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Modulation of motor and premotor cortices by actions, action words and action sentences

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ABSTRACT

Recent research has indicated that processing different kinds of action verbs, such as those related to arm or leg movements (e.g. *grab*, *kick*), engages regions along the motor strip responsible for the execution of the corresponding actions. It has been proposed that this activation reflects action-related meaning and that these regions are automatically triggered whenever action words are encountered. However, this view is not universally shared by cognitive studies that have shown that the representation of verbs is highly dependent on the interactions with the semantic context. We investigated these views in a set of fMRI studies, in which participants performed a movement localiser task and listened to arm- and leg-related verbs that were presented in isolation (e.g. *kick*), in literal sentences (as in *kick the ball*) and idiomatic sentences (as in *kick the bucket*). We found significant activation in motor regions when action verbs were presented in isolation, and, to a lesser extent, in literal sentential contexts. When the same verbs were presented in idiomatic contexts, activation was found in fronto-temporal regions, associated with language processing, but not in motor and premotor cortices. These results suggest that motor responses were context-dependent, rather than automatic and invariable. These findings lend support to cognitive theories of semantic flexibility, by showing that the nature of the semantic context determines the degree to which alternative senses and particularly relevant features are processed when a word is heard.

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1. Introduction

A prominent view of the cognitive and neural bases of conceptual knowledge proposes that sensory and motor properties underpin the meaning of concepts and that the relative contribution of these types of properties varies across domains. For example, our concept for an animal such as *elephant* may be made up of many visual properties (e.g. *has a trunk*, *is grey*), and relatively few motor properties. On the other hand, concepts for tools such as *hammer* rely more heavily on motor properties like *hammering* and *beating*, and action verbs such as *grab* may be almost entirely based on motor properties (Warrington & McCarthy, 1983). Although there are a number of variants of this view that differ in important ways, they all share the assumption that conceptual knowledge is grounded in modality-specific neural systems for perception and action (Barsalou, 1999; Barsalou, Simmons, Barbey, & Wilson, 2003; Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Martin & Chao, 2001; Martin, Wiggs, Ungerleider, & Haxby, 1996; Pulvermüller, 2001).

In addition to these sensory and motor network dissociations across conceptual domains, further fine-grained distinctions have been proposed for the neural representation of action words in the motor and premotor cortices. It has been claimed that producing and comprehending verbs denoting actions performed with different body parts engages regions along the motor strip, which overlap with those involved in the actual performance of those actions (Hauk, Johnsrude, & Pulvermüller, 2004; Pulvermüller, 1999, 2001; Tettamanti et al., 2005). This research has been taken as evidence that motor and premotor sites are critically engaged, not only in sensory–motor operations, but also by the neural system underpinning the conceptual foundations of language. Pulvermüller and colleagues have hypothesised that neurons processing the word form (e.g. *grasp*) and those processing the corresponding body movements (the action of *grasping*) frequently fire together and thus become strongly linked (Pulvermüller, 1999, 2001). According to this view, the action-related aspects of a word's meaning are represented in and around the motor strip and these regions are automatically and invariably activated when action words are encountered, and should not be modulated by attentional demands

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(Pulvermüller, 2005; Pulvermüller, Shtyrov, & Ilmoniemi, 2005). In a study where motor activation was reported for action words in a paradigm where subjects had to focus their attention on a distractor task, the authors concluded that such brain processes "are to a large degree automatic" (Pulvermüller et al., 2005).

In partial support of this view, activation of the motor properties of action words has also been reported both when these words occur in isolation and in some types of sentential context. Action words occurring in sentences (e.g. *I grasp the knife*; *I kick the ball*) and phrases (e.g. *biting the peach*) which convey their action meaning, activate the fronto-parietal motor network that subserves action execution relative to rest (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006) and relative to sentences with an abstract content (e.g. *I appreciate sincerity*; Tettamanti et al., 2005). However, the automaticity of motor-related activity for action words has been challenged by two studies which failed to find effects in motor and premotor areas for action compared to object words (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Kable, Lease-Spellmeyer, & Chatterjee, 2002). The authors argued that this may have occurred because subjects were not explicitly attending to the motor attributes of the words, raising the possibility that motor cortex modulation may occur only when participants directly attend to the actions and their motor properties. Thus, although motor areas may be activated by action verbs under certain experimental settings, it is not clear whether this activation is as truly automatic and invariable as is claimed.

In the present study, we asked whether motor regions are automatically and invariably involved in the processing of action words or whether the activation of meaning attributes of words (including their sensory–motor properties) is a more flexible and contextually dependent process. In an fMRI study, we had volunteers perform arm/hand and leg/foot actions to identify neural regions involved in motor movements in each volunteer individually. The same participants listened to action words that were presented in isolation (e.g. *kick*) or embedded in sentences with literal or idiomatic meanings. Critically, in the literal sentences, the verbs denoted actions performed either by arm/finger movements or by leg/foot movements (e.g. *After six minutes, the new recruit kicked the ball*), whereas in the idiomatic sentences, the same verbs were not related to any body movements (e.g. *After six months, the old man kicked the bucket*). Behavioural studies have shown that idioms do not take longer and are not more difficult to process than literal sentences (Gibbs, 2002; Keysar, 1989), suggesting that the idiomatic meaning is processed automatically, and similar language areas are involved in literal and idiomatic sentence comprehension (Giora, 2002; Oliveri, Romero, & Papagno, 2004). Comparing action words presented in isolation and in literal and idiomatic sentences enables us to contrast the processing of the same words under very different processing demands. Extensive behavioural priming studies have shown that sentential context affects the activation of the specific meaning attributes of a word. For example, when hearing the word *lemon* in the sentence: "*The little boy shuddered eating a slice of lemon*" only the contextually relevant attributes of lemon (e.g. *sour*) were primed and not contextually irrelevant attributes (e.g. *yellow*; Tabossi, 1988; Tabossi, Colombo, & Job, 1987). Cognitive studies suggest that language comprehension may not be based on a full word-by-word analysis, but instead the contextual meaning of the sentence may influence the semantic processing of the upcoming words (Ferreira, Ferraro, & Bailey, 2002; Marslen-Wilson & Tyler, 1980; Tyler & Wessels, 1983; Sanford & Sturt, 2002), highlighting the importance of the sentential context in which a word occurs. In contrast with previous fMRI studies which have used very short, predictable sentences (*I grasp the knife*) or phrases (*biting the peach*) thus minimising the contribution of the semantic, syntactic and pragmatic context, we used longer and less predictable sentential contexts to ensure that participants fully engaged in the processing of contextual information, and that their attention was not directed towards specific words.

If action words automatically activate their motor properties irrespective of their context, as may be assumed on a "fire together wire together" view (Pulvermüller, 1999, 2001), then we should observe activation in motor/premotor cortex for all three conditions—single action verbs, literal and idiomatic sentences. If, however, the meaning of words is modulated by the sentential context, we expect the neural processing of verbs to vary, depending on whether the same action word is processed in isolation, or in literal or idiomatic contexts. Based on previous results, we expect single action words (Hauk et al., 2004; Rüschemeyer, Brass, & Friederici, 2007) and literal action-related sentences (Aziz-Zadeh et al., 2006; Tettamanti et al., 2005) to activate motor regions in a somatotopic fashion. Contextual effects should be maximal for idiomatic sentences, since context is *not* consistent with the action-related meaning and therefore no motor activity is expected.

2. Method

2.1. Participants

We tested 22 right-handed, healthy, British English speakers (mean age 23 years). All gave informed consent and were paid for their participation. The study was approved by Addenbrookes NHS Trust Ethical Committee. All participants took part in the body movement localiser task and in the action sentences study. The localiser task always followed the sentence experiment in order not to bias the participants' attention toward action-related aspects of the stimuli. In order to avoid repetition effects, subjects were tested in the single word experiment in a separate scanning session one month after the first session. Fourteen of the original subjects participated in this second study. Given the differences in the conditions (words vs. sentences and localiser) participants were unaware of the relationship between the two studies, therefore performance on the single word task is unlikely to have been influenced by the motor localizer task.

2.2. Materials and procedure

2.2.1. Body movement localiser task

Instructions were presented visually on a computer screen indicating which body part participants should move. Subjects were asked to move their: (a) right-index finger; (b) left-index finger; (c) right foot; and (d) left foot. Each movement was performed in a self-paced manner for 21 s and repeated four times in a pseudo-randomised order, as in Hauk et al. (2004). DMDX software (Forster & Forster, 2003) was used to present the instructions.

2.2.2. fMRI study of action words

The stimuli consisted of 112 single spoken words, which denoted action ($n = 56$) and non-action verbs ($n = 56$). Half of the action verbs were arm-related (e.g. *grab*) and half were leg-related (e.g. *trample*). Non-action verbs, used as a control condition, were abstract verbs with no arm- or leg-related meaning (e.g. *think*). The degree of semantic relatedness between words and body movements was determined in a pre-test, in which 15 native speakers of British English (none of whom took part in the neuroimaging studies) rated how related in meaning each word was to actions performed with: (a) arms or hands; and (b) legs or feet using a 7-point scale (see Table 1). Verbs in the arm-related condition were rated as significantly more related to arm and hand movements, while leg-related verbs were rated as significantly more related to leg and foot movements ($p < .001$), with no significant differences between words in the other conditions ($p > .05$). Words were matched for lemma frequency (Baayen & Pipenbrook, 1995) and familiarity (Coltheart, 1981; see Table 1). We included 28 baseline items, to control for speech-related activity, by randomly selecting a subset of action and non-action words and converting them to signal correlated noise (SCN, Schroeder, 1968) using Cool Edit 96 (http://www.colledit.com). These items retained the same spectral profile and amplitude envelope as the original speech, but since all spectral details were replaced with noise, they were unintelligible.

Participants were asked to listen passively to single words and noise. A sparse-imaging technique was used, in which the words/noise bursts were presented in the silent period between successive scans, minimising interference from scanner noise (Hall et al., 1999). Participants heard a word (or noise equivalent) in the 1.4 s silent period before a single EPI volume of 1.6 s. Stimuli were pseudo-randomised in a single scanning session and were presented dichotically using DMDX software (Forster & Forster, 2003). At the beginning of the session, there were five

Table 1
Descriptive statistics of stimuli characteristics. Action-relatedness refers to the rated arm- and leg-relatedness (for arm and leg contexts respectively), where 1 = unrelated, 7 = highly-related. Underlined verbs are examples of the actions words employed in each condition.

	N	Action-relatedness	Frequency action word	Familiarity action word	Length (words)	Naturalness
Arm verb e.g. *Grab*	28	6.4	62	566	–	–
Arm literal e.g. *The fruit cake was the last one so Claire grabbed it.*	28	5.4	62	566	10.8	5.9
Arm idiomatic e.g. *The job offer was a great chance so Claire grabbed it.*	28	3.1	62	566	10.6	5.6
Leg verb e.g. *Trample*	28	6.4	64	562	–	–
Leg literal e.g. *The muddy children trampled over Sarah's clean floor.*	28	5.4	64	562	10.9	5.9
Leg idiomatic e.g. *The spiteful critic trampled over Sarah's feelings.*	28	3.3	64	562	10.8	5.6

lead-in trials to allow for T1 equilibrium. The session lasted approximately eight minutes.

2.2.3. fMRI study of action sentences

We constructed sentences using the same action verbs as in the single word study. There were four types of sentence in this experiment. The literal sentences contained a verb that described an action performed with arms and hands (e.g. *The fruit cake was the last one so Claire grabbed it*) or legs and feet (e.g. *The muddy children trampled over Sarah's clean floor*). The same verbs also appeared in idiomatic sentences, matched in structure to the literal sentences, in which the verb's meaning was not related to actions performed by body movements (e.g. *The job offer was a great chance so Claire grabbed it*; *The spiteful critic trampled over Sarah's feelings*). The idioms were taken from the Cambridge Dictionary of Idioms (http://dictionary.cambridge.org).

Each sentence contained a phrase before the verb whose role was to disambiguate the meaning of the verb (i.e. whether or not it was related to body movements). This allowed us to look the role of the previous context in the activation of the upcoming action words. The relatedness of the sentences to body movements was confirmed in a pre-test (Table 1). Sentences in the literal arm-related condition were rated as significantly more related to actions performed with arms and hands than all other sentence types ($p < .001$). Sentences in the literal leg-related condition were rated as significantly more related to actions performed with legs and feet than sentences in the other conditions ($p < .001$). As it can be seen from the examples in Table 1, the critical action word appeared embedded in the sentence (either in the middle or towards the end). Importantly, the word's position in the literal and the corresponding idiomatic sentence was matched, ruling out any word position effects across different contexts. Sentences were matched for number of words and rated naturalness. The critical action words in the sentences were matched for lemma frequency (Baayen & Pipenbrook, 1995) and familiarity (Coltheart, 1981) (see Table 1).

There were 112 experimental items: 56 literal sentences (28 arm-related, 28 leg-related verbs) and 56 idiomatic sentences (28 arm-related, 28 leg-related verbs). We included 28 baseline items which were created by randomly selecting a subset of sentences and converting them to SCN. An additional 112 filler sentences were created (56 literal, 56 idiomatic) containing verbs with non-action meanings (e.g. *Despite their spending, the boys' mother had saved some money*; *Despite their embarrassment, the boys' mother had saved the day*) to avoid focusing the participants' attention on the action-related aspects of the sentences. The filler items were matched to the experimental sentences on the relevant variables. There were a total of 252 trials.

We selected a task which has been previously shown to be sensitive to the meaning of individual words in sentences (Davis et al., 2007; Rodd, Davis, & Johnsrude, 2005). In this task participants listen to sentences and on half of them (randomly assigned) a visual probe word is presented on the screen a few seconds after the end of the sentence. Participants press a response key to indicate whether the visual probe is related to the meaning of the sentence. This task picked up greater activity due to target words which were semantically ambiguous (e.g. *bank*) compared to unambiguous words in sentences, showing its sensitivity to the semantic properties of individual words. Moreover, it elicited similar activations as a passive listening task. Our study was modelled on these previous studies such that the visual probe words occurred on average four seconds after the end of the sentence. Related and unrelated probes were matched for familiarity and number of letters across conditions ($p > .05$ for all comparisons).

A sparse-imaging technique was used to minimise interference from scanner noise. Participants heard a single sentence (or noise equivalent) in the 8.6 s silent period before a single 1.6 s scan. The critical words (i.e. action words) were jittered relative to the scan onset by temporally aligning the offset of the word with the onset of the scan, ensuring that scans were obtained five seconds after the critical word was heard, to coincide with the peak of the hemodynamic response evoked by the word (Hall et al., 1999). In Rodd et al. (2005) and Davis et al. (2007) these timing relationships between the critical words and the peak of the haemodynamic response ensured that the task was sensitive to the processing of the critical word along with the preceding context. The visual relatedness probe appeared at the start of the scan, thereby ensuring that very little of the hemodynamic response to the probe word would be observed in the scan.

The items were pseudorandomly organised into four sessions of 63 trials each. Literal and idiomatic sentences that shared the same verb were presented in different sessions with an average of 104 trials (about 18 min) interspersed in between. The order of the sentences was pseudo-randomised such that half of the action words were presented in the literal form first, while the other half were first shown in the idiomatic form. The relatively long lag between word repetition and the randomization of the context order indicate that repetition suppression effects are unlikely and not specific to a particular condition. Stimuli were presented dichotically using DMDX software (Forster & Forster, 2003). Session order was counterbalanced across participants.

2.3. MRI acquisition and imaging analysis

Scanning was conducted on a 3-Tesla Brucker Medspec MR system by using a head gradient, echo-planar imaging sequence (24 slices, 4 mm thick, interslice gap of 1 mm, 2 mm × 2 mm in-plane resolution, FOV = 25 cm × 25 cm, matrix size = 90 × 90, TE = 27 ms). We used continuous acquisition for the body movement localiser task, with acquisition time = 1.6 s and TR = 1.6 s. For the single word and sentence experiments, we used a sparse-imaging technique, with a TR of 3 s and 10.2 s, respectively. Acquisition was transverse-oblique, angled away from the eyes, and covered the entire brain.

Preprocessing and statistical analysis of the data were performed using Statistical Parametric Mapping software (SPM2, Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk), implemented in Matlab (Mathworks Inc., Sherborn MA, USA). Initial preprocessing of the body movement localiser scans consisted of slice timing correction by resampling slices in time relative to the first slice collected. For the word and sentence experiments, slice timing correction was not used, because of the long repetition time. For each experiment, all images were realigned to the first image (excluding the lead-in scans) to account for head motion. The images were spatially normalised to a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain, using a 12-parameter linear affine transformation (translation, rotation, zoom and shear in x, y and z directions) and a linear combination of three-dimensional discrete cosine transform basis functions to account for nonlinear deformations. The spatially normalised images were smoothed with an isotropic 8 mm full-width half-maximal Gaussian kernel.

Data for each subject was modelled with the general linear model using the canonical hemodynamic response function. Parameter estimate images from each subject were combined into a group random-effects analysis. Results were thresholded at $p < .001$ and only clusters that survived $p < .05$ corrected for multiple comparisons across the entire brain volume were considered significant. For the ROI analyses, we took a more liberal approach given the *a priori* hypothesis of activation in these regions, and thus results were thresholded at .001 uncorrected at the voxel level (Bailey, Jones, Friston, Colebatch, & Frackowiak, 1991; Tettamanti et al., 2005). Montreal Neurological Institute coordinates are reported. Beta values were obtained for the peak activations. These data were further analyzed using off-line statistical software.

3. Results

3.1. *fMRI study of body movements*

To determine the pattern of neural activation specifically associated with each body movement, we contrasted left and right finger movement with left and right foot movement. Finger movements produced significant activation in dorsolateral regions, including the pre- and postcentral gyrus bilaterally. Activation was also seen in the precuneus, R amygdala and cerebellum. Foot movements showed activation in centrodorsal regions on the midline, namely in paracentral lobule and medial frontal gyrus bilaterally (Fig. 1 and Table 2). These regions have been associated with finger and foot movement in previous neuroimaging studies (Fink, Frackowiak, Pietrzyk, & Passingham, 1997; Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998) and they correspond to the well-established somatotopic organisation of the motor circuit.

3.2. *fMRI study of action words*

We investigated the hypothesis that action word processing is associated with motor and premotor activation by contrasting all action words (arm- and leg-related) with non-action words (see Fig. 2 panel A and Table 3). Two clusters of significant activation were found. One was located in precentral gyrus and paracentral lobule. The peak activation was in the right hemisphere, but the cluster extended to similar regions of the left hemisphere, as shown in Fig. 2A. The other cluster was in R amygdala, extending to the hippocampus. Non-action words did not show significant activation over and above action words.

We next examined whether different types of action words elicited activation in the motor strip that overlapped with the respective body movements, as revealed by the body movement (localiser) task. We first tested if arm-related words (e.g. *grab*) showed significant activation in finger movement regions, over and above non-action words (e.g. *think*). A mask that included the motor and premotor regions activated for finger movements was defined in Marsbar toolbox (http://marsbar.sourceforge.net), using a threshold of .01 uncorrected. A region of interest (ROI) analysis was carried out in this *a priori* defined area. The results showed significant activation for arm-related words relative to non-action words in two clusters: one in the L inferior parietal lobule (LIPL), and the other in R precentral gyrus. Plots of signal change show that finger movement regions were modulated in a greater extent by arm-related words relative to leg-related words (Fig. 2 panel B and Table 3).

Table 2
fMRI study of body movements. Results were thresholded at $p < .001$ and clusters significant at $p < .05$ corrected for multiple comparisons were considered significant. The highest peaks from each cluster are shown.

Region	Extent	*Z* score	MNI coordinates		
			x	*y*	*z*
Finger movements					
L postcentral gyrus	1240	6.11	−40	−24	50
R postcentral gyrus	872	5.61	40	−24	50
Cerebellum	792	4.33	−38	−66	−18
R precuneus	331	3.96	2	−44	−22
R amygdala	198	3.87	28	−4	−16
Foot movements					
R dorsomedial frontal gyrus	1367	4.93	10	−18	68
L paracentral lobule		4.73	−10	−20	66

Table 3
fMRI study of action words. Action words compared to non-action words. For whole brain analysis, results were thresholded at $p < .001$ and clusters significant at $p < .05$ corrected for multiple comparisons were considered significant. For ROI analysis, results were thresholded at $p < .001$ uncorrected (voxel level). The highest peaks from each cluster are shown.

Region	Extent	*Z* score	MNI coordinates		
			x	*y*	*Z*
Action words > non-action words					
R amygdala	124	4.32	26	0	−16
R precentral gyrus	119	3.83	22	−26	64
ROI analysis					
Arm words > non-action words					
L inferior parietal lobule	8	3.36	−44	−36	44
R precentral gyrus	3	3.15	36	−14	46
Leg words > non-action words					
L paracentral lobule	6	3.48	−6	−16	72

A similar ROI analysis was carried out for leg-related words (e.g. *kick*) relative to non-action words, using a mask that combined the regions activated for foot movements. The results showed significant activation in a small cluster in L paracentral lobule, in the dorsomedial frontal gyrus. Plots of signal change demonstrate that

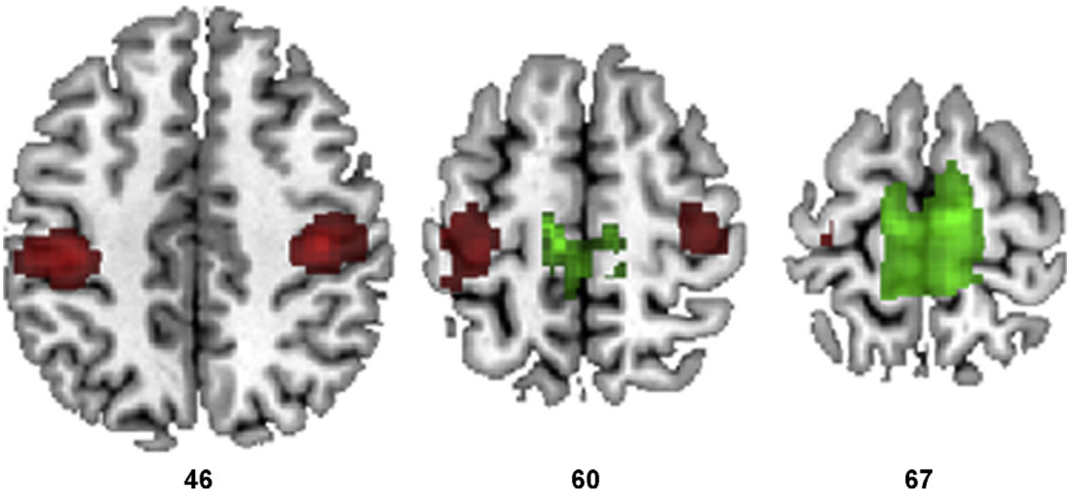

Fig. 1. fMRI study of body movements. Cortical regions activated during finger (red) and foot (green) movements. Results were thresholded at $p < .001$ voxel level and clusters that survived $p < .05$ corrected for multiple comparisons were considered significant. MNI coordinates are reported.

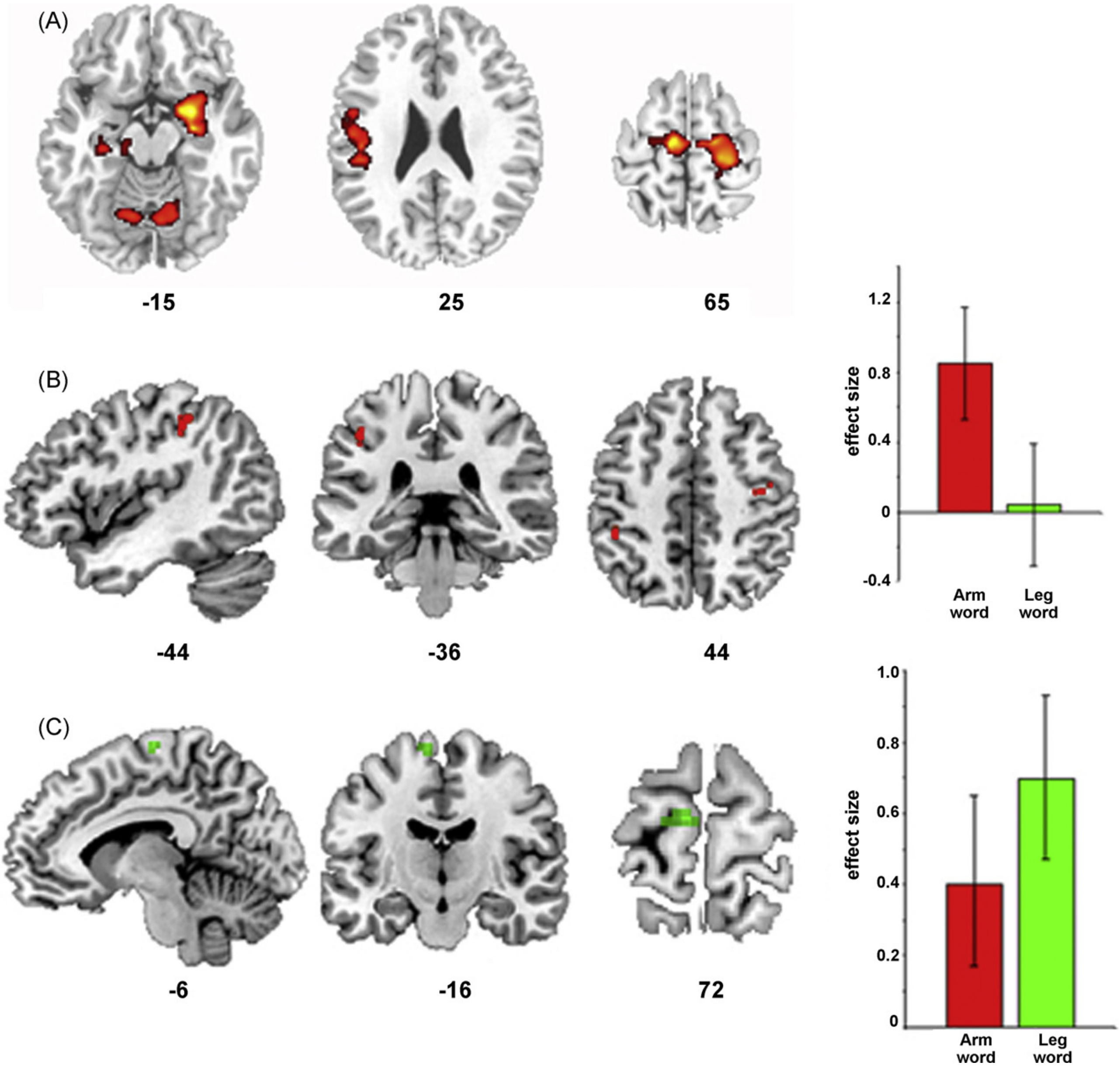

Fig. 2. fMRI study of action words. (Panel A) Cortical regions activated for action words relative to non-action words. Results were thresholded at $p < .01$ voxel level for display purposes. (Panel B) Cortical regions activated for arm-related words relative to non-action words in a finger movement region ROI analysis. The plots show effect sizes and standard deviations for arm- and leg-related words in a finger movement region. (Panel C) Cortical regions activated for leg-related words relative to non-action words in a foot movement region ROI analysis. The plots show effect sizes and standard deviations for arm- and leg-related words in a foot movement region. MNI coordinates are reported.

foot movement regions were modulated in a greater extent by leg-related than arm-related words (Fig. 2 panel C and Table 3). There were no significant activations for non-action words compared to arm- and leg-related words in any of the regions of interest. These effects suggest that motor strip activation is modulated by the semantic content of the words, with arm and leg words activating different regions in a somatotopic fashion.

3.3. *fMRI study of action sentences*

Participants button-press responses were significantly faster in the arm-related literal than idiomatic sentences (1039 ms, 1146 ms, $p < .05$). For the leg-related condition, there were no significant differences between sentential contexts (1104 ms, 1110 ms, $p > .1$). Overall, reaction times for arm-related and leg-related conditions did not differ. As expected, participants' responses were significantly faster in the baseline noise condition (870 ms) compared to the speech conditions (all $p < .001$). There were no significant differences in accuracy among conditions (87% for arm literal, 86% for arm idiomatic, 90% for leg literal, 93% for leg idiomatic, 94% for SCN).

We first investigated the brain regions engaged during processing of sentences, by comparing all sentences (both action and non-action in literal and idiomatic contexts) against noise. Sentence processing was associated with significant activation in L middle temporal gyrus (MTG), extending to superior and inferior temporal gyri and posteriorly to angular and supramaginal gyri. Activation was also found in L inferior frontal gyrus (IFG) and L precentral gyrus. A smaller cluster was centred in similar regions of the right hemisphere, including the RMTG and RSTG (Fig. 3 panel A and

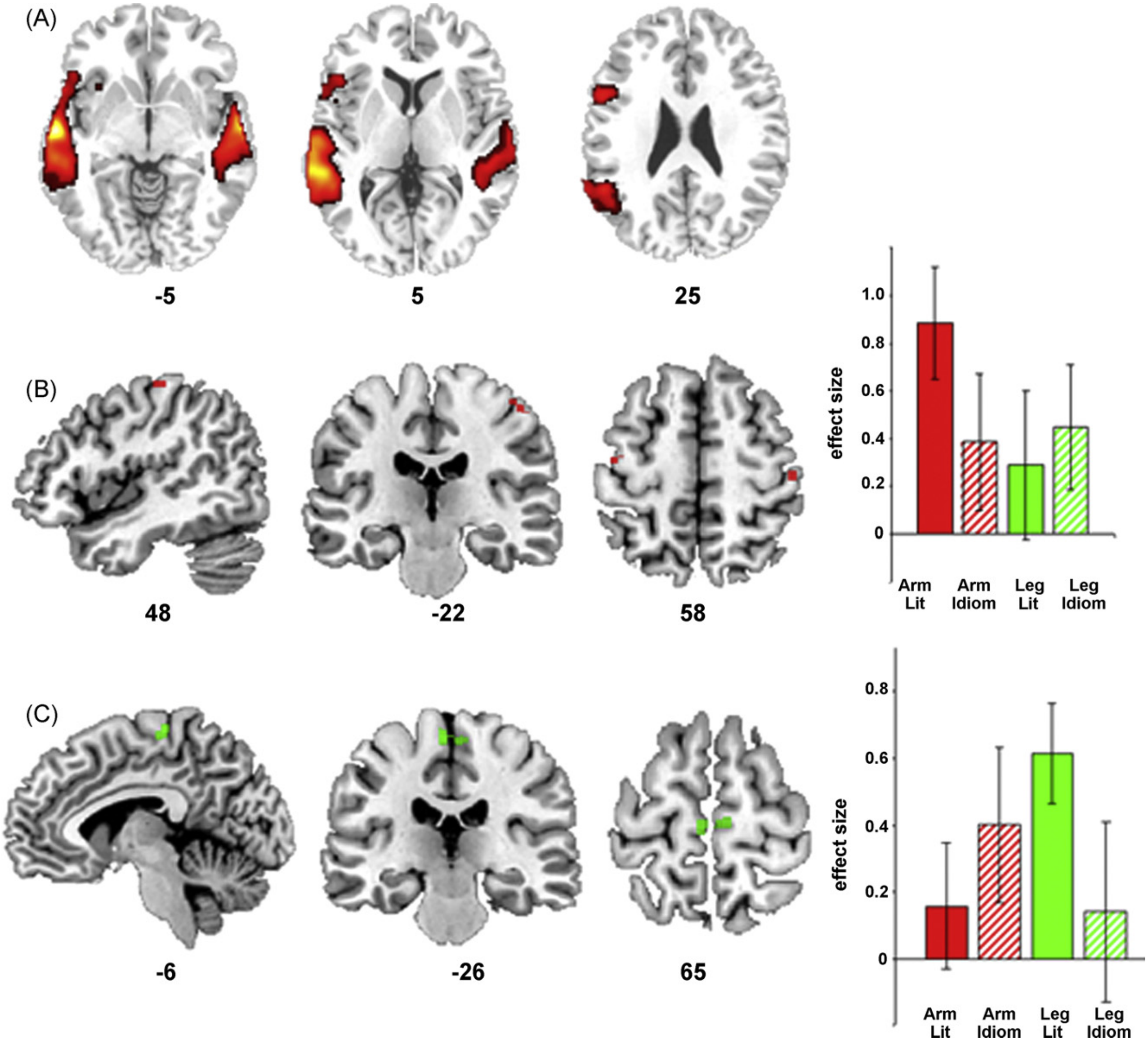

Fig. 3. fMRI study of action sentences. (Panel A) Cortical regions activated for all action sentences relative to signal correlated noise. Results were thresholded at $p < .01$ voxel level for display purposes. (Panel B) Cortical regions activated for arm-related literal sentences relative to noise in a finger movement region ROI analysis. The plots show effect sizes and standard deviations for arm- and leg-related sentences in a finger movement region. (Panel C) Cortical regions activated for leg-related literal sentences relative to noise in a foot movement region ROI analysis. The plots show effect sizes and standard deviations for arm- and leg-related sentences in a foot movement region. MNI coordinates are reported. Lit = literal; Idiom = idiomatic.

Table 4). Activation in these regions has been consistently reported in fMRI studies of spoken language processing (Davis & Johnsrude, 2003; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005), and importantly in studies investigating the processing of word meanings (Rodd et al., 2005), suggesting that this experiment successfully tapped into the language processing system. The direct contrast between literal and idiomatic sentences showed a single cluster which was more strongly activated for literal sentences, centred in the L hippocampus and extending to the L fusiform gyrus and cerebellum. Idiomatic sentences did not activate any cortical region over and above literal sentences (Table 4).

To investigate whether action words invariably activate motor/premotor cortex or whether their activation is modulated by the context in which they occur, we compared action words in literal sentences against noise, and action words in idiomatic sentences versus noise. Action literal sentences were associated with bilateral activation in MTG, STG and ITG, as well as L hippocampus, parahippocampus and fusiform gyrus. An ROI analysis using the *a priori* motor areas, as defined by the finger and foot movement task, showed activation in the L postcentral and R dorsomedial frontal gyrus (Table 4). Similar analyses carried out for action words in idiomatic contexts revealed whole brain activity in bilateral regions of MTG, superior temporal pole, and LIFG. Importantly, the ROI analysis in the *a priori* defined areas showed no activation in motor or premotor regions for idiomatic action sentences.

To examine in greater detail the neural patterns in motor and premotor regions we conducted a more exploratory analysis, in which we relaxed the threshold. Specifically, we looked at arm- and leg-related sentences separately at a lower significance threshold of $p < .005$ uncorrected at the voxel level, as in Tettamanti et al. (2005). As for the single word study, we used the motor areas identified by the body movement task as our ROI. Arm-related literal sentences compared with SCN showed significant activation in postcentral gyrus bilaterally. Similarly, leg-related sentences relative to SCN

Table 4
fMRI study of action sentences. For whole brain analysis, results results were thresholded at $p < .001$ and clusters significant at $p < .05$ corrected for multiple comparisons were considered significant. For ROI analysis, results were thresholded at $p < .005$ uncorrected.

Region	Extent	*Z* score	MNI coordinates		
			x	*y*	*z*
All sentences > noise					
L middle temporal gyrus	2434	6.37	−60	−12	−4
R middle temporal gyrus	708	5.77	62	−10	−4
Literal > idiomatic sentences					
L hippocampus	723	3.71	−32	−22	−14
ROI analysis					
Action literal sentences > noise					
L postcentral gyrus*	21	3.61	−60	−20	38
R dorsomedial frontal gyrus*	15	3.12	6	−22	62
Arm literal sentences > noise					
R postcentral gyrus	8	2.75	48	−22	58
L postcentral gyrus	3	2.73	−44	−14	56
Leg literal sentences > noise					
L paracentral lobule	18	2.96	−6	−26	68
R dorsomedial frontal gyrus	4	2.71	6	−22	64

* Denotes clusters also activated at threshold of $p < .001$ uncorrected. The highest peaks from each cluster are shown.

showed activation in L paracentral lobule and R dorsomedial frontal cortex. For idiomatic sentences, we found no differences in activity between arm-related or leg-related sentences and SCN in the *a priori* ROI defined by the respective body movements, even at the low threshold of .005 uncorrected. The plots of the effect sizes for each condition against the baseline show that finger and foot movement regions were sensitive to the context in which action words occurred (Table 4 and Fig. 3 panels B and C). We inspected the effect sizes of these peak activations to further explore the differences between literal and idiomatic contexts. Repeated measures ANOVAs were carried out on the beta values by comparing sentence conditions (arm literal vs. arm idiomatic vs. leg literal vs. leg idiomatic) and neural region (finger vs. foot movement regions). Critically, there was a significant interaction between sentence type and neural region ($F(12, 252) = 1.74$, $p = .05$). Interactions were significant for literal sentences on both left ($F(1, 21) = 10.26$, $p = .004$) and right hemisphere regions ($F(1, 21) = 5.05$, $p = .03$). In contrast, for idiomatic sentences there was no significant interaction between arm- and leg-related sentences, and neural region ($F(1, 21) = .41$, $p > .1$ in the left hemisphere; $F(1, 21) = .005$, $p > .1$ in the right hemisphere). This indicates that each region responded most to sentences relating to a specific body movement, and significantly more so in literal than idiomatic contexts.

Finally, we carried out a correlation analysis to examine the regions that showed modulation in activity as a function of the degree of action-relatedness. In this model, we entered the rated relatedness of the single words, literal and idiomatic sentences to body movements (as determined by the pre-tests) as a parametric modulator with linear expansion for each item. We found no significant effects in any neural regions hence we observed no direct link between the degree of relatedness of the words/sentences to body movements and neural activity.

4. Discussion

In this study we investigated the role of motor and premotor cortices in the processing of action words and sentences. We found that motor activation was modulated by the context in which action words were heard. Although we found somatotopic organisation for action words when they were presented as single words and, to a lesser extent, when embedded in literal sentences, these same words did not generate activity in premotor or motor regions when they were presented in idiomatic contexts.

Listening to action words when presented in isolation activated a fronto-parietal system known to be involved in action execution. Within this system, activation for arm- and leg-related words partially overlapped with the activation pattern of the respective body movement. Our findings are consistent with previous studies which showed motor circuit activation for passive viewing of action words (Hauk et al., 2004; Rüschemeyer et al., 2007). Similarly to the single word data, we found activation in somatosensory cortex for literal sentences that denoted arm and leg movements, when the threshold was reduced ($p < .005$). The peak activation for arm sentences was anterior to the motor activation for single arm words, while the peak for leg sentences was slightly posterior to that for leg words presented in isolation. Nonetheless, in both single word and literal sentence contexts, activity overlapped with those regions which were activated in the body movement task. In contrast, processing action words in idiomatic contexts did not recruit motor or premotor regions. No differences were detected in these areas for arm- and leg-related words in idiomatic sentences relative to noise, even at a very liberal threshold. Factors associated with the relatedness judgment task employed during the sentence experiment cannot account for the effects observed. First, this task was presented four seconds after the end of the sentences, with each scan set to coincide with the peak activation for the action word in the sentence. Thus, it is unlikely that activation associated with a task that occurred several seconds later contaminated the results. Moreover, as the motor task was equally required for all sentence conditions as well as baseline conditions, the contrasts presented here should not reveal task specific activations. Finally, the motor task only occurred for half of the sentences, and therefore preparatory activity (e.g. attentional demands, motor preparation) is unlikely as the subject did not know when they would be asked to respond. Our results thus suggest an essential difference in motor cortex modulation for action words in isolation, in literal and idiomatic contexts.

The activation that we observed for the literal sentences is consistent with that reported by other studies, which have proposed a somatotopically organised pattern in the motor and preomotor cortex for action-related sentences (Aziz-Zadeh et al., 2006; Tettamanti et al., 2005). According to this view, the meaning of action words is represented in a cortical network including areas typically associated with the execution of the actions described. However, the lack of activation in motor-related regions for the idiomatic sentences suggests that motor representations are only engaged under specific conditions and that their effects are variable and context-dependent. These findings provide some neural support for the cognitive theories of semantic flexibility, by showing that the nature of the semantic context determines the degree to which alternative senses and particularly relevant features are processed when a word is heard (Gentner, 1981; Kersten & Earles, 2004; Tyler, Moss, Galpin, & Voice, 2002).

One possibility is that motor regions are only recruited when processing demands emphasise the motor features of the verb, as suggested by previous neuroimaging studies which have failed to find activation in motor and premotor areas for action words when the task stressed visual rather than motor semantic information (Kable et al., 2002, 2005). In a study carried out in German, Rüschemeyer et al. (2007) found motor effects to be associated with simple action verbs (e.g. *greifen*, to grasp). In contrast, morphologically complex verbs built on motor stems (e.g. *begreifen*, to comprehend) showed no motor effects. These results also reinforce the view that motor systems are engaged only when the overall meaning of word is specifically related to body movements. In a study using pictograms of actions and objects, Assums, Giessing, Weiss, & Fink (2007) reported significant activation in premotor regions for actions relative to object pictograms. Interestingly, a subsequent analysis of psychophysiological interactions was carried out to identify co-dependent changes in neural activity during retrieval of action knowledge. This analysis revealed that semantic processing in the fusiform gyrus coupled with activity in temporal-parietal regions but not with premotor activity. In the present study, the literal and idiomatic sentences contained the same action words and were designed to have similar acoustic, phonological and syntactic properties. By manipulating the contextual information we directed participants' attention toward or away from the actions. It is plausible that in the idiomatic action sentences, the motor features of the actions were not emphasised enough to activate (pre)motor regions of the brain. In contrast, in our study with single words, participants were focussed on the individual words and thus may have attended more directly to the actions and their motor properties, which may have resulted in engagement of motor and premotor cortices. Similarly, in literal sentences, where the sentence meaning was consistent with the motor properties of the verbs, participants' attention may have been more focussed on this aspect of the word's meaning. Results from our pre-tests lend support to this interpretation. In these pre-tests participants were asked how related in meaning each word/sentence was to body movements on a 7-point scale. Participants rated action verbs presented in isolation as significantly more related to motor properties than literal sentences, and these more than idiomatic sentences ($p < .001$ in all cases). Even though the correlation analysis between action-relatedness and brain activity showed no significant effects, possibly because the relatedness ratings clustered around two values of the scale rather than in a continuum, the results from the direct contrasts mirrored the behavioural data. We found more reliable activation in motor regions for single words than for literal sentences, and no above threshold activation for idiomatic contexts. These findings suggest that the degree to which context emphasises motor properties contributes to the neural patterns observed in motor and premotor regions during action word processing.

An important factor to take into account when investigating the overlapping activations for body movements and action word/sentence processing is that of motor imagery. Voluntary motor imagery has been shown to involve the primary motor and premotor areas (Ehrsson, Geyer, & Naito, 2003; Gerardin et al., 2000). Importantly, perspective taking has been shown to be an essential component in mental imagery of actions, with earlier studies finding that first-person perspective in motor imagery recruits LIPL and somatosensory-motor regions relative to third person perspective (Ruby & Decety, 2001). In the present study, and in contrast with previous ones, we used sentences that always referred to a third-person (e.g. *The fruit cake was the last one so Claire grabbed it*), thus reducing the likelihood of imagery effects.

It is worth noting that in this study processing action words in both sentential contexts (relative to noise), generated robust activity in left middle and superior temporal gyri. These regions have been identified as being central to the processing of spoken language (Rodd et al., 2005; Tyler et al., 2005). Furthermore, LMTG activation has been consistently associated with the processing of verbs (Kable et al., 2005; Longe, Randall, Stamatakis, & Tyler, 2007; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Tranel, Adolphs, Damasio, & Damasio, 2003; Tyler & Marslen-Wilson, 2008; Tyler, Randall, & Stamatakis, 2008; Tyler et al., 2005). It has been proposed that LMTG reflects linguistic aspects of language comprehension, namely lexical aspects of verb processing. Verbs are central in sentential interpretation as they carry tense, specify the relations between elements of a phrase and engage processes of linguistic integration. It is therefore likely that verbs strongly engage the language system. Consistent with this view, recent fMRI studies have shown that inflected verbs (e.g. *hears*) generate greater LMTG activation than inflected nouns (e.g. *snails*) (Longe et al., 2007; Tyler et al., 2005), and verbs generate greater LMTG activation than nouns, but only when they occur in a phrasal contexts such as in *to lock* vs. *the lock* (Tyler et al., 2008). Thus, it is plausible that LMTG activation observed in the present study is related to lexical aspects of verb processing.

Our results also speak to the neural bases of literal and idiomatic meanings during spoken language comprehension. We found that both types of meaning activate similar regions along the bilateral MTG and STG, which is in line with studies that have shown that idioms and literal sentences recruit overlapping regions of the L temporal cortex (e.g. Lauro, Tettamanti, Cappa, and Papagno (2008); Oliveri et al., 2004). Some recent studies have argued that understanding idioms does not necessarily require additional neural activation, namely in the RH, especially when idioms are highly familiar and opaque, as was the case in our task (Oliveri et al., 2004). These findings do not exclude that other brain regions may be activated during the processing of transparent, ambiguous idioms. The only exception in the current study was in the L fusiform gyrus and hippocampus, where greater activation was found for literal relative to idiomatic sentences. Previous cognitive studies have argued that familiar idiomatic phrases often become lexicalised and are therefore treated as a single lexical unit, requiring less semantic and syntactic processing than literal phrases (Giora, 2002). Our results support this hypothesis, suggesting that the literal meanings may require more extensive activation and possibly greater processing demands than idioms. The lack of idiom-specific activations could indicate that these were processed in a shallow manner. However, our behavioural data argues against this prediction, as the overall responses were similar, both in accuracy and reaction times, between literal and idiomatic conditions. The only exception was for the arm-related condition where responses to idioms were slower, the opposite pattern of what would have been expected if the processing of idioms would have been shallow.

In summary, in this study the same subjects performed motor movements and listened to action words occurring in different contexts. We found that, while spoken sentences activated the typical left fronto-temporal language system, this activation only included motor regions when an action verb occurred in a sentence consistent with its literal meaning. This may be due to the influence of semantic context in determining which aspects of a word's meaning are activated during sentence processing. This idea is consistent with models of spoken word recognition that claim that context effects emerge early during selection of word candidates and affect the lexical and semantic information that is accessed and integrated into an utterance as it is heard (Gaskell & Marslen-Wilson, 2001; Marslen-Wilson, 1987; Marslen-Wilson & Tyler, 1980; Zwitserlood, 1989). An interesting goal for future research includes finer-grained analyses of the time course of neural activation associated with literal and idiomatic sentence comprehension, using MEG or EEG. An open question is whether idioms activate motor cortex, along with other regions, at an early stage of the sentence processing, and that such activation is quickly suppressed as other features become relevant to the current context.

Our results challenge the view that "the same cell assembly is activated when any part of the network is activated" (Pulvermüller, 1999; Pulvermüller et al., 2005). Action words appear to activate motor regions only when they occur in isolation or in sentences that emphasise body movements. When attention is not focussed on motor properties, we do not observe any activity in motor regions associated with action word processing. Our findings suggest that access and integration of meaning is a flexible process, which depends on the sentential context and, more generally, on the information that one needs to extract from the representations as a function of the cognitive task at hand.

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