemmerer & Gonzalez-Castillo, 2010). As Table 1 and Figure 1 indicate, only 28 of the 51 peaks (55%) are located within M1 and PM cortex. When the peaks are fractionated according to their respective body parts, it is apparent that the assignments of the orofacial (mouth/face) peaks are least accurate, with only 2 of 12 (17%) in cytoarchitectonic motor areas, followed by 14 of 25 arm/hand peaks (56%). The accuracy appears to improve considerably for foot/leg peaks with 12 of 14 (86%) in M1 and PM cortices. However, more than half (7) of those 12 peaks are on the lateral surface rather than medial wall (i.e., the posterior paracentral lobule) where the leg/foot motor representations are located according to electrocortical stimulation techniques and neuroimaging studies (e.g., Chainay et al., 2004; Sahyoun, Floyer-Lea, Johansen-Berg, & Matthews, 2004; Allison, McCarthy, Luby, Puce, & Spencer, 1996).

Additionally, we collated 49 peaks from 19 neuroimaging investigations of written and auditory nonword perception and nonword production conducted during a similar period (Table 2) and rendered them on an identical cortical surface (Figure 2). As the rendered data in Figure 2 indicate, a majority (39 of 49) of these peaks are located in PM and M1 cortices (80%). The assignment of PM and M1 labels to peaks is demonstrably more accurate for the nonword perception/production studies than for the action word meaning studies. Thus, nonword processing activates motor cortex much more reliably. Most (35) of the peaks are located in PM rather than M1 cortex. More importantly, the reported peaks occupy much of the motor strip, including those areas proposed to be body part specific (cf. Carota et al., 2012). Furthermore, as nonword production involves articulatory motor

movements following processing of nonfamiliar phoneme sequences, these peaks can serve as an anatomical marker for orofacial representations. Note that these peaks are not restricted to the ventral portion of the motor strip as predicted by a somatotopic organization.

Thus far, the debate in the neuroimaging literature has been largely concerned with establishing whether the motor activity observed in conjunction with action word processing is necessary or context dependent; it has been framed exclusively in terms of semantic and syntactic information (e.g., Papeo, Corradi-Dell'Acqua, & Rumati, 2011; Willems & Casasanto, 2011; Tomasino et al., 2010). However, as Figures 1 and 2 indicate, there is little more than chance probability of this activity actually localizing to motor cortical areas that have been defined cytoarchitectonically. Even if we accept the results of just those studies with accurate labeling of motor area activity, the reported peaks do not demonstrate a consistent somatotopic organization and overlap with those reported for nonword perception and production (refer to Figures 1 and 2). This raises the possibility that the motor activity elicited by action word processing might not necessarily be related to semantic representations and/or implicit motor simulation.

### **Probabilistic Orthographic and Phonological Cues to Grammatical Category**

There is now considerable evidence that orthography (spelling) influences both auditory word perception and spoken word production in addition to written word recognition (e.g., Bürki, Spinelli, & Gaskell, 2012; Perre, Bertrand, & Ziegler, 2011; Rastle, McCormick, Bayliss, & Davis, 2011; Peereman, Dufour, & Burt, 2009). The language system is therefore highly interactive, with bidirectional activation flow between phonological and orthographic representations. Neuroimaging and lesion studies have established a role for the PM cortex in converting this sublexical information (e.g., Cloutman, Newhart, Davis, Heidler-Gary, & Hillis, 2011; for a review, see Taylor, Rastle, & Davis, in press). Common activation in PM cortex for written and auditory nonword perception and production (Table 2 and Figure 2) is consistent with this role.

To support an inference of a necessary and selective involvement of the motor system in conceptual processing of action words, embodied language researchers have frequently contrasted this class of words with non-body-part-related nouns in investigations of patients with lesions or degenerative disorders affecting the motor system (e.g., Boulenger et al., 2008; Bak et al., 2006; Neiningner & Pulvermüller, 2003) and in TMS investigations of healthy participants (e.g., Willems, Labruna, D'Esposito, Ivry, & Casasanto, 2011). In addition, researchers have often described action words as being grammatically ambiguous when presented in isolation, that is, they may be understood as either nouns or verbs (e.g., Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005).

**Table 1.** Peak Coordinates Reported as PM or M1 Cortex Activity across Studies Investigating Conceptual Processing of Arm/Hand, Face/Mouth, and Leg/Foot Words and Their Cytoarchitectonic Probabilities Depicted in Figure 1

Authors	Stimuli	Task	MNI Coordinates			PM Cortex Probability	M1 Cortex Probability
			x	y	z		
Hauk et al., 2004	Arm-related verbs	Silent reading	−22	2	64 <sup>a</sup>	40	—
			−38	−20	48	10	80
	Leg-related verbs		−8	−26	64	50	50
			−22	−30	64 <sup>a</sup>	40	40
			−22	−34	62	10	30
Face-related verbs	−50	10	20	—	—		
Tettamanti et al., 2005	Arm-related sentences	Listening	−30	−2	56	30	—
			−62	−26	36	—	—
	Leg-related sentences		−26	4	64	30	—
			−64	−32	28	—	—
	Face-related sentences		−44	2	24	—	—
Aziz-Zadeh et al., 2006	Arm-related sentences	Silent reading	−60	−34	32	—	—
			−30	−6	46	10	—
	Leg-related sentences		−40	6	28	—	—
			−54	4	26	—	10
	Face-related sentences		−54	4	26	—	10
Rüschemeyer, Brass, & Friederici, 2007	Arm-related verbs	Silent reading and lexical decision	−46	−9	63 <sup>b</sup>	—	—
			−49	−2	60 <sup>b</sup>	—	—
Tomasino, Werner, Weiss, & Fink, 2007	Arm-related sentences	Action imagery	−50	−24	56	—	—
Kemmerer, Gonzalez-Castillo, Talavage, Patterson, & Wiley, 2008	Arm-related verbs	Semantic similarity judgment	−46	10	40	—	—
			−28	−30	62	20	40
	Leg-related verbs		−28	−32	60	10	50
			−19	−29	61	40	40
	Face-related verbs		−50	18	20	—	—
Boulenger et al., 2009	Arm-related sentences	Silent reading	−54	4	44	50	—
			Leg-related sentences	−5	−18	75	80
Pulvermüller, Kherif, Hauk, Mohr, & Nimmo-Smith, 2009	Arm verbs (Experiment 1)	Silent reading	−32	−5	52	20	—
	Arm verbs (Experiment 2)		−34	−10	50	50	20
	Leg verbs (Experiment 1)		−19	−29	61	40	40
	Leg verbs (Experiment 2)		−20	−26	57	30	40

Table 1. (continued)

Authors	Stimuli	Task	MNI Coordinates			PM Cortex Probability	M1 Cortex Probability
			x	y	z		
	Face verbs (Experiment 1)		−49	11	16	–	–
	Face verbs (Experiment 2)		−32	−38	58	–	–
	Face verbs (Experiment 2)		−44	−29	40	–	–
	Face verbs (Experiment 2)		−50	9	10	–	–
			−38	−34	51	–	–
Raposo et al., 2009	Arm-related sentences	Listening: sentences or single words	−44	−14	56	60	30
	Leg-related sentences		−6	−26	68	70	50
	Leg-related verbs		−6	−16	72	100	20
Willems et al., 2010	Manual movement related words	Lexical decision	−22	−5	56 <sup>c</sup>	20	–
			−20	−29	58 <sup>c</sup>	–	–
Desai, Binder, Conant, & Seidenberg, 2010	Hand/arm motor-verb sentences	Listening correlation with hand ratings	−12	13	63 <sup>d</sup>	40	–
Tomasino et al., 2010	Imperative hand-related phrases	Sentence verification	−38	−25	59 <sup>e</sup>	30	40
			−35	−20	68 <sup>e</sup>	90	–
Yang, Shu, Bi, Liu, & Wang, 2011	Hand- and tool-related verbs	Silent reading	−38	2	34 <sup>f</sup>	–	–
			−1	10	53 <sup>f</sup>	60	–
Hauk & Pulvermüller, 2011	Unimanual- and bimanual-related hand verbs	Silent reading	−50	−8	50	90	20
			−58	−18	22	–	–
Pulvermüller et al., 2012	Arm-related sentences		−46	−2	48	50	–
	Leg-related sentences		−44	0	50	60	–
			−20	−18	60	90	10
	Face-related sentences	Silent reading	−50	20	16	–	–
			−56	−2	40	90	20

Peak cytoarchitectonic probabilities for PM and M1 cortex were calculated using the SPM Anatomy toolbox (Eickhoff et al., 2006, 2007).

<sup>a</sup>The y coordinates for these peaks were apparently misreported in the original article. The coordinates here are accurate according to Kemmerer and Gonzalez-Castillo's (2010) personal communication with the authors (see the caption to their Table 2).

<sup>b</sup>The original coordinates [−44 −15 59; −47 −9 57] are in the stereotaxic space of Talairach and Tournoux (1988) and are here converted to MNI space using the *tal2icbm* transform (Lancaster et al., 2007). Note that the coordinates were not transformed in the previous reviews by Carota et al. (2012) and Kemmerer and Gonzalez-Castillo (2010).

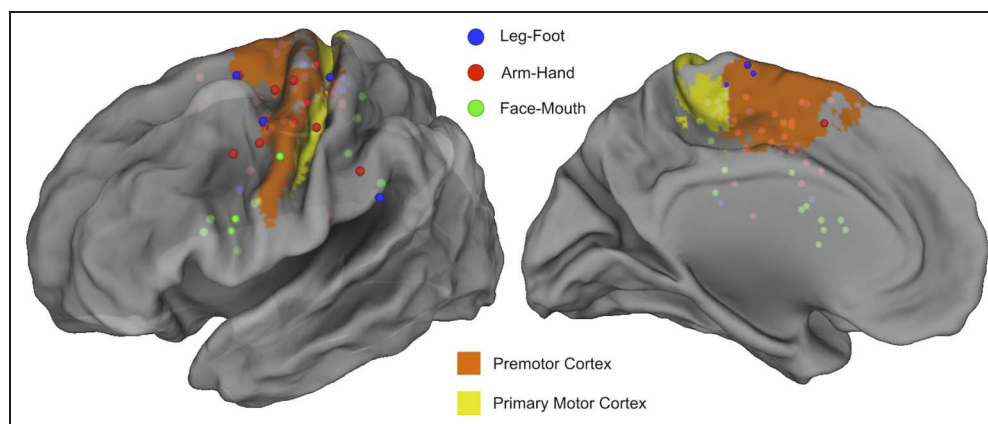
<sup>c</sup>These are the mean subject-specific coordinates reported in the caption to their Figure 4.

<sup>d</sup>The original coordinates [−13 5 61] are in the stereotaxic space of Talairach and Tournoux (1988) and are here converted to MNI space using the *tal2icbm* transform (Lancaster et al., 2007). Note that the coordinates [−55 −34 37] listed by Carota et al. (2012) do not appear in Desai et al.'s (2010) Appendix II table of significant peaks or elsewhere in the published article.

<sup>e</sup>Group mean coordinates of peaks in motor cortex ROIs.

<sup>f</sup>The original coordinates [−37 −3 34] and [−1 3 52] are in the stereotaxic space of Talairach and Tournoux (1988) and are here converted to MNI space using the *tal2icbm* transform (Lancaster et al., 2007).

**Figure 1.** (From left to right) Renderings of the lateral and medial cortical surfaces of the left hemisphere with peak maxima from fMRI studies reporting motor cortex activity for action word meaning representations, color-coded according to their respective body part relations. The renderings are made partially transparent to illustrate peak depth in relation to the cytoarchitecturally defined MPMs of primary motor and premotor cortices (comprising BA 4a, BA 4p, and BA 6, respectively; Eickhoff et al., 2006, 2007). Refer to Table 1 for details of the depicted studies and coordinates.



However, there is a substantial body of psycholinguistic research involving large-scale corpus analyses and behavioral measurements demonstrating that verbs tend to show distinct, nonmorphologically derived, orthographic and phonological (henceforth ortho-phonological) properties that are different from those exhibited by nouns. It has been shown that these probabilistic cues can affect both word and sentence level processing (e.g., Arciuli, McMahon, & de Zubicaray, 2012; Arciuli & Monaghan, 2009; Kemp, Nilsson, & Arciuli, 2009; Arciuli & Cupples, 2006, 2007; Farmer, Christiansen, & Monaghan, 2006; Monaghan, Chater, & Christiansen, 2005; Kelly, 1992).

For example, Arciuli and Cupples' (2006, 2007) analyses of disyllabic words in the CELEX English language corpus (Baayen, Piepenbrock, & Gulikers, 1995) found orthographic cues in words' beginnings (the letters corresponding to the onset and first vowel) and also in words' endings (the letters corresponding to the rime of final syllable) that were highly predictive of grammatical category. In these analyses, words' "beginnings" and "endings" were not determined morphologically. For example, *cu-* is more likely to appear at the beginning of a noun, and *be-* is more likely to appear at the beginning of a verb. In addition, over 90% of words ending in *-age* are nouns, whereas 80% ending in *-end* are verbs. A similar corpus analysis of trisyllabic words found category consistent cues in both words' beginnings and endings (Arciuli & Monaghan, 2009). Thus, these kinds of probabilistic cues are likely relevant for the majority of words in an adult lexicon. For example, around 85% of the 40,000 words represented in the English lexicon project have more than one syllable (eLexicon; Balota et al., 2007; see Arciuli, Monaghan, & Seva, 2010). Yet even within monosyllabic words, the arrangement of phonemes is such that verbs are closer to one another in terms of their phonology than to nouns and vice versa (Farmer et al., 2006).

Sensitivity to ortho-phonological probabilistic cues has been demonstrated in lexical decision and speeded

grammatical judgment tasks, with words that have cues consistent with their grammatical category exhibiting advantaged processing (e.g., Arciuli et al., 2012; Arciuli & Monaghan, 2009). Farmer et al. (2006) provided a demonstration of behavioral sensitivity to probabilistic phonological cues to grammatical category that operate at the single word level even in sentential contexts. In addition, when nonwords contain probabilistic orthographic cues, participants are more likely to assign them noun- or verb-like status in grammatical judgment tasks and use them consistently as nouns or verbs in sentences (e.g., Kemp et al., 2009; Arciuli & Cupples, 2006, 2007). Given the substantial neuroimaging evidence indicating that motor system activity is elicited in response to ortho-phonological manipulations (Table 2 and Figure 2), a demonstration that PM and M1 cortices are responsive when reading both action words and nonwords that contain probabilistic cues to grammatical category would point to an alternate mechanism for motor system activity elicited by the former stimuli.

We tested this alternate explanation in an fMRI experiment in which participants performed grammatical category judgments on disyllabic words denoting manual actions (e.g., *carry*) or non-body-part-related nouns (e.g., *canyon*) and on disyllabic nonwords containing endings predictive of verb (e.g., *-eve*) or noun status (e.g., *-age*) identified by Arciuli and Cupples' (2006) corpus analysis and used by Kemp et al. (2009) in their behavioral investigations. We employed word endings, as there is evidence that these cues play a more important and consistent role than word beginnings (Arciuli & Monaghan, 2009). Further, we employed written stimuli as most embodied language studies have employed reading tasks (14 of 18 studies; see Table 1), and we investigated words referencing manual actions, as all embodied language studies to date have examined these words in relation to other items. Finally, we combined functional localizer scans and cytoarchitectonic maps of left PM and M1 cortices to examine responses solely within defined hand motor areas

**Table 2.** Peak Coordinates Reported as PM or M1 Cortex Activity across Studies Investigating the Perception and/or Production of Nonwords and Their Cytoarchitectonic Probabilities Depicted in Figure 2

Authors	Stimuli	Task	MNI Coordinates			PM Cortex Probability	M1 Cortex Probability
			x	y	z		
Dietz, Jones, Gareau, Zeffiro, & Eden, 2005	Monosyllabic	Silent reading vs. fixation	−55	−1	39 <sup>a</sup>	70	20
Valdois et al., 2006	Mono-, di-, and trisyllabic	Lexical decision and silent reading vs. fixation	−47	−17	56 <sup>b</sup>	10	–
			−48	−2	37	10	–
			−51	−28	52	–	–
			0	6	50	70	–
			−44	3	51	30	–
Carreiras, Mechelli, Estevez, & Price, 2007	Mono- and polysyllabic (number of syllables not reported)	Lexical decision vs. false font	−2	−4	60	80	–
			−50	−4	50	100	–
			−56	0	34	50	10
			−46	8	28	–	–
Rauschecker, Pringle, & Watkins, 2008	Di- and quadrisyllabic	Silent repetition of auditory presentation, repetition suppression	−50	6	16	–	–
			−2	4	60	70	–
			−2	0	62	80	–
Buchsbaum et al., 2005	Monosyllabic	Listening and silent reading	−55	−2	41	90	20
			−65	2	33	–	–
Baciu et al., 2001	Mono-, di-, and trisyllabic	Silent reading vs. fixation, peak common with words	−60	−5	28	30	10
			−59	−4	26	30	10
McGettigan et al., 2011	Di- and quadrisyllabic	Silent repetition of auditory presentation vs. tones, 4 > 2	−54	−9	48	70	20
			−51	−6	48	100	10
			−60	0	24	40	10
Tomasino et al., 2010	Monosyllabic non-verbs (e.g., gralp vs. grasp)	Silent reading/sentence judgment	−38	−25	59	30	40
			−35	−20	68	90	–
Pulvermuller et al., 2006	Monosyllabic	Listening vs. spectrotemporal noise	−54	−3	46	100	–
			−60	2	25	50	–
Wilson & Iacoboni, 2006	Monosyllabic, native and non-native	Listening vs. rest	−62	−4	38	–	–

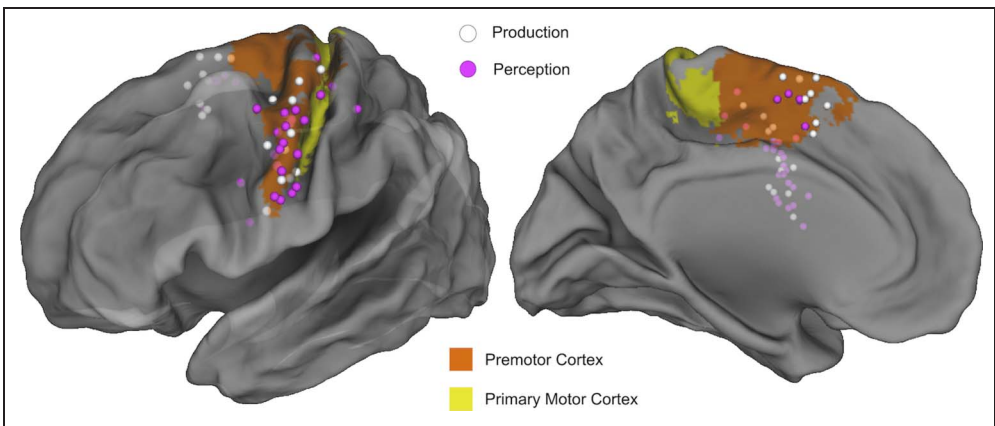
Wilson, Saygin, Sereno, & Iacoboni, 2004	Monosyllabic	Listening vs. nonspeech noise	−50	−6	47	100	10
Ghosh, Tourville, & Guenther, 2008	Mono- and disyllabic	Reading aloud vs. fixation	−54	2	20	10	10
		di- vs. monosyllable	−2	8	62	70	–
			−52	−6	30	10	50
			−46	−8	54	80	20
			−6	4	68	70	–
Bohland & Guenther, 2006	Trisyllabic	Reading aloud	−46	−10	60	–	–
			−60	0	30	50	10
			−44	−18	64	60	10
			−34	−6	54	30	–
			−2	−2	68	80	–
			−2	6	50	60	–
			−6	10	52	50	–
Sörös et al., 2006	Mono- and trisyllabic	Reading aloud vs. baseline	−2	6	60	60	–
Papoutsis et al., 2009	Di- and quadrisyllabic	Silent and aloud	−56	−4	44	100	20
		repetition following	−4	10	68	60	–
		auditory presentation	−52	2	40	20	–
			−4	14	58	30	–
Peeva et al., 2010	Disyllabic	Repetition of reading reordered and resyllabified stimuli	−52	−8	32	–	40
Osnes, Hugdahl, & Specht, 2011	Monosyllabic	Listening vs. nonspeech music noise	−54	−6	51	–	–
Callan, Callan, Gamez, Sato, & Kawato, 2010	Monosyllabic	Reading aloud and listening	−54	−3	39	90	20
			−6	9	48	30	–
McNealy, Mazziotta, & Dapretto, 2006	Trisyllabic	Listening vs. rest	−6	4	60	60	–
			−50	−2	44	50	–

Peak cytoarchitectonic probabilities for PM and M1 cortex were calculated using the SPM Anatomy toolbox (Eickhoff et al., 2006, 2007).

<sup>a</sup>Peak from conjunction analysis. Although the MNI template was used in this study, the authors used the *mni2tal* Brett, Lancaster, & Christoff (2001) transformation to report their coordinates [−54 1 36] in the stereotaxic space of Talairach and Tournoux (1988). The coordinates here are converted back to MNI space using the inverse *tal2mni* transform.

<sup>b</sup>Data reported as normalized into the stereotaxic space of Talairach and Tournoux (1988) despite using an MNI template in SPM99. MNI atlas space thus assumed here.

**Figure 2.** (From left to right) Renderings of the lateral and medial cortical surfaces of the left hemisphere with peak maxima from fMRI studies reporting motor activity for nonword/phoneme manipulations, color-coded according to perception or production tasks. The renderings are made partially transparent to illustrate peak depth in relation to the cytoarchitecturally defined MPMs of primary motor and premotor cortices (comprising BA 4a, BA 4p, and BA 6, respectively; Eickhoff et al., 2006, 2007). Refer to Table 2 for details of the depicted studies and coordinates.



to evaluate their proposed category specificity (e.g., Tomasino et al., 2010; Willems, Toni, Hagoort, & Casasanto, 2010; Postle et al., 2008).

## METHODS

### Participants

Twenty-one participants (15 women) were recruited from among University of Queensland students and staff (mean age = 25 years, range = 21–35 years). All were right-handed, native English speakers, with no history of neurological or psychiatric disorder, substance dependence, or hearing deficits. All had normal or corrected-to-normal vision. Written informed consent was obtained for all participants before commencing the experiment. The University of Queensland medical research ethics committee approved the experimental protocol.

### Materials

The critical stimuli comprised 80 disyllabic words, selected without reference to probabilistic ortho-phonological cues to grammatical class, and 80 disyllabic nonwords. Of the words, half were regular, transitive verbs denoting manual actions (e.g., *carry*, *fondle*, *inscribe*, *tighten*), and the other half were nouns denoting nonmanipulable entities (e.g., *cavern*, *forest*, *iceberg*, *typhoon*). Grammatical class assignment was established using a percentage measure of the dominant part of speech relative to total frequency (Brysbaert, New, & Keuleers, 2012). Verb transitivity was established using the on-line Wordsmyth dictionary (Parks, Ray, & Bland, 1998). In a separate rating study with an independent group of 10 right-handed, native English-speaking participants, the nouns and verbs were randomized within a single list and rated according to a scale of 1 (*does not remind me of an action I can perform with my hand*) to 7 (*reminds me very much of an action I can perform with my hand*). Participants were undergraduate

psychology students who completed the ratings study for course credit. They were given as much time to rate the words as they required. Mean ratings differed significantly for verbs (5.64,  $SD = 1.69$ ) versus nouns (1.1,  $SD = 0.51$ ),  $F(1, 9) = 255.75$ ,  $MSE = 16.14$ ,  $p < .001$ , partial  $\eta^2 = .97$ . The nouns and verbs were matched on a range of psycholinguistic variables including letter length, lexical frequency (SUBTL<sub>WF</sub>; Brysbaert & New, 2009), orthographic Levenstein distance (OLD), mean bigram frequency, morphemes and phonemes according to the on-line English Lexicon Project (Balota et al., 2007), imageability (Schock, Cortese, & Khanna, 2012) and age of acquisition (Kuperman, Stadthagen-Gonzalez, & Brysbaert, 2012; see Table 3). Corpus probability data from Arciuli and Cupples (2006) were available for 31 of the nouns and 28 of the verbs. A post hoc analysis of the available word endings revealed that, on average, noun endings were significantly more

**Table 3.** Psycholinguistic Properties of the Word Stimuli

Item Property	Verbs	Nouns
Letters	6.78	6.8
Phonemes	5.28	5.4
Morphemes	1.41	1.43
Orthographic Levenstein distance	2.32	2.55
Frequency (per million) <sup>a,b</sup>	4.1	4.35
Bigram frequency	3811	3459
Imageability <sup>b</sup>	4.77	4.92
Age of acquisition <sup>c</sup>	9.2	8.1
Dominant part of speech <sup>d</sup>	93%	92%

<sup>a</sup>Brysbaert and New (2009).

<sup>b</sup>Schock et al. (2012).

<sup>c</sup>Kuperman et al. (2012).

<sup>d</sup>Brysbaert et al. (2012).

prominent in our noun stimuli compared with our verb stimuli ( $t(57) = 4.732, p < .001$ ). Verb endings were significantly more prominent in our verb stimuli compared with our noun stimuli ( $t(57) = 5.164, p < .001$ ).

The 80 disyllabic nonwords were selected from those used in behavioral testing by Kemp et al. (2009) and Arciuli and Cupples (2006), which derived from the corpus analysis of Arciuli and Cupples (2006). Of these, half had endings that were probabilistically associated with verb status and the other half had endings that were probabilistically associated with noun status. For example, word endings such as *-iff* and *-oon* are strongly associated with noun status, whereas endings such as *-ieve* and *-erge* are strongly associated with verb status. All nonwords conformed to English orthotactic and phonotactic conventions. Each consonant before the defined “ending” was different to ensure that any effects were for that ending only. The nonwords did not differ significantly in the “noun-likeness” or “verb-likeness” of their beginnings, based on the frequency with which each of these beginnings occurs in nouns, verbs, or both, in real English words (Arciuli & Cupples, 2007). They were matched according to vowel/consonant structure, mean letter length, and mean bigram frequency (Balota et al., 2007). Words and nonwords were randomly distributed into 20 different lists of 160 items using the Mix program (van Casteren & Davis, 2006).

The motor localizer video stimuli were selected from a subset created by Postle et al. (2008) and consisted of 20 silent movie clips, half of which involved a right hand performing simple intransitive actions repeatedly for 5 sec. The other half depicted a series of frequently encountered natural and man-made stimuli in motion (e.g., tree branches moving in the wind, rotating fan blades, elevator doors closing). No humans or animals were depicted in these latter videos that were employed to control for generic motion processing. However, it should be acknowledged that these control stimuli might elicit activity because of nonmanipulable object processing, particularly for the comparison opposite to that employed below (i.e., nonbiological motion > manual action).

## Procedure

There were two experimental tasks with event-related designs: grammatical category judgment and the motor localizer, administered consecutively. For the grammatical category judgment task, participants were presented with a list of 160 stimuli comprising the nouns, verbs, noun-like nonwords, and verb-like nonwords described above, split into two consecutive runs/sessions of 80 trials. Following Kemp et al. (2009), they were instructed to identify whether a letter string on the screen seemed more likely to be a noun or a verb. During each trial, a fixation point (crosshair) appeared at the center of the screen for 500 msec, followed by the word/nonword for 750 msec and

a blank screen for 1250 msec. Participants were instructed to withhold their response until the word/nonword disappeared from the screen and response options appeared. Next the categories “verb” and “noun” were presented on either side of the center of the screen, remaining for up to 2 sec depending on the speed of the participant’s response. This served both as a prompt to respond and to indicate which button should be pressed for a given response, as the left/right positions of the categories were randomized and counterbalanced across trials to prevent consistent response mappings (Pulvermüller, Lutzenberger, & Preissl, 1999). Participants responded using their right hand by pressing one of two buttons corresponding to their decision on a similarly arranged response pad. The selected category changed color to red for 200 msec to provide response feedback, and a blank screen was presented for the remainder of the 2 sec period. The trial timed-out if a response was not made within the 2 sec period. Thus, each trial lasted for 4.5 sec. A blank inter-trial interval was jittered pseudorandomly using five different delays between 2 and 6 sec (mean = 3.6 sec) to optimize the estimation of the BOLD response. Whereas in the bore of the MRI system and before the experimental run, participants were provided with a brief practice version of the task involving a pseudorandomized series of two trials of each stimulus type. The practice stimuli were not included in the experimental task.

For the motor localizer, trials involving manual or nonbiological motion conditions were presented in pseudorandom order, with participants instructed to observe all videos then execute manual movements with their right hand following a delayed prompt (see Postle et al., 2008). Each video was displayed for 10 sec, followed by a blank delay period jittered pseudorandomly between 2 and 6 sec (mean = 3.6 sec). A green or red dot was next presented in the center of the screen for 10 sec. The green dot served as a prompt to execute the manual action depicted in the video until the dot disappeared, whereas the red dot indicated no response was required. The red dot appeared following half of the videos depicting manual movements and following all depicting nonbiological motion. The purpose of the jittered delay and 50% response probability was to minimize response preparation during manual action observation.

## Image Acquisition

Whole-brain images were acquired using a Siemens MAGNETOM Trio TIM System (Siemens Medical Solutions, Erlangen, Germany) operating at 3 T and equipped with a standard 12-channel Matrix head coil. Functional T2\*-weighted images depicting BOLD contrast were acquired using a gradient-echo EPI sequence (36 slices, repetition time = 2.5 sec, echo time = 36 msec,  $64 \times 64$  matrix,  $3.3 \text{ mm} \times 3.3 \text{ mm}$  in plane resolution, 3 mm slice thickness with 0.3 mm gap and flip angle =  $80^\circ$ ). A point-spread function (PSF) mapping sequence was acquired before

the EPI data to correct geometric distortions (Zaitsev, Hennig, & Speck, 2004). In each of two consecutive functional imaging series, 269 EPI volumes were acquired for the grammatical judgment task. An additional series of 224 volumes was acquired subsequently for the hand motor localizer task. The first five volumes in each functional series were acquired for magnetization to stabilize and were subsequently discarded. A T1-weighted structural image was acquired before the hand motor localizer using a magnetization-prepared rapid acquisition gradient-echo sequence ( $512 \times 512$  matrix, in-plane resolution  $0.45 \times 0.45$  mm, 192 slices, slice thickness = 0.9 mm, flip angle =  $9^\circ$ , inversion time = 900 msec, repetition time = 1900 msec, echo time = 2.32 msec).

### Image Analysis

The functional and structural image volumes from each participant were preprocessed and analyzed with statistical parametric mapping software (SPM8; Wellcome Department of Imaging Neuroscience, Queen Square, London, UK). Each functional time series was first resampled using generalized interpolation to the acquisition of the middle slice in time to correct for the interleaved acquisition sequence and then realigned to the first image of the initial series using the INRIAAlign toolbox (Freire, Roche, & Mangin, 2002). A mean image was generated and used to coregister the realigned series to the T1-weighted image. The “New Segment” procedure was next applied to the T1-weighted image and the “DARTEL” toolbox (Ashburner, 2007) employed to create a custom group template from the gray and white matter images. The resulting individual flow fields were used to normalize the realigned fMRI volumes to the MNI atlas T1 template. Normalized images were resampled to  $2 \text{ mm}^3$  voxels and smoothed with an 8-mm FWHM isotropic Gaussian kernel. A voxel-level linear model was employed to estimate and remove global signal effects (Macey, Macey, Kumar, & Harper, 2004).

Statistical analyses were conducted according to two-level, mixed effects models. At the first level, separate fixed effects analyses were conducted for each participant and task. For the grammatical judgment task, trial types corresponding to correctly classified stimuli were defined and modeled as effects of interest with delta functions representing each onset, in addition to nuisance regressors consisting of onsets for the delayed responses (to permit condition-specific effects to be estimated) and trials involving misclassifications/omissions. The trial types for the two observation, two delay, and two execution conditions of the motor localizer were likewise modeled as effects of interest along with a parametric regressor corresponding to the delay intervals. Trial onsets were convolved with a canonical hemodynamic response function. Low-frequency noise and signal drift were removed from the time series in each voxel with high pass filtering (1/128 Hz). Temporal autocorrelations were estimated

and removed with an autoregressive (AR1) model. For each task, linear contrasts were applied to each participant’s parameter estimates for each experimental condition of interest relative to baseline and then entered in second-level group repeated-measures ANOVAs in which covariance components were estimated using a restricted maximum likelihood procedure to correct for nonsphericity (Friston et al., 2002).

As we had a priori hypotheses concerning BOLD signal responses in the hand area of the left hemisphere cytoarchitectonic PM and M1 cortices, we restricted the second-level voxel-wise analysis of the localizer task to an explicit mask comprising maximum probability maps (MPMs) of these regions (combining BA 6, BA 4a, and BA 4p; Eickhoff et al., 2006). We targeted left-lateralized regions because of the known language dominance of this hemisphere in right-handed individuals (see Postle et al., 2013). To identify voxels in these motor areas responsive to both observation and execution of hand actions, we employed a conjunction analysis (i.e., execute hand > fixation  $\cap$  observe hand > non-body motion) testing the conjunction null as defined by Nichols, Brett, Andersson, Wager, and Poline (2005). A height threshold of  $p < .001$  was adopted for this analysis with a spatial cluster extent threshold of  $p < .05$  (family-wise error [FWE]-corrected). The significant voxels identified by this analysis then served as an explicit mask for the second-level analysis of the grammatical judgment task. For the latter analysis, we first performed planned  $t$  contrasts examining activity in each word and nonword condition versus baseline to be consistent with prior studies (e.g., Hauk & Pulvermüller, 2011; Willems et al., 2010; Boulenger, Hauk, & Pulvermüller, 2009; Hauk et al., 2004), followed by planned comparisons to identify grammatical category effects for the two classes of stimuli (i.e., verbs vs. nouns and verb-like vs. noun-like nonwords and vice versa). A height threshold of  $p < .001$  and spatial cluster extent threshold of  $p < .05$  (FWE-corrected) were likewise adopted for this analysis. We also performed exploratory whole-brain analyses of the grammatical judgment task using identical alpha thresholds. Results were rendered on cortical surfaces for visualization purposes using Caret software (v5.65; Van Essen et al., 2001).

## RESULTS

### Behavioral Data

Data sets from two participants were excluded because of incidental findings on radiological examination. All analyses reported below were therefore conducted on a final sample of 19 participants (6 men), mean age = 25 years (range = 21–35 years). Omitted responses and outliers (RTs > 2000 msec and < 200 msec) accounted for 0.5% and 1.4% of trials, respectively. Mean percent accuracies for the word and nonword grammatical category judgments are shown in Table 4. Because of the mean

**Table 4.** Mean Percent Accuracies for the Word and Nonword Grammatical Category Judgements

	<i>Words</i>		<i>Nonwords</i>	
	<i>Nouns</i>	<i>Verbs</i>	<i>Noun-like</i>	<i>Verb-like</i>
Proportion (%)	98 (1.3)	96 (1.9)	79 (4.1)	57 (5)

SDs in parentheses.

accuracy rates being near ceiling, the classification data for the nouns and verbs were not subjected to further analysis.

We conducted one-way ANOVAs to determine sensitivity to probabilistic cues to grammatical category in the nonword endings with  $F_1$  treating participants as a random factor and  $F_2$  treating items as a random factor. Two-way ANOVAs were not employed because the percentage of nonwords categorized as nouns and the percentage of nonwords categorized as verbs provide redundant information (see Kemp et al., 2009; Arciuli & Cupples, 2006). The single factor, ending type, was repeated in the participant analysis and nonrepeated in the item analysis. Significantly, more nonwords with verb-like endings were classified as verbs than nonwords with noun-like endings  $F_1(1, 18) = 105.13$ ,  $MSE =$

119.87,  $p < .001$ , partial  $\eta^2 = .85$ ;  $F_2(1, 78) = 71.23$ ,  $MSE = 0.04$ ,  $p < .001$ , partial  $\eta^2 = .48$  indicating that the participants were sensitive to the probabilistic cues to grammatical category embedded in the endings of the nonwords, replicating prior results (Kemp et al., 2009; Arciuli & Cupples, 2006).

### Imaging Data

The conjunction analysis conducted to identify regions of the left cytoarchitectonically defined PM and M1 cortices involved in both observation and execution of hand actions (i.e., execute hand > fixation  $\cap$  observe hand > non-body motion) revealed significant activity in three large clusters with peaks in medial (corresponding to SMA), dorsal and ventral middle lateral areas (see Table 5 and Figure 3). All three peaks and majority of the voxels within each cluster were situated in PM cortex. Within these voxels, planned  $t$  contrasts of each condition of the grammatical category judgment task versus baseline revealed significant BOLD signal responses in identical peaks in the left SMA for all stimuli types, with additional responses in the midlateral PM cortex for manual verbs and verb-like nonwords—also with identical peaks (Table 5).

**Table 5.** MNI Coordinates for Comparisons Showing Significant Motor Activity

<i>t Contrast</i>	<i>Peak MNI (x y z)</i>			<i>Z Score</i>	<i>Cluster (Voxels)</i>
<i>Localizer (Execute Hand &gt; Fixation <math>\cap</math> Observe Hand &gt; Non-body Motion)</i>					
Left medial precentral gyrus (SMA)	−4	4	50	5.14	265
Left lateral precentral gyrus	−26	−2	62	5.05	472
	−58	4	32	4.82	82
<i>Manual Verbs &gt; Non-body-Part-related Nouns</i>					
Left medial precentral gyrus, pre-SMA	−4	14	50	4.27	30
Left lateral precentral gyrus	−54	−2	42	4.96	21
<i>Verb-like &gt; Noun-like Nonwords</i>					
Left medial precentral gyrus, SMA	−6	6	56	4.49	79
Left lateral precentral gyrus	−54	−2	42	4.3	17
<i>Manual Verbs &gt; Non-body-Part-related Nouns <math>\cap</math> Verb-like &gt; Noun-like Nonwords)</i>					
Left lateral precentral gyrus	−54	−2	42	4.3	17
Left medial precentral gyrus, pre-SMA	−4	14	50	4.0	30
<i>Manual Verbs &lt; Non-body-Part-Related Nouns <math>\cap</math> Verb-like &lt; Noun-like Nonwords)</i>					
Left posterior middle temporal gyrus	−44	−60	18	4.46	471*

$p < .001$  and  $p < .05$  (FWE cluster-corrected).

\* $p < .001$  and  $p < .05$  (FWE cluster-corrected; whole-brain analysis).

Note that the coordinates for this lateral peak at  $-52, -2, 42$  are consistent with those reported for comparisons of manual verbs versus baseline conditions within PM cortex regions activated by functional motor localizer tasks, for example,  $-54, 4, 44$  (Boulenger et al., 2009);  $-50, -8, 50$  (Hauk & Pulvermüller, 2011); and  $-46, -2, 48$  (Pulvermüller, Cook, & Hauk, 2012).

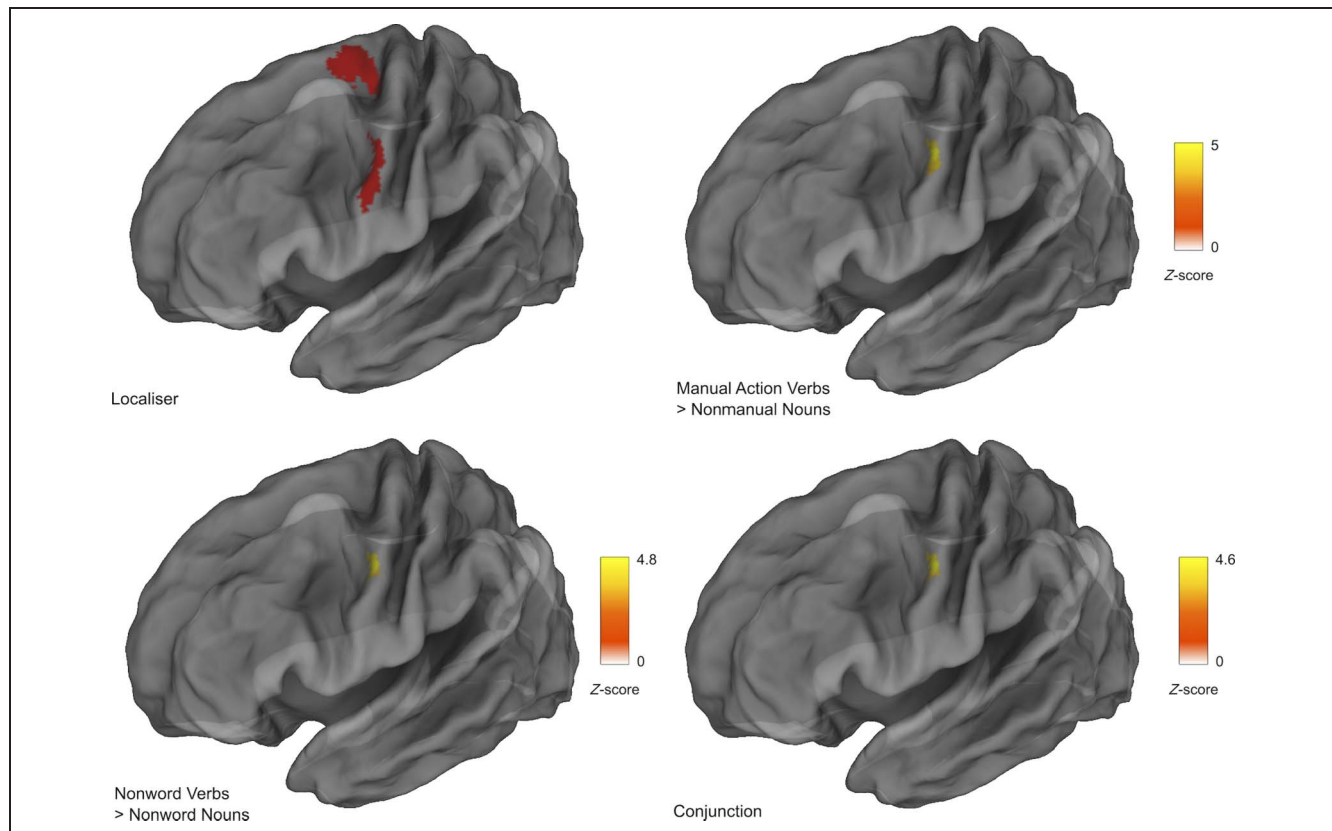
We next evaluated grammatical class effects by contrasting hand-related verbs with non-body-part-related nouns and verb-like nonwords with noun-like nonwords. Both verb and verb-like nonwords showed increased activation in the left SMA and middle lateral PM cortex compared with nouns and noun-like nonwords, respectively (Table 5 and Figure 3). None of the reverse contrasts were significant (i.e., nouns > verbs; noun-like > verb-like nonwords). To establish whether these PM cortex regions responding across word and nonword contrasts overlapped, we tested the conjunction null as defined by Nichols et al. (2005), that is, Manual verbs > Non-body-part-related nouns  $\cap$  Verb-like > Noun-like nonwords. The results of this conjunction analysis revealed identical voxels in lateral and medial (SMA) regions of PM cortex were responding, despite the absence of manual semantic content in the nonwords.

## Whole-brain Exploratory Analyses

The results for the whole-brain exploratory analyses are shown in Figure 4. In addition to the regions identified in the ROI analyses above, we identified a region in the left posterior temporal cortex demonstrating significant activity for the conjunction of Non-body-part-related nouns > Manual verbs  $\cap$  Noun-like > Verb-like nonwords (see Table 5).

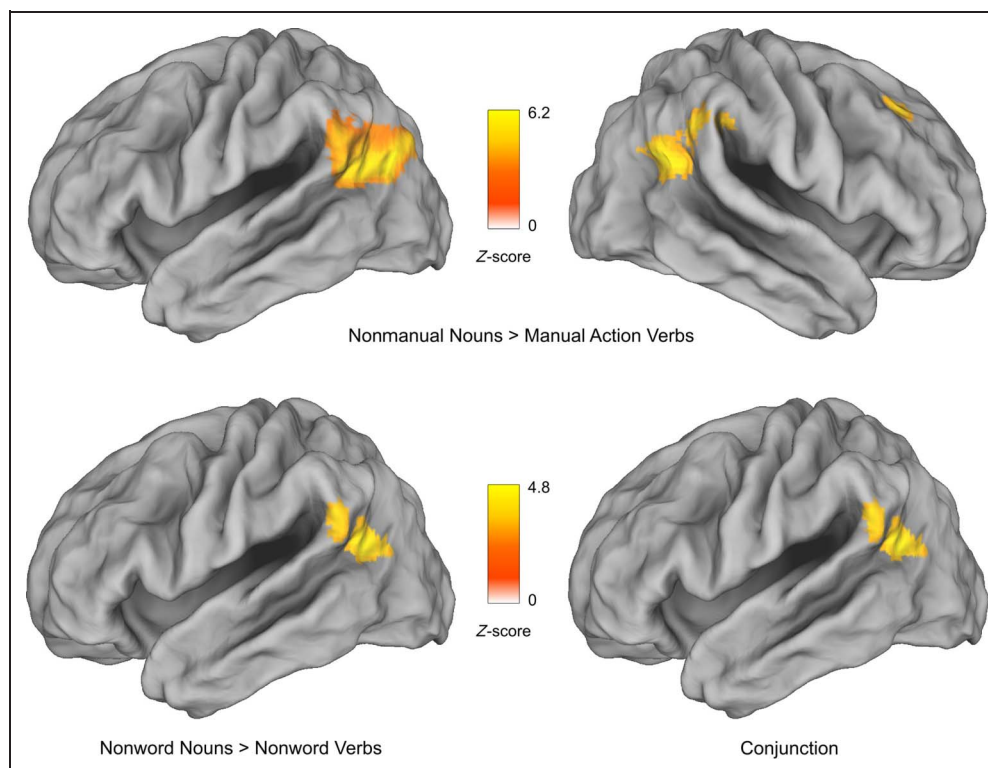
## DISCUSSION

The aim of this study was to investigate the motor cortex activity elicited during action word processing; in particular, whether this activity selectively reflects motor-semantic content and/or its simulation, as is often assumed. We drew upon recent corpus and behavioral research demonstrating the relevance of probabilistic ortho-phonological cues to grammatical category to determine whether motor cortex activity elicited during action word processing might also reflect sensitivity to these statistical regularities. Our results demonstrate for the first time that PM cortex responds differentially to these probabilistic ortho-phonological cues when they are embedded in the



**Figure 3.** Renderings of the left hemisphere lateral cortical surface depicting: (top left) the motor localizer ROI determined by conjunction analysis (i.e., execute hand > fixation  $\cap$  observe hand > non-body motion); (top right) increased activity elicited by manual action verbs compared with non-body-part-related nouns; (bottom left) increased activity elicited by verb-like nonwords compared with noun-like nonwords; and (bottom right) significant overlapping activity revealed by the conjunction analysis of Manual verbs > Non-body-part-related nouns  $\cap$  Verb-like > Noun-like nonwords.

**Figure 4.** (Top) Renderings of the left and right hemisphere lateral cortical surfaces depicting significant activity revealed by the contrast of Non-body-part-related nouns > Manual verbs in the whole-brain analysis. (Bottom) Renderings of the left hemisphere lateral cortical surface depicting significant activity revealed by the contrast of Noun-like > Verb-like nonwords and significant overlapping activity revealed by the conjunction analysis of Non-body-part-related nouns > Manual verbs  $\cap$  Noun-like > Verb-like nonwords.



endings of nonwords. Specifically, verb-like nonwords evoked increased activity compared with noun-like nonwords. Crucially, this differential activity overlapped with that observed for disyllabic verbs denoting manual actions compared with nouns denoting non-body-part-related concepts. In what follows, we discuss the implications of these results for neuroscientific investigations of language embodiment and of grammatical class more generally.

### Probabilistic Ortho-phonological Cues and PM Cortex

Our behavioral data confirmed that participants were sensitive to the probabilistic nonmorphologically derived ortho-phonological cues to grammatical class embedded in the endings of the disyllabic nonwords, replicating prior results (Kemp et al., 2009). Similar effects have been observed for these types of nonwords across naming, stress assignment, sentence construction, and sentence judgment tasks (Arciuli et al., 2012; Arciuli & Monaghan, 2009; Kemp et al., 2009; Arciuli & Cupples, 2006). Hence, there is considerable evidence that participants exploit this sublexical information even when an explicit grammatical category judgment is not required.

We identified a significant increase in PM cortex for processing of disyllabic verbs denoting manual actions compared with non-body-part-related nouns. This activity was evoked in an identical region of PM cortex to that reported by several prior studies employing these types of words across word reading and sentence comprehension tasks (e.g., Pulvermüller et al., 2012; Hauk &

Pulvermüller, 2011; Boulenger et al., 2009). Consequently, we can be confident that the motor activity identified in this study is consistent with that reported previously for manual action words, at least when it has been assigned accurately to a motor cortex region. This activity is typically attributed to conceptual processing. However, a demonstration of significant motor activity for this class of words cannot, in isolation, address the nature of the mechanisms responsible (Postle et al., 2008, 2013; Mahon & Caramazza, 2008). It is therefore essential that researchers test alternate hypotheses to explain this activity.

We first reviewed the results of neuroimaging studies showing the activity for nonwords overlapped with regions often reported to be action category specific, thus providing evidence that ortho-phonological processing is sufficient for eliciting activity along the motor strip. Next, as a new finding, our data showed that PM cortex is differentially sensitive to probabilistic ortho-phonological cues to grammatical class embedded in the endings of disyllabic nonwords, with verb-like stimuli resulting in significantly increased activity compared with noun-like stimuli. Moreover, the regions of PM cortex demonstrating this sensitivity overlapped with those showing increased activity for manual action verbs compared with non-body-part-related nouns. This latter result, the critical test of our novel hypothesis, indicates motor activity evoked during processing of action words cannot be attributed selectively to conceptual representations and/or their motor simulation. This interpretation extends to demonstrations of processing impairments for action words, compared with nouns, in patients with motor

system disorders (e.g., Boulenger et al., 2008; Bak et al., 2006; Neiningner & Pulvermüller, 2003).

As the overlap in activity was calculated via Nichols et al.'s (2005) method for a logical AND conjunction, it represents the intersection of the identically thresholded statistical maps from the nonword and word comparisons. As an anonymous reviewer of this article noted, the spatial extent of the cluster for the contrast of manual action verbs versus non-body-part-related nouns was slightly larger than the similar contrast for the nonwords (four voxels). This difference might be interpreted as reflecting the additional demands of semantic processing and/or simulation for the action words. Alternatively, this could possibly be related to the additional demands of processing probabilistic cues present in beginnings (see Kemp et al., 2009; Arciuli & Cupples, 2007) across our words and nonwords. However, as we noted in the Introduction, we have focused here on endings as there is evidence that these cues might play a more consistent role in denoting grammatical class than beginnings (Arciuli & Monaghan, 2009).

### **Implications for Theory and Experimental Research**

The fact that the observed overlap with ortho-phonological activity occurred in a cytoarchitecturally and functionally defined hand motor area is relevant for theories proposing a role for mirror neurons in the representation of action meaning (e.g., Gallese & Lakoff, 2005; Glenberg & Kaschak, 2002). We defined our motor-localizer ROI based on a conjunction analysis of manual action observation and execution conditions. The localizer task activity was thus consistent with prior reports of PM cortex activity interpreted as reflecting mirror neuron (MN) system engagement for these types of actions (e.g., Grézes, Armony, Rowe, & Passingham, 2003). A key challenge for MN theories of action understanding has been to demonstrate whether this activity reflects processing of the intentional structure of action by detecting the statistical regularities of others' behavior or is instead more akin to recognition of mere statistical regularity (e.g., Borg, in press; Gallese, Rochat, Cossu, & Sinigaglia, 2009). Behavioral demonstrations of sensitivity to probabilistic ortho-phonological cues to grammatical category are evidence that language processing is an example of implicit learning of statistical regularities present in language input (e.g., Arciuli et al., 2012; Arciuli & Cupples, 2006; Farmer et al., 2006; Monaghan et al., 2005; Kelly, 1992). Thus, the overlap of activity observed for MN system operations and processing of probabilistic ortho-phonological cues in this study would appear to indicate that PM cortex activity is more likely to reflect recognition of statistical regularity, given the absence of action meaning content in the nonword stimuli. This is consistent with the increasing evidence demonstrating that PM cortex responds to statistical regularities

among actions, irrespective of the body part employed (e.g., extension–flexion movements; Lorey et al., in press; Rijntjes et al., 1999).

If PM cortex activity reflects recognition of statistical regularities more generally, it should also be sensitive to probabilistic ortho-phonological cues embedded in other open class words (adjectives and adverbs). For example, adjectives are more likely to end with *-ed* than other words (Monaghan et al., 2005). We speculate that PM cortex might contribute to grammatical class processing by using ortho-phonological statistical regularities embedded in single words in a predictive manner, across perception and production (e.g., von Helmholtz, 1860/1962; see Clark, 2013). The relatively greater activity observed for verb-like stimuli in this study may reflect the relative difficulty of processing verbs compared with other grammatical classes (see Kemp et al., 2009). If our results are reflecting greater difficulty processing verbs, this could be related to the fact that there are more nouns than verbs in English, and that it is likely that our participants had been exposed to more of the noun-typical than verb-typical endings during their reading experience. In terms of developing neural networks, this differential cue exposure could influence the plasticity of representations, resulting in some cues being processed/accessed more quickly. Alternatively, differential cue exposure during development might influence the probability of connecting new representations to existing ones, resulting in some cues to grammatical class having more central, highly connected representations, facilitating processing (see Romberg & Saffran, 2010).

Although the current result in PM cortex is directly relevant to comparisons of action words and noun classes, probabilistic ortho-phonological cues are also likely to affect comparisons of different lists of words within a given grammatical class; for example, comparisons of action versus state verbs (e.g., Willems et al., 2010), comparisons of verbs denoting actions performed by different body parts (e.g., Hauk et al., 2004), and comparisons of object nouns with different sensory or functional properties (e.g., Carota et al., 2012). As we noted in the Introduction, verbs or nouns that are ortho-phonologically typical for their grammatical class elicit advantaged processing compared with nontypical stimuli, across a range of tasks (e.g., Kemp et al., 2009; Arciuli & Cupples, 2006; Farmer et al., 2006; Monaghan et al., 2005). To date, none of the studies investigating activation of motor areas during verb or object noun processing have employed lexical stimuli matched for these ortho-phonological variables. This was also the case in this study. Although we deliberately constructed our word lists without reference to probabilistic ortho-phonological cues to grammatical category, a post hoc analysis indicated the respective word endings were more typical of their category (Arciuli & Cupples, 2006). Consequently, differential motor activity evoked by different lists of words can be expected to reflect differences in the extent to which each list

contains words with typical or atypical cues, unless they are matched explicitly for these variables.

Of course, as we employed only manual action words, it remains to be demonstrated whether PM cortex responses for foot/leg or mouth/face words likewise reflect sensitivity to probabilistic ortho-phonological cues to grammatical class. We think this is quite likely as our review of the available neuroimaging data revealed little evidence in support of a proposed somatotopic organization of action word meanings in PM cortex. Similarly, as we employed written stimuli as per the majority of embodied language investigations, our results do not necessarily generalize to auditorily presented stimuli which have been employed in a minority of studies (e.g., Desai et al., 2010; Raposo, Moss, Stamatakis, & Tyler, 2009; Tettamanti et al., 2005). However, as we noted in the Introduction, there is now considerable evidence that orthography influences both auditory word perception and spoken word production in addition to written word recognition (e.g., Bürki et al., 2012; Perre et al., 2011; Rastle et al., 2011; Peereboom et al., 2009).

Our results also have broader implications for the large and equivocal literature documenting attempts to demonstrate a fronto-temporal cortex dichotomy between verb and noun processing, respectively (Crepaldi, Berlingeri, Paulesu, & Luzzatti, 2011; Pillon & d'Honin, 2011). The differentiation between nouns and verbs is perhaps the most common grammatical distinction across the world's languages (Baker, 2001). Most studies have investigated semantic (e.g., object/action), syntactic, and morphological variables. A recent review proposed grammatical category distinctions instead emerge from a combination of variables including both semantic constraints and co-occurrences within language, including distributional cues at the phrasal level (Vigliocco, Vinson, Druk, Barber, & Cappa, 2011). However, probabilistic cues embedded within single words have typically been neglected (cf. Arciuli et al., 2012). Although noun processing has been linked to temporal lobe areas with varying levels of success (see Crepaldi et al., 2011), our conjunction analysis revealed overlapping activity in left posterior temporal cortex for nouns and noun-like versus verb and verb-like nonword stimuli, respectively. This suggests cue typicality may be an important moderating variable for grammatical class-related activity in this region.

### Additional Issues

Aside from demonstrating the equivocal nature of the neuroimaging evidence that has been cited to support grounding of action word conceptual processing in a body part specific organization of motor cortex, our review also identified a number of issues concerning how this evidence has been presented across individual studies and reviews. Inaccurate anatomical labeling of peaks is a prominent issue for embodied language studies, being demonstrably less accurate than for studies using ortho-

phonological manipulations. In an earlier review, Postle et al. (2008) noted that some studies reported significant effects for only a subset of their body part categories and/or reported nonsignificant trends, raising questions about the reliability of results and their task-dependent nature. These issues remain salient. Null results have also not been considered in previous reviews, leading to an overestimate of the reliability of body part specific conceptual-motor activity. For example, in an early study Perani et al. (1999) failed to observe significant motor activity for object manipulation verbs relative to state verbs (cf. Willems et al., 2010). The issue of reliability also extends to the assumed motor properties of object nouns. Whereas Carota et al. (2012) reported motor cortex activity for passive reading of nouns denoting manipulable objects, other recent studies have failed to observe such activity even when the task explicitly directs attention to motor features (Bonner, Peelle, Cook, & Grossman, 2013; van Dam, van Dijk, Bekkering, & Rueschmeyer, 2012; see also Perani et al., 1999).

### Conclusions

In summary, the combined empirical data we have presented demonstrate that the motor cortex activity evoked by action words cannot be assumed to selectively reflect motor-semantic content and/or its simulation. Ortho-phonological manipulations evoke motor activity reliably and probabilistic cues to verb status embedded in non-words evoke increased PM cortex activity akin to verbs denoting manual actions. Although embodied language theories place strong emphasis on semantic content and its simulation, investigations of statistical learning have long indicated that infants and children are sensitive to a range of probabilistic cues in language input (e.g., Saffran, Aslin, & Newport, 1996) and patterns of brain activity can be expected to reflect this sensitivity. Thus, it may be more profitable to adopt an emergentist approach to inform the design of future neuroimaging investigations of action word processing as well as grammatical class more generally.

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