She runs, the road runs, my mind runs, bad blood runs between us: Literal and figurative motion verbs: An fMRI study

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ABSTRACT

The role of sensory–motor components in language processing is a central topic in cognitive neuroscience. Recent studies showed that the processing of action words recruits cortical motor regions involved in the planning and execution of the described actions. However, it remains unclear to what extent the abstract versus concrete nature of the described motion modulates the activation of premotor and motor areas and how the agent affects this modulation.

Here, we contribute to this line of research by investigating the comprehension of motion verbs, used in a literal versus figurative context, in an fMRI study with normal subjects in which the somatotopy of activation was investigated by presenting motion verbs that involve upper vs. lower limbs. A set of sentences including a motion verb used in a literal, fictive (only lower limb), metaphorical, or idiomatic way was studied. Cognition verbs were also included as control. We found that figurative sentences compared to literal ones produced a greater activation of a bilateral fronto-temporal network, in line with previous studies. Moreover, fictive motion activated a more posterior region, involving primary visual areas and motion sensitive visual areas, but also the left middle frontal gyrus. Crucially, the left precentral gyrus was activated in the case of the upper limb for literal and metaphorical motion sentence types, but not idiomatic sentences. For fictive motion, we found a lower limb-related somatotopic effect, also present for literal sentences, while the evidence for metaphorical and idiomatic sentences was less strong. In conclusion, our results confirm that premotor areas are activated by language understanding, but to a different degree depending on the specific literal versus figurative context in which motion verbs appear. Therefore, they support weak embodied views suggesting that the motor system enhances the comprehension of linguistically encoded actions.

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Introduction

When someone says *The road suddenly turned left*, it is evident that she/he does not refer to a physical entity moving (this represents a *fictive motion*, see Talmy, 2000). A real movement is instead implied in literal sentences such as *The man suddenly turned left*. But what does it happen when the verb *turn* is used in a metaphorical context such as *The lady turned her thought away from sorrow*? The aim of the present study is to investigate the involvement of the action representation neural system in a figurative versus literal motion sentence context, clearly distinguishing between different types of figurative (idiomatic, metaphorical, and fictive motion) expressions, and by employing a multilevel set of control conditions, such as literal motion and sentences with a mental verb.

In recent years, the relationship between language and action, and specifically the hypothesis that the neural circuitries associated with action representation are recruited when processing action-related words and sentences, has been a topic of debate, opposing traditional *amodal*/*disembodied* models of conceptual knowledge to *embodied* models of cognition. The first type of model suggests that conceptual knowledge is fundamentally amodal and abstract and is represented separately from modality-specific systems recruited for perception and action (e.g., Fodor, 1975; Jackendoff, 2002). In contrast, *embodied* models of cognition posit that sensory–motor processes are part of the mental representation of concrete and possibly also abstract concepts (e.g., Barsalou, 1999; Borghi et al., 2004; Glenberg and Kaschak, 2002; Pecher et al., 2003, 2004; Vigliocco et al., 2004), with disagreements between advocates of strong versus weak embodied views, as to whether sensory–motor processes form, respectively, a constitutive- or context-dependent flexible component of conceptual representations (Meteyard et al., 2012). Evidence in favour of the weak embodied view suggests that while the motor system does appear to enhance or deepen the understanding of linguistically encoded actions, it may not be necessary for basic comprehension (Tettamanti and Moro, 2012;

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van Dam et al., 2012). In embodied models, language understanding is seen as a result of the Hebbian correlation learning between perisylvian language areas and motor regions (Pulvermüller, 2005; Kiefer and Pulvermüller, 2012; Ghio and Tettamanti, 2010), or as a form of mental simulation of actions that involves the mirror neuron system (Glenberg and Kaschak, 2002; Rizzolatti and Arbib, 1998) with direct or indirect link between language and sensory–motor systems (Fischer and Zwaan, 2008; Kemmerer and Gonzalez-Castillo, 2010; Vigliocco et al., 2004).

Consistent evidence has shown that the motor schemata associated with action words are embedded in the corresponding cortical representations (for reviews, see Kemmerer and Gonzalez-Castillo, 2010; Pulvermüller, 2005; Willems and Hagoort, 2007). The neural architecture of language-induced *motor resonance* would therefore comprise regions encoding information that is not purely linguistic or conceptual but reflects the sensory–motor properties associated with the underlying concept. In other words the motor and premotor regions would be somatotopically engaged in the production as well as in the comprehension of action-related words and sentences (Hauk et al., 2004; Pulvermüller, 1999, 2005; Tettamanti et al., 2005).

Despite the growing amount of evidence on the involvement of sensory–motor systems in language processing, important questions remain unsolved (for overviews see Mahon and Caramazza, 2005, 2008; Negri et al., 2007). For instance, it is not yet clear whether and to what extent embodied models can account for abstract concepts that are not grounded in action or perception. Also, the time course of the intervention of sensory-motor information is not yet established despite claims of automaticity and early activation (e.g., Pulvermüller et al., 2009; Boulenger et al., 2012) that did not receive univocal empirical support (e.g., Papeo et al., 2009; Kable et al., 2002, 2005). Recently, it has been underlined that early motor regions are not involved in understanding action-verbs nor is the primary motor area activated by linguistic descriptions of actions (Bedny and Caramazza, 2011). Bedny et al. (2008) argued that the posterior lateral temporal cortex recruited when participants read or listen action verbs does not overlap with visual–motion regions, and is activated for any type of verb, thus suggesting that its involvement is only due to the retrieval of grammatical information associated with verbs. In addition, it is still questionable whether the motor system is activated by any occurrence of a motion verb in a sentence or whether such activation is modulated by the linguistic context in which the motion verbs occur.

Different methods have been applied to investigate the relationship between language and the motor system: neuropsychological studies on patients with Parkinson's disease (PD) (Boulenger et al., 2008; Cotelli et al., 2007; Rodrìguez-Ferreiro et al., 2009; Fernandino et al., in press), amyotrophic lateral sclerosis (Grossman et al., 2008), neurodegenerative disorders (Silveri and Ciccarelli, 2007), and vascular lesions (Arévalo et al., 2012; Kemmerer et al., 2012); fMRI studies with Alzheimer's disease (AD) patients (Grossman et al., 2003); single-pulse TMS and fMRI studies with neurologically-unimpaired subjects. Yet, the results do not provide a consistent picture. This is partially due to the different tasks used (e.g., morphological tasks, semantic judgements, mental simulation) and to the comparison of different grammatical classes (concrete nouns and action verbs), which introduces an additional variable. More recently, Fernandino et al. (in press) in a study on PD patients found that these patients were selectively impaired for action verbs as compared with abstract ones both in a lexical decision task, which does not require an explicit semantic processing, and in semantic similarity judgements. In some TMS studies (e.g., Buccino et al., 2005; Oliveri et al., 2004) action-related verbs modulated activation in the primary motor cortex depending on the effector involved in the action (foot–leg or hand). In other studies (e.g., Glenberg et al., 2008), no differences were found between concrete transfer verbs (e.g., *to give cards to someone*) and abstract transfer verbs (e.g., *to delegate responsibilities to someone*), since both modulated the MEP amplitude when compared with non-transfer verbs. A specific effect of the motion verb

emerged but only when participants were asked to perform a mental simulation (Tomasino et al., 2007; 2008) or at a later stage (500 ms) than previously reported (Papeo et al., 2009).

When considering these experiments on the involvement of the sensory–motor cortices in processing action language, the most salient result is that such an involvement appears to be task- and context-dependent (Tettamanti and Moro, 2012; van Dam et al., 2012; Willems and Francken, 2012). As Willems and Francken underline, beyond the involvement of the sensory–motor cortices in understanding action-related and perception-related language, it is essential to study when and how this occurs. Therefore, we aimed at thoroughly investigating the role of the linguistic context, by comparing figurative versus literal sentences.

In a recent study, Cacciari et al. (2011) used single-pulse TMS to assess whether reading literal, non-literal (metaphorical and idiomatic) and fictive motion sentences modulated the activity of the motor system. Since MEPs were larger when participants were presented with literal, fictive and metaphorical motion sentences than with idiomatic motion or mental verb sentences, they suggested that the motor component of the verb is preserved in fictive and metaphorical motion sentences. While metaphorical use of a verb preserves the basic semantic component of the verb's meaning (Torreano et al., 2005), it is less clear why fictive motion should. In fact, previous studies with fictive motion (Saygin et al., 2010; Wallentin et al., 2005, 2011) found activation of motion-sensitive visual areas and not of primary motor areas. This result was interpreted as evidence that in fictive motion sentences the hearer/reader applies motion to the depicted scenario by scanning it egocentrically. fMRI findings also offer a complex picture (e.g., Aziz-Zadeh et al., 2006; Boulenger et al., 2009; Chen et al., 2008; Raposo et al., 2009; Tettamanti et al., 2005). In general, whereas it is commonly accepted that action related sentences elicit activation in the premotor and motor cortex with a somatotopically-congruent distribution, evidence for the recruitment of the same regions in metaphorical and idiomatic sentences is more controversial. In Aziz-Zadeh et al. (2006)'s study, a clear congruence was found between effector-specific activations of visually presented actions and actions described by literal phrases, but no effects were found for metaphorical sentences (although the examples provided by the authors are idioms and idioms do not appear to activate the motor component as reported above).

Concerning idioms, Boulenger et al. (2009) found that idiomatic and literal sentences elicited activation along the motor strip in the central and precentral cortices that somatotopically corresponded to the body part reference of the words. More recently, Boulenger et al. (2012) investigated the time-course of cortical activation during the comprehension of literal and idiomatic sentences using MEG and showed that, compared to literal sentences, processing of idioms in a silent reading task modulates anterior fronto-temporal activity very early, already 150–250 ms after the critical disambiguating words. Similarly, in the same time windows significant ROIs × body part interactions appeared. The authors suggest that parallel compositional and abstract context-driven semantic processes contribute to the understanding of the idiom's meaning, since the meaning of action words embedded in sentences is reflected by somatotopic activation of the precentral motor system. However, only sentences including arm verbs were seen to reliably recruit the arm motor region, whereas the effect in the leg ROI fell short of reaching significance. Crucially, no control sentences, namely mental sentences, were included; therefore it cannot be excluded that participants were "expecting" action verbs for all items and did not "switch-off" from an action verb mode of processing. Also, the rate of presentation was very slow, so that possibly subjects performed a word level processing and not a real sentence-level processing.

To sum up, positive but also negative evidence exists for an involvement of motor regions in processing motion verbs without any actual motor behaviour. The different results are due at least in part to the type of task and methodology used, and to a non-uniform selection of

stimulus material, especially in the case of figurative verbs. A clear definition of what an idiom is, for example, has seldom been provided in the reviewed studies, and the same can be said about making explicit the differences between idioms and other types of figurative expressions (e.g., metaphors and proverbs). In particular, there has been an underestimation of the role played by the linguistic characteristics of the stimuli employed in experimental and clinical studies. Yet, idioms and metaphors differ from both a semantic and a syntactic point of view, and both factors need to be accounted for (see Papagno and Caporali, 2007 for a discussion). Moreover, in studies on PD patients, action naming has been opposed to object naming, thus introducing, as already mentioned, an additional uncontrolled grammatical variable. Péran et al. (2009) in an fMRI study challenged this possibility and supported a motor hypothesis based on a significantly different activation in the premotor and prefrontal cortices with action generation and object naming. However, the two tasks are qualitatively different and Péran et al.'s results may simply suggest that there is more activation in active generation tasks than in passive picture naming.

In the present study we investigated whether the activation of the motor system was sensitive or not to the literal vs. figurative nature of the motion verbs used in sentences, and whether the types of non-literal (i.e., fictive, metaphorical, idiomatic) motion sentence modulate the activity of the motor system. At variance with previous fMRI studies, we compared all the different linguistic contexts together, as in a recent TMS experiment (Cacciari et al., 2011). In addition, at odds with most studies that only required silent reading or answering to occasional questions, we included a delayed semantic judgement task, in order to make sure that participants semantically processed the experimental sentences.

Material and methods

Participants

Twenty-four healthy volunteers with no history of mental or psychiatric disorders took part in the fMRI experiment. All participants were Italian native speakers and right-handed (Oldfield, 1971). They all gave written consent prior to their participation and the study was approved by the San Raffaele Hospital Ethics Committee.

Stimuli

Twenty-one motion verbs describing actions involving the upper limb (e.g. to cut) and twenty-one motion verbs describing actions involving the lower limb (e.g. to stumble) were selected. Stimuli for the lower limb were taken from a previous study (Cacciari et al., 2011); however, since additional stimuli for the upper limb were included, they were all checked again. A rating study was performed on a sample of 30 experimental subjects who did not participate to the fMRI study: they were asked to evaluate on a 5-point scale (1 = "not at all", 5 = "highly associated") how much each upper limb-related verb was specifically associated with a hand movement and each lower limb-related verb was specifically associated with a foot movement. The results showed that both upper and lower limb-related verbs were judged to be strongly associated with the appropriate body parts (mean rating 3.7 for upper limb- and 3.2 for lower limb-related verbs), with a relatively stronger association for upper as compared to lower limb-related verbs [t(29) = −4.8, p < .001].

(1) Each upper and lower limb motion verb was used to generate three different sentence types: idiomatic (Idi), metaphorical (Met), and literal sentences (Lit), yielding 21 sentences per type. For example, for the upper limb verb "*gettare*" ("to throw"), the idiomatic sentence was "*L'investigatore getta la spugna subito*" (*The detective throws away the sponge immediately*), the metaphorical "*Matilde getta la tristezza lontano*" (*Matilde throws her sadness far away*), and the literal "*Marco getta la legna nel camino*" (*Marco throws wood in the fireplace*). Since almost all idioms were ambiguous (with a plausible literal interpretation), we run an additional pilot study to verify whether the figurative meaning was indeed the dominant one. A different group of twenty participants was presented with the list of idiomatic sentences intermingled with literal sentences and asked to write down the first meaning they thought about for each sentence. In 93% of their answers, the participants produced the idiomatic meaning first.

(2) Lower limb motion verbs were also used to generate 21 fictive motion sentences (FicL). An example of it for the verb "*entrare*" (*to move forward*) was "*Il sentiero entra nella valle fiorita*" (*The path moves forward into the valley*). According to Talmy (1996, 2000), in fictive motion some intangible entity continues along its emanation path and terminates by impinging on some distal object; therefore, in a strict sense, fictive motion sentences require lower limb actions, and consequently, upper-limb fictive motion sentences were not included. As a replacement, in order to obtain a balanced design, we included 21 filler sentences with upper limb figurative motion verbs, which were not analysed in the contrasts of interest. Moreover, 42 sentences with mental verbs (e.g. to think) were included as a control condition. An example of sentence with a mental verb was "*Il capo promette un aumento all'impiegato*" (*The manager promises an increase of salary to the employee*).

Twenty participants (different from those involved in the fMRI experiment) were asked to rate how concrete was the meaning of each sentence including a motion verb (Idi, Met, FicL, and Lit), ranging from 0 (no concrete action at all) to 10 (totally concrete action). In order to explore whether there was any difference in concreteness ratings among these four types of sentence we run a repeated measures ANOVA with limb (2 levels: Upper vs. Lower limb) and sentence type (4 levels: Idi, Met, FicL/Filler and Lit) as main within factors. Mean concrete ratings are reported in Table 4. The main factor limb [F(11, 19) = 7.51, p < .05] as well as the interaction limb × sentence type [F(3, 57) = 5.61, p < .005] was significant, showing higher mean concreteness ratings for upper than lower limb in all sentence types, except for Idi. Also the main effect of sentence type was significant [F(3, 72) = 78.4, p < .001]. Briefly, whereas literal sentences were judged as conveying a more concrete action, this was much less so for the metaphorical and idiomatic ones, whereas fictive motion lied in-between.

(3) Each target sentence was associated with a second sentence, either semantically congruent or semantically incongruent. For instance, the sentence "*Il bimbo inciampa nelle stringhe slacciate*" (*The boy stumbles in the untied laces*) was associated with the semantically congruent sentence "*Infatti cade per terra all'improvviso*" (*Indeed he suddenly falls down*); whereas the sentence "*Il maestro attacca l'avviso alla bacheca*" (*The teacher puts the advertisement on the board*) was associated with the semantically incongruent sentence "*perché deve nasconderlo*" (*Because he needs to hide it*). The associated sentences (henceforth, "task sentences") requiring a semantic judgement were included in order to monitor that the participants were processing the semantic content of the experimental sentences during the fMRI scan. Fifty volunteers, who did not take part in the fMRI experiment, rated the congruency between the target and the task sentences. More specifically, they were asked to judge, for each pair of target-task sentences, on a scale from 0 = "not at all" to 4 = "highly congruent", whether the second sentence of the pair was semantically congruent with the first. Task sentences with a rating score higher than 2 (congruent pairs) or lower than 1.5 (incongruent pairs) were selected for the fMRI experiment.

Table 1

Limb-related sentence specific effects (p < 0.05, FWE corrected; uncorrected p values marked by an asterisk). Percent values and labels next to anatomical locations refer to cytoarchitectonic probabilities as reported in the SPM Anatomy toolbox.

Anatomical location	Cluster	Voxel level		MNI coordinates		
	k	p value	Z score	x	y	z
[(IdiU + MetU + LitU) − CtrU] excl. mask by [(IdiL + MetL + FicL + LitL) − CtrL]						
R/L med. sup. front. gyrus	73	0.0415	4.6	−4	28	44
R/L mid. cing. cortex	73	2.6 e−04	5.7	6	16	44
L inf. front. gyrus (20% BA45)	63	1.7 e−05	6.2	−44	34	8
L inf. front. gyrus (40% BA44)	132	3.3 e−08	7.1	−52	12	16
L precentral gyrus	132	5.4 e−04	5.6	−38	8	32
L insula	5	0.0184	4.8	−28	24	4
R insula	28	1.4 e−04	5.8	30	26	4
L mid. temp. gyrus	66	2.5 e−04	5.7	−62	−58	4
[(IdiU + MetU + LitU) − CtrU] excl. mask by [(IdiL + MetL + FicL + LitL) − CtrL]						
Small volume correction at hand-related sentence effect in Tettamanti et al. (2005)						
L precentral gyrus (30% BA6)	66	0.002	3.8	−28	−4	60
L mid. front. gyrus	66	0.016	3.2	−26	2	56
[(IdiL + MetL + FicL + LitL) − CtrL] excl. mask by [(IdiU + MetU + LitU) − CtrU]						
		n.s.				
[(IdiL + MetL + FicL + LitL) − CtrL] excl. mask by [(IdiU + MetU + LitU) − CtrU]						
Small volume correction at leg-related sentence effect in Tettamanti et al. (2005)						
L mid. front. gyrus (20% BA6)	1	0.0380*	1.8	−28	6	64
[IdiU − CtrU] excl. mask by [IdiL − CtrL]						
L inf. front. gyrus (20% BA45)	4	0.0033	5.2	−44	34	8
L inf. front. gyrus (60% BA44)	4	0.0135	4.9	−58	12	16
L mid. temp. gyrus	8	0.0023	5.3	−60	−58	4
[IdiU − CtrU] excl. mask by [IdiL − CtrL]						
Small volume correction at hand-related sentence effect in Tettamanti et al. (2005)						
L precentral gyrus (30% BA6)	40	0.0531	2.7	−28	−4	60
[IdiL − CtrL] excl. mask by [IdiU − CtrU]						
L inf. front. gyrus (80% BA45)	42	9.9 e−05	5.9	−54	26	20
L inf. front. gyrus (50% BA44)	8	0.0072	5.0	−54	14	24
L precentral gyrus	3	0.0129	4.9	−42	2	44
L mid. temp. gyrus	1	0.0464	4.6	−56	−32	0
[IdiL − CtrL] excl. mask by [IdiU − CtrU]						
Small volume correction at leg-related sentence effect in Tettamanti et al. (2005)						
L mid. front. Gyrus (20% BA6)	1	0.0263*	1.9	−28	6	64
[MetU − CtrU] excl. mask by [MetL − CtrL]						
L inf. front. gyrus (80% BA45)	695	3.7 e−07	6.8	50	20	16
L inf. front. gyrus (40% BA44)		2.8 e−10	7.7	−52	12	16
R/L suppl. mot. area (30% BA6)	236	1.7 e−09	7.5	4	16	48
R insula	88	1.4 e−08	7.2	30	26	4
L mid. temp. gyrus	79	6.3 e−04	5.5	−48	−50	8
[MetU − CtrU] excl. mask by [MetL − CtrL]						
Small volume correction at hand-related sentence effect in Tettamanti et al. (2005)						
L precentral gyrus (30% BA6)	70	2.2 e−04	4.4	−30	−4	60
[MetL − CtrL] excl. mask by [MetU − CtrU]						
L mid. temp. gyrus	7	0.0025	5.3	−54	−30	0
[MetL − CtrL] excl. mask by [MetU − CtrU]						
Small volume correction at leg-related sentence effect in Tettamanti et al. (2005)						
		n.s.				
[FicL − (Idi + Met)][a]						
Small volume correction at leg-related sentence effect in Tettamanti et al. (2005)						
L sup. front. gyrus (30% BA6)	46	0.0410	3.0	−22	4	60
[LitU − CtrU] excl. mask by [LitL − CtrL]						
L inf. front. Gyrus (20% BA45)	11	0.0031	5.2	−42	36	8
L inf. front. gyrus (40% BA44)	3	0.0260	4.7	−52	12	16
L mid. temp. gyrus	1	0.0348	4.7	−52	−60	0
L supramarg. gyrus (60% IPC)	2	0.0315	4.7	−56	−26	32
[LitU − CtrU] excl. mask by [LitL − CtrL]						
Small volume correction at hand-related sentence effect in Tettamanti et al. (2005)						
L precentral gyrus (30% BA6)	36	0.0312	2.9	−28	−4	60
[LitL − (Idi + Met)][a]						
Small volume correction at leg-related sentence effect in Tettamanti et al. (2005)						
L sup. front. gyrus (40% BA6)	19	0.050	3.0	−22	2	64

[a] For FicL, given the lack of a corresponding upper-limb condition, we used a different hypothesis-driven approach than for the IdiL and MetL conditions. We tested whether the processing of lower limb fictive motion sentences involved leg-related somatotopic activations significantly more than IdiL and MetL; the body-part specificity in this contrast was ensured by also including the upper-limb conditions IdiU and MetU in the contrast's subtraction term: [FicL − (Idi + Met)]. With a similar hypothesis, we also computed the corresponding contrast for LitL: [LitL − (Idi + Met)].

Table 2A
Activations for figurative (Idi + Met + FicL) minus literal (Lit + Ctr) sentences (p < 0.05, FWE corrected). Percent values and labels next to anatomical locations refer to cytoarchitectonic probabilities as reported in the SPM Anatomy Toolbox.

Anatomical location	Cluster	Voxel level		MNI coordinates		
	k	p value	Z score	x	y	z
R/L medial sup. front. gyrus	70	8.0 e−04	5.7	−4	26	44
R/L suppl. mot. area (50% BA6)	70	8.0 e−04	5.7	−2	18	48
L inf. front. gyrus (60% BA44)	1165	1.0 e−12	8.0	−46	14	24
L inf. front. gyrus (70% BA45)		1.2 e−11	8.0	−50	24	20
L insula		0.0063	5.3	−32	20	0
R inf. front. gyrus (80% BA45)	132	2.0 e−06	6.6	56	28	20
L mid. temp. gyrus	297	9.7 e−09	7.4	−60	−54	4
L inf. temp. gyrus	8	0.0160	5.1	−48	−36	−20
L temp. pole	39	1.9 e−07	7.0	−50	14	−20
R temp. pole	15	4.1 e−06	6.5	52	16	−16
L inf. occ. gyrus (50% hOC4v)	12	0.0054	5.3	−38	−86	−8
L calcarine gyrus (70% BA17)	13	7.7 e−04	5.7	−10	−90	0
L mid. occ. gyrus	75	1.8 e−04	5.9	−26	−62	32
L sup. par. lobule		0.0012	5.6	−28	−64	44
L inf. par. lobule (50% hIP3)		4.5 e−04	5.8	−28	−56	48
L cerebellum (57% lobule VIIa)	17	6.4 e−04	5.7	−6	−80	−28
R cerebellum (79% lobule VI)	23	9.9 e−05	6.0	12	−76	−24

Table 2B
Activations for literal (Lit + Ctr) minus figurative (Idi + Met + FicL) sentences (p < 0.05, FWE corrected).

Anatomical location	Cluster	Voxel level		MNI coordinates		
	k	p value	Z score	x	y	z
R/L medial superior frontal gyrus	67	0.001	5.6	−6	56	0
R/L ant. cingulate cortex		0.002	5.5	−4	42	−4
R mid. frontal gyrus	15	0.003	5.4	40	42	8

(4) All sentences were balanced with respect to number of syllables and frequency of content words (COLFIS, Bertinetto et al., 2005) across the five conditions for both upper and lower limbs. The total stimuli were 210 sentences and were presented in a semi-randomized order in four separate fMRI runs (two fMRI runs for the upper limb and two for the lower limb condition). At the end of the experiment all the participants filled a questionnaire in which the familiarity of each Idi, Met and FicL sentence was rated on a 4-point scale ranging from 0 (not at all) to 3 (highly familiar), with a score of 1 corresponding to "heard, but I am not sure about the exact meaning" and 2 "familiar, I know its meaning". The results showed that on average the participants found all types of sentence familiar, since for all of them the mean score was above 2 (Idi: 2.3, Met: 2.1, FicL: 2.2). To verify whether there was any difference in familiarity among these three types of sentence a repeated measures ANOVA was run on subjects' mean familiarity rating with limb (2 levels: Upper vs. Lower limb) and sentence type (3 levels: Idi, Met and Filler/FicL) as main within factors.

The main effect of limb was significant [F(1, 20) = 11.9, p < 0.005] with a higher familiarity for sentence involving lower limb actions. The

Table 2C
Figurative minus literal: areas of common activation in the present and in the 2008 study by Romero Lauro et al. (2008) (p < 0.05, FWE corrected).

Anatomical location	Cluster	Voxel level		MNI coordinates		
	k	p value	Z score	x	y	z
L medial superior frontal gyrus	4	0.0113	5.2	−8	50	36
L inferior frontal gyrus	208	1.0 e−12	8.0	−48	26	0
L temporal pole		1.0 e−12	8.0	−50	14	−20
R temporal pole	8	0.0039	5.4	52	12	−24
L mid. temporal gyrus	40	2.1 e−07	6.9	−54	0	−20
R mid. temporal gyrus	4	0.0079	5.3	56	−8	−16

main effect of sentence was also significant [F(2, 40) = 4.3, p < 0.05] as well as the interaction limb × sentence type [F(2, 40) = 7.1, p < 0.005]. Post hoc analyses showed that familiarity was significantly lower for upper-limb Met (MetU) in comparison to upper-limb Idi (IdiU) (p < 0.001).

In order to account for the possible effects due to differences in familiarity ratings among the experimental conditions, we performed a set of control fMRI data analyses (see below).

Task

The experiment was designed as an event-related paradigm, with separate events for the presentation of the experimental target

Table 3A
Brain regions differentially activated by the three figurative sentence types (Idi vs Met vs FicL) (p < 0.05, FWE corrected).

Anatomical location	Cluster	Voxel level		MNI coordinates		
	k	p value	Z score	x	y	z
R/L med. sup. front. gyrus	71	1.4 e−08	7.3	−8	52	36
L mid. front. gyrus	6	0.0089	5.2	−22	6	52
L inf. front. Gyrus (40% BA45)	179	1.1 e−04	6.0	−50	26	8
R inf. front. Gyrus (70% BA45)	6	0.0039	5.4	50	22	20
L temp. pole	109	2.2 e−07	6.9	−54	10	−20
L mid. temp. gyrus	75	9.3 e−06	6.4	−60	−8	−8
L mid. temp. gyrus	92	2.5 e−09	7.5	−54	−60	−4
L mid. temp. gyrus	90	6.4 e−04	5.7	−52	−38	0
R temp. pole	11	8.1 e−04	5.7	52	12	−24
R/L post. cing. cortex	25	2.5 e−04	5.9	−4	−50	28
L precuneus	227	1.0 e−12	8.0	−12	−56	16
R precuneus	229	1.0 e−12	8.0	12	−54	12
R sup. par. lobule (50% 7A)	6	0.0139	5.1	−16	−68	52
L fusiform gyrus	193	1.0 e−12	8.0	−30	−40	−16
R fusiform gyrus	123	1.0 e−12	8.0	28	−32	−20
L mid. occ. gyrus (40% PGp)	269	1.0 e−12	8.0	−36	−78	32
R mid. occ. gyrus (80% PGp)	105	1.3 e−10	8.0	44	−74	32
R calcarine gyrus (100% BA17)	46	5.5 e−05	6.1	12	−82	4

Table 3B
Activations for (Idi + Met) minus FicL sentences (p < 0.05, FWE corrected).

Anatomical location	Cluster	Voxel level		MNI coordinates		
	k	p value	Z score	x	y	z
R/L med. sup. front. gyrus	88	6.4 e−09	7.4	−8	54	36
L inf. front. gyrus (50% BA45)	39	2.6 e−04	5.8	−48	24	8
L temp. pole	273	2.2 e−08	7.2	−50	8	−28
L mid. temp. gyrus		3.9 e−06	6.5	−60	−8	−8
L mid. temp. gyrus	92	1.6 e−04	5.9	−56	−38	0
R temp. pole	22	5.3 e−05	6.1	52	12	−24
R sup. temp. gyrus	8	6.0 e−04	5.7	58	−4	−12
R/L post. cing. cortex	8	0.0033	5.4	−4	−50	28

Table 4
Mean concreteness ratings for the different sentence types.

Sentence types	Limb	Mean concreteness ratings	SD
Idi	U	4.63	1.3
Met	U	4.88	1.6
Fic	U	6.03	1.4
Lit	U	8.72	0.9
Idi	L	4.89	1.3
Met	L	4.36	1.3
Fic	L	5.85	1.2
Lit	L	8.29	0.9

sentence and for the presentation of the associated task sentence. Target sentences were presented in white Courier font on a black background, size 24 for 2500 ms, and were followed by the task sentences that appeared in yellow font for 5000 ms. The two sentences were interleaved with a black screen of random duration between 2000 and 5000 ms. This interval allowed separating the activations of target sentence processing from the confounding activations elicited by task sentence processing and associated button press responses. Trials were divided by a variable inter-stimulus interval (ISI) between 5000 and 12,000 ms. The participants were instructed to read both sentences of each trial and to judge whether the second (i.e. task) sentence was semantically congruent or incongruent with the first (i.e. target). A fibre-optic response box was placed in the MRI scanner near the participants' right hand. The participants responded by pressing either the left (congruent) or right (incongruent) button with the index or middle finger, respectively. Stimulus presentation and response collection were controlled by E-prime software. The stimuli were back-projected on a screen located in front of the scanner visible to the participants through a mirror placed on the head coil above their eyes. Accuracy and reaction times (RTs) were measured.

fMRI acquisition

Scanning was performed with a 3 T Intera Philips body scanner (Philips Medical Systems, Best, NL) using an 8-channel SENSE head coil (sense reduction factor = 2). Whole-brain functional images were obtained with a gradient-echo echo-planar T2* sequence, using blood oxygenation level-dependent (BOLD) contrast. Each functional image comprised 30 contiguous axial slices, each 3.2 mm thick (0.8 mm gap), acquired in ascending mode, with a repetition time of 2000 ms and an echo time of 30 ms (field of view: 240 mm × 240 mm; matrix size: 128 × 128). Each participant underwent 4 functional scanning runs (2 with the upper limb and 2 with the lower limb conditions). The duration of each run was 320 scans, preceded by 5 dummy scans that were discarded prior to data analysis.

We also acquired a high-resolution whole-brain structural T1 weighted scan (resolution 1 mm × 1 mm × 1 mm) of each participant for anatomical localization and visualization of brain activations.

Table 3C
Activations for FicL minus (Idi + Met) sentences (p < 0.05, FWE corrected).

Anatomical location	Cluster	Voxel level		MNI coordinates		
	k	p value	Z score	x	y	z
L sup. front. gyrus	14	8.0239 e−04	5.66	−20	6	48
L mid. temp. gyrus	75	4.7474 e−09	7.46	−56	−62	−4
L precuneus	230	1.0 e−12	Inf	−14	−58	16
R precuneus	228	1.0 e−12	Inf	12	−54	12
L fusiform gyrus	205	1.0 e−12	Inf	−28	−40	−16
R fusiform gyrus	137	1.0 e−12	Inf	28	−32	−20
L mid. occ. gyrus (40% PGp)	264	1.0 e−12	Inf	−36	−78	32
R mid. occ. gyrus (80% PGp)	138	1.2049 e−11	Inf	44	−74	32

fMRI data analysis

Preprocessing of fMRI data

Statistical parametric mapping (SPM8, Wellcome Department of Imaging Neuroscience, London, UK) was used for image realignment and unwarping (Andersson et al., 2001), normalization to the Montreal Neurologic Institute (MNI) standard space, smoothing by a 6-mm full-width half-maximum Gaussian kernel, and General Linear Model statistical analysis (Friston et al., 2002). We adopted a 2-stage random-effects approach to ensure generalizability of the results at the population level (Penny and Holmes, 2003).

First-level statistical analysis

At the first stage, in SPM8 the time series of each participant were high-pass filtered at 128 s and prewhitened by means of an auto-regressive model AR(1) (Andersson et al., 2001). No global scaling was applied. The first-level individual design matrices included the data of all 4 scanning sessions of each participant. Hemodynamic evoked responses for all experimental conditions were modelled as a set of hemodynamic response functions, including the canonical response function, its first derivative (modelling for temporal latency effects), and its second derivative (modelling for dispersion effects). The experimental conditions were modelled with the onset of the hemodynamic response functions time locked to the presentation of the experimental sentence, and, as a separate event/experimental condition regressor, to the presentation of the associated target sentence (not further considered in the second-level statistical analysis).

For the two upper limb-related fMRI sessions, we modelled the following 5 experimental conditions: 1. Idiomatic upper limb-related sentences [IdiU], 2. Metaphorical upper limb-related sentences [MetU], 3. Filler sentences with upper limb motor verbs, 4. Literal upper limb-related sentences [LitU], 5. Control sentences [CtrU]. For the two lower limb-related fMRI sessions, we modelled the following 5 experimental conditions: 1. Idiomatic lower limb-related sentences [IdiL], 2. Metaphorical lower limb-related sentences [MetL], 3. Fictive-motion lower limb-related sentences [FicL], 4. Literal lower limb-related sentences [LitL], 5. Control sentences [CtrL]. t-Test contrasts were used to identify the network of activation for each sentence type. The t-contrasts only spanned the canonical response function, excluding first and second derivative regressors.

For each subject, we also specified two additional first-level design matrices that served to perform a set of control analyses to account for possible confounding effects due to significant differences (see Stimuli section) in familiarity ratings among the experimental conditions (for details, see inline Supplementary Materials and methods, Inline Supplementary Tables S1–S3 and Inline Supplementary Figs. S1–S3).

Inline Supplementary Table S1 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.06.050.

Inline Supplementary Table S2 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.06.050.

Inline Supplementary Table S3 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.06.050.

Inline Supplementary Fig. S1 can be found online at http://dx.doi. org/10.1016/j.neuroimage.2013.06.050.

Inline Supplementary Fig. S2 can be found online at http://dx.doi. org/10.1016/j.neuroimage.2013.06.050.

Inline Supplementary Fig. S3 can be found online at http://dx.doi. org/10.1016/j.neuroimage.2013.06.050.

Second-level statistical analysis

At the second stage of the analysis, the contrast images obtained at the single-subject level were used to compute a full factorial ANOVA in SPM8, assessing their significance at the group level (n = 24 participants). The ANOVA included two factors, namely Sentence Type (Idi, Met, Filler/Fic, Lit, Ctr) and Limb (Upper, Lower), both modelled with equal variance and non-independent levels.

We used F-contrasts and t-Student's contrasts to assess the following effects of interest: i) somatotopic effects for upper and lower limb-related verbs in the figurative and literal sentence conditions; ii) main effect of figurative versus literal and control sentences; iii) variance among figurative sentences (i.e. a mass-univariate F-contrast testing for all possible differences between the three figurative sentence types, Idi, Met, and FicL). For the sake of clarity, the detailed procedure adopted to assess these second-level effects will be described in the Results section in association to the corresponding findings.

In addition, in order to confirm the results of the analysis of the somatotopic effects, we also used the SPM Marsbar toolbox (www. marsbar.sourceforge.net) to extract percent BOLD signal changes for each subject and for each of the 9 experimental conditions, from limb specific ROIs derived from previous studies (Hauk et al., 2004; Tettamanti et al., 2005).

All reported effects relate to voxel-level statistics with p < .05, Family Wise Error (FWE) type corrected for multiple comparisons. We assessed the cytoarchitectonic probability of activated areas, using the SPM Anatomy Toolbox (http://www.fz-juelich.de/ime/spm_anatomy_ toolbox).

Results

fMRI results

Somatotopic effects for motion verbs

In order to test whether the upper and lower limb-related sentences elicited body-part specific somatotopic activations in the left-hemispheric motor and premotor areas, either as an overall effect or as a sentence type-specific effect, we performed two types of statistical contrasts.

i) The first type of contrasts allowed for inferences limited to the present study, in which the comparison of limb-specific sentences minus Ctr sentences (e.g. [IdiU − CtrU]) was exclusively masked by the corresponding contrast for the other limb (e.g. [IdiL − CtrL]) with a mask threshold of p < 0.001 uncorrected for multiple comparisons. This procedure (described in Tettamanti et al., 2005) allows excluding that the brain regions significantly activated by sentences related to one body part are also activated by sentences related to the other body parts. In general (see Table 1 for the detailed results), the results showed a left-hemispheric network of activation encompassing in particular the inferior frontal gyrus and the posterior middle temporal gyrus. In some, but not all sentence types, the left-hemispheric network extended to the precentral gyrus, the supplementary motor area, and the antero-lateral parietal cortex. The effects for lower limb-related sentences were much less pronounced than for upper-limb related sentences.

ii) The second type of contrasts was based on a priori hypotheses derived from the study by Tettamanti et al. (2005) to test for limb-specific activations in the premotor cortex. We used Small Volume Correction in SPM8 and defined search spherical volumes

of radius 6 mm around the hand-related (x = −30, y = −2, z = +56) and leg-related (x = −26, y = +4, z = +64) coordinates reported in Tettamanti et al. (2005). This second type of contrast showed upper-limb specific effects for all upper limb-related sentence types (MetU and LitU, although IdiU only showed a trend, p = 0.053). For lower limb-related sentences there was a statistical trend at an uncorrected significance level for all lower limb-related sentences pooled together; more specifically, there was a significant effect for LitL and FicL compared to IdiL, which only showed a statistical trend at an uncorrected significance level, and MetL, which did not show any significant effect.

Finally, in order to confirm the results of the second type of contrasts, we extracted percent BOLD signal changes for each subject and for each of the 9 experimental conditions, from limb specific ROIs. Two ROI pairs were used: one consisting again of the two spherical ROIs of radius 6 mm around the hand-related (x = −30, y = −2, z = +56) and leg-related (x = −26, y = +4, z = +64) coordinates reported in Tettamanti et al. (2005). In addition, in order to generalize to the available literature as much as possible, a second ROI pair was defined by computing a micro-meta-analysis with ALE software (www. brainmap.org/ale), based on the activation clusters for hand-related and leg-related language effects reported in Hauk et al. (2004) and Tettamanti et al. (2005). For both ROI pairs, for upper and lower limb, we run separately a repeated measure ANOVA with type of sentence (4 levels: Idi, Met, Filler/Fic, Lit) as a main factor. This ROI analysis testing for left premotor somatotopic effects confirmed the previous pattern of results. For percent signal change values extracted from the ROI centred on the hand-related coordinates reported in Tettamanti et al. (2005), we found a significant main effect of sentence type [F(3, 75) = 7.9, p < 0.001]. Paired post-hoc tests between sentence types showed significant higher effect for MetU compared to CtrU (p < 0.001 Bonferroni corrected). No significant effects were found in the leg-related ROI [F(4, 100) = 0.51, p = 0.73]. For values extracted from the ROI based on the micro-meta-analysis on hand-related and language effects reported in Hauk et al. (2004) and Tettamanti et al. (2005), we found a significant main effect of sentence type [F(3, 75) = 5.9, p = 0.001]. Paired post-hoc tests between sentence types showed significant higher effects for MetU compared to CtrU (p = 0.002 Bonferroni corrected). No significant effects were in turn found for the ROI based on the leg-related micro-meta-analysis [F(4, 100) = 0.37, p = 0.8].

Main effect of figurative versus literal and control sentences

We used t-tests to compare the three types of figurative sentences to literal and control sentences for both upper and lower limbs: [(Idi + Met + FicL) − (Lit + Ctr)] and [(Lit + Ctr) − (Idi + Met + FicL)]. The main effect of figurative (Idi + Met + FicL) minus literal (Lit + Ctr) sentences showed a widespread bilateral network, including the medial superior frontal gyrus, extending to the supplementary motor area, the left inferior frontal gyrus (Brodmann's Area (BA) 44/45) and the right inferior frontal gyrus (BA 45), the temporal poles, and the cerebellar hemispheres. Activation clusters in the left middle and inferior temporal gyri, in the left inferior and superior parietal lobules, and in the left occipital lobe were also found (Table 2A, Fig. 1A).

Literal minus figurative sentences yielded activations in the medial superior frontal gyri, extending to the anterior cingulate cortex, and in the right middle frontal gyrus (Table 2B, Fig. 1B).

As a further characterization of the activation differences between figurative and literal sentence processing, we statistically compared the results of the present study with those obtained in our previous study (Romero Lauro et al., 2008). In our previous study, the contrast between idiomatic and literal sentences revealed activations in the medial anterior prefrontal cortex, and bilaterally in the inferior frontal gyri, and in the anterior and posterior temporal cortices. Given
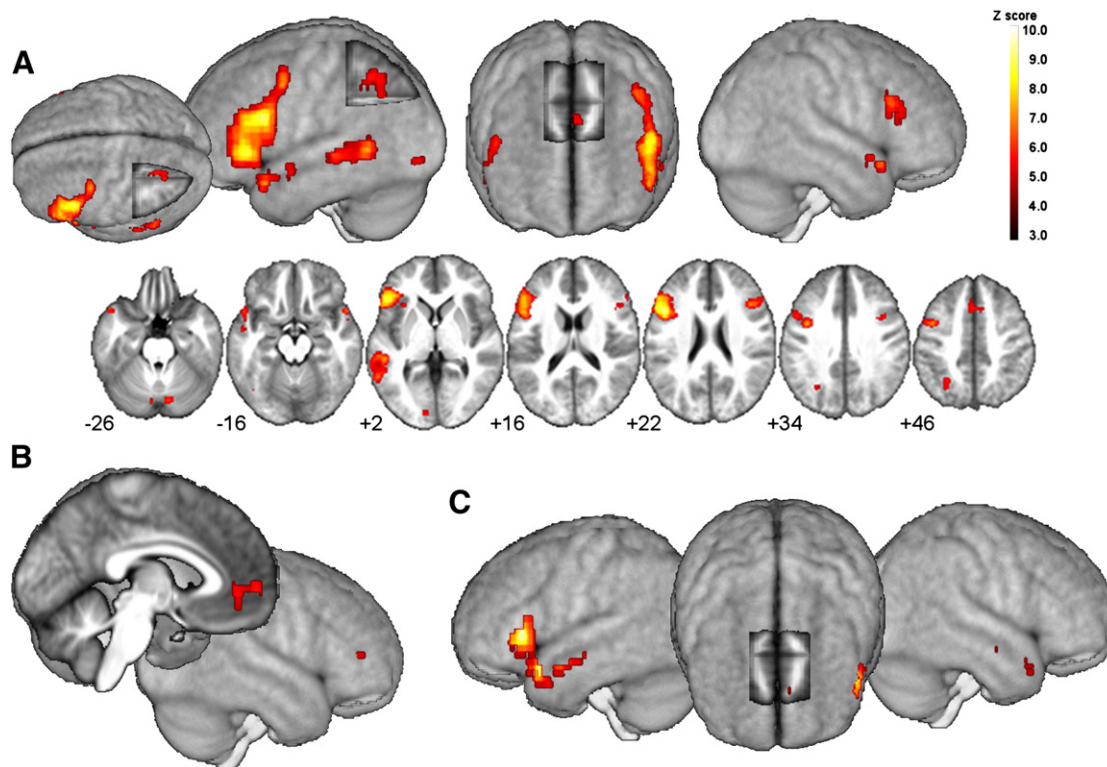
Fig. 1. Main effects of figurative vs literal sentences. Significant activations (p < 0.05, FWE corrected for multiple comparisons) are displayed on lateral and medial cortical renderings and on axial (z coordinate levels in mm) slices of the average anatomical image of all participants (warped to the MNI coordinate space). (A) Higher activations for figurative (Idi + Met + FicL) minus literal (Lit + Ctr) sentences. (B) Higher activations for literal (Lit + Ctr) minus figurative (Idi + Met + FicL) sentences. (C) Statistical comparison showing the common activations between the contrast [(Idi + Met) − Lit] in the present study and the contrast [Idi − Lit] in the study by Romero Lauro et al. (2008).

the lack of significant differences between Idi and Met in the present study (see next paragraph), we pooled Idi and Met together and inclusively masked the F-contrast of figurative versus literal sentences [(Idi + Met) − Lit] with the network of activations (at p < .05, FWE) obtained in the previous study in the F-contrast [Idi − Lit]. The results showed a common pattern of activation, which included the left fronto-temporal network, the medial superior prefrontal cortex, and the right temporal cortex. The only difference concerned the activation of the right inferior frontal gyrus in the previous study that was absent at a comparable location in the present study (Table 2C, Fig. 1C).

Variance among figurative sentences

We first computed a mass-univariate F-contrast testing for all possible differences between the three figurative sentence types (Idi vs Met vs FicL), which showed a widespread network of activation encompassing frontal, temporal, parietal, and occipital areas (Table 3A, Fig. 2A).

In order to attribute each of these effects to an activation increase for a particular figurative sentence type, we computed a set of post-hoc t-Student's contrasts, testing for sentence type specific effects: [Idi − Met] and [Met − Idi], and [(Idi + Met) − FicL] and [FicL − (Idi + Met)]. The direct comparison between Idi and Met did not show any significant cluster of activation. Idi and Met compared to FicL showed increased activation in the medial superior frontal cortex, left inferior frontal gyrus, bilateral anterior temporal cortices, and posterior cingulate cortex (Table 3B, Fig. 2B). In turn, FicL compared to Idi and Met activated a largely bilateral network of posterior areas, including the precunei, the fusiform gyri, and the middle occipital gyri, as well as the left superior frontal gyrus and the posterior left middle temporal gyrus (Table 3C, Fig. 2C).

Control fMRI analyses for the possible confounding effect of familiarity

In order to account for the possible effects due to differences in familiarity ratings among the experimental conditions, we performed a

set of control fMRI data analyses co-varying familiarity ratings from the condition-specific activations, as well as correlating the level of activation with the familiarity ratings. No significant effects of familiarity on the results provided in Tables 1, 2A, 2B, 2C, 3A, 3B and 3C were found (see Inline Supplementary results, Inline Supplementary Tables S1–S3 and Inline Supplementary Figs. S1–S3).

Behavioural results

A repeated measures ANOVA was run on mean percentage of correct responses and mean RTs with Limb (2 levels: Upper vs. Lower) and Sentence Type (5 levels: Idi, Met, Filler/FicL, Lit and Ctr) as within factors.

Regarding accuracy, the main effect of Limb was not significant [F(1, 25) = 1.75, p = n.s.]. The main effect of Sentence Type was significant [F(4, 100) = 16.4, p < 0.001] with a higher accuracy for Lit (M: 97%, SD: 5%) and Ctr (M: 95%, SD: 5.3%) than for FicL (M: 87%, SD: 5.7%), Met (M: 95%, SD: 6%) and Idi (M: 92%, SD: 8.3%). Post hoc analyses (Duncan's tests) showed that accuracy for Lit was significantly higher than for all the other sentence types, while it was significantly lower in the case of FicL; accuracy for Ctr and Idi was significantly higher than for Met (p < 0.05).

The interaction Limb × Sentence Type was significant [F(4, 100) = 23.2, p < 0.001]. Post hoc analyses (Duncan's tests) showed that the accuracy for MetU was significantly lower than for MetL (p < 0.005), in line with the analyses performed to check the experimental material (see Material and methods section). In contrast, no difference was found in the accuracy between LitU and LitL and between IdiU and IdiL.

Regarding RTs, the main effect of Limb was significant [F(1, 25) = 8.2, p < .05] with slower RTs for sentences with motion verbs denoting lower limb actions. The main effect of Sentence Type was also significant [F(4, 100) = 41.6, p < 0.001]. The interaction Limb × Sentence Type approached significance [F(4, 100) = 2.3, p = 0.06]. Post hoc
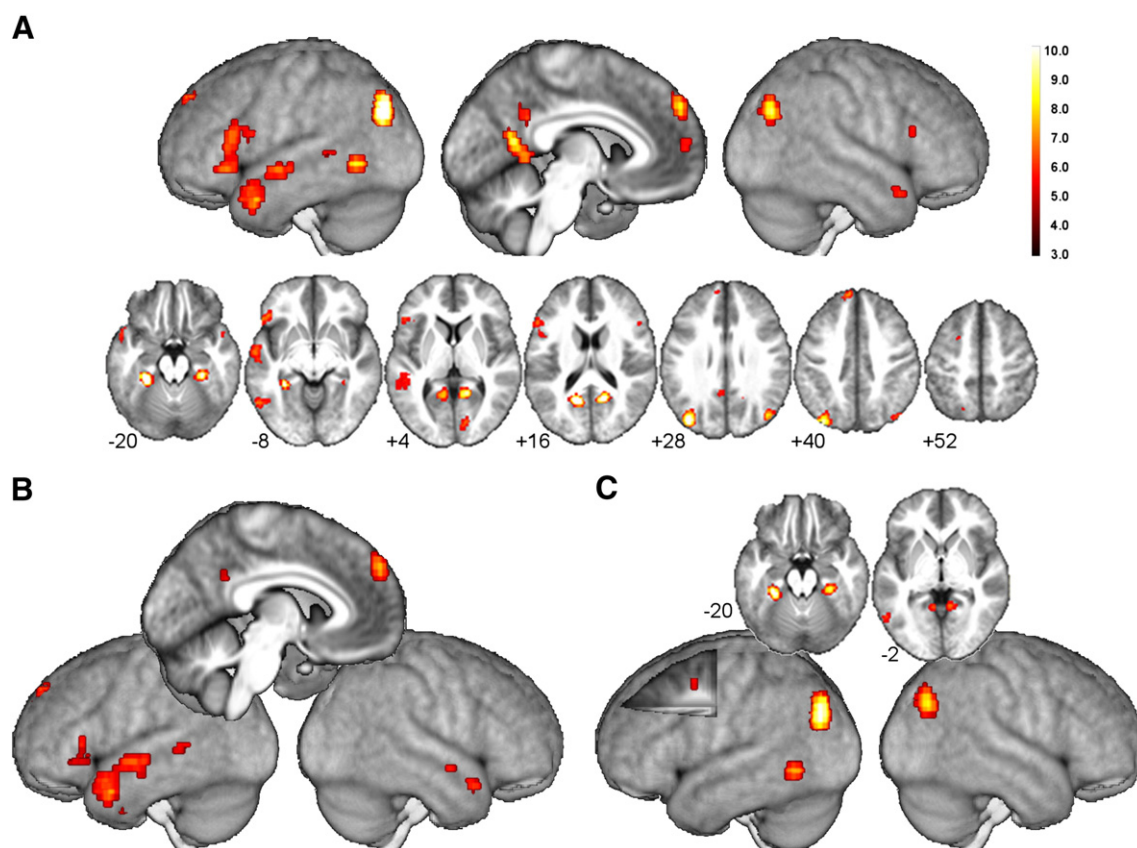
Fig. 2. Differences between the three figurative sentence types. Graphical conventions are the same as in Fig. 1. (A) Brain regions of differential activation between the three figurative sentence types (Idi vs. Met vs. FicL). (B) Higher activations for Idi and Met compared to FicL sentences. (C) Higher activations for FicL compared to Idi and Met sentences.

analyses showed that subjects were significantly slower with FicL (M: 2243 ms, SD: 78 ms) than with Ctr (M: 1943 ms; SD: 74 ms), Lit (M: 1996 ms, SD: 70 ms), Met (M: 2055 ms; SD 75 ms) and Idi (2056 ms; SD: 76). Moreover, Idi and Met were associated to significantly slower RTs than Ctr.

There was no correlation between familiarity rating and accuracy and RTs in Idi, Met and Ctr.

Discussion

In this study we aimed at verifying whether motion verb processing involves activation of motor areas, regardless from the context in which the motion verb appears, namely literal or figurative sentences. For the latter, we compared three different types of sentence in which a motion verb can be used: fictive, metaphorical, and idiomatic sentences. For the first time, all these different figurative sentences were compared in the same fMRI experiment.

The effects for lower limb related sentences were much less pronounced than for upper limb related sentences. A possible explanation can rely on the fact that sentences including upper limb motion verbs were rated as conveying a significantly more concrete and specific motion than those concerning lower limb motion.

Literal and metaphorical motion sentences activated the left precentral gyrus in the case of the upper limb, while idiomatic sentences only approached significance. This result might represent either a *quantitative* or a *qualitative* difference among idiomatic sentences and metaphorical ones. The fact that among sentences including upper limb motion verbs the idiomatic ones were those rated as less concrete might account for the lower somatotopic effect. A recent MEG experiment (Boulenger et al., 2012) showed that idiom processing in a silent reading task produced a somatotopic activation of the precentral motor systems. The results were interpreted as a neural reflection of

constituent parts of idiomatic sentences. However, as mentioned in the Introduction, there are several critical points of this study that do not allow, in our opinion, a straightforward interpretation, the main problem being the absence of control sentences. Moreover, the lack of a significant somatotopic effect in the case of idioms suggests that there is a substantial difference among idiomatic and metaphorical sentences, with a motion involvement only in the latter, in accordance with a previous TMS study (Cacciari et al., 2011).

The results with respect to the somatotopic activation of the motor system for fictive-motion sentences, although limited to lower limb-related meanings (since, as highlighted in the Material and methods section, fictive sentences by definition cannot refer to upper limb-related meanings), are interesting. Fictive-motion sentences were associated with an activation of the premotor cortex overlapping with the somatotopic lower limb effect of Tettamanti et al. (2005); this activation was comparable to that for lower limb-related literal sentences, with both conditions eliciting significantly higher effects than idiomatic and metaphorical sentences. This somatotopic activation which was obtained for both literal and fictive motion sentences challenges the hypothesis of a premotor activation due to a grammatical class effect (Bedny et al., 2008), since sentences were carefully matched for syntactical features, and suggests that an activation of the motor system is involved in processing motion verbs. Again, the lack of a somatotopic effect for metaphorical and idiomatic sentences in the case of lower limb motion verbs can be explained by the fact that these sentences were rated significantly less concrete as compared to literal and fictive motion sentences. Certainly, the confound with concreteness for this result could be critical. However, this possible effect of concreteness speaks in favour of our hypothesis, namely a motor involvement dependent on the specific context: the more the motion verb loses its concrete meaning and acquires an "abstract" connotation, as is presented in a figurative context, the lesser the effect is found. The comparison of

figurative sentences to literal ones showed a greater activation of a bilateral fronto-temporal network, in line with previous studies using either metaphors (Lee and Dapretto, 2006; Rapp et al., 2004; Stringaris et al., 2007) or idioms (Romero Lauro et al., 2008; Zempleni et al., 2007) but different experimental paradigms. With respect to our previous study on idioms (Romero Lauro et al., 2008), we found a minimal difference concerning the right IFG: although in the present study an activation in the right IFG for the figurative minus literal comparison (Table 2A) was present, it did not spatially overlap with that of the previous study (Table 2C). This subtle difference might be due to the different types of experimental paradigm employed in the two studies: here, the participants silently read the sentences (although they performed a semantic congruency task, the hemodynamic response was modelled with the onset of the experimental sentence), whereas in our previous experiment they performed a sentence-to-picture matching task; neuroimaging studies have shown that the activity in the right inferior prefrontal cortex is modulated by the complexity of language tasks, suggesting that this structure plays a role when cognitive demands are particularly high (Jung-Beeman, 2005); silent reading probably did not require additional resources. Alternatively, according to Cardillo et al. (2012), the right prefrontal cortex activation decreases when familiarity of metaphors increases; our metaphors as well as idioms were rated sufficiently familiar, and, probably, the level of salience of the figurative meaning did not require the inhibition of the literal one which has been related to the activity of the right IFG (see Aron et al., 2004). However, this alternative explanation seems unlikely, since also in the previous study idioms were judged familiar.

Moreover, the same network of activation was found for different types of material, namely ambiguous idioms and predicate metaphors. Previous studies have evaluated both ambiguous and non-ambiguous idioms; nominal metaphors were commonly used, with the exception of Chen et al. (2008), who tested predicate metaphors and Cardillo et al. (2012) who directly compared nominal and predicate metaphors and found no evidence for a neural differentiation between them. One could suggest that what appears to be the effect of figurative language may at least in part be the effect of relatively abstract language, since the sites of activation are similar to those found in studying neural representation of abstract concepts (see Wang et al., 2010 for a meta-analysis). This pattern of activation, including both Broca's area and the superior sector of the left temporal pole, was for instance found in our previous experiment (Romero Lauro et al., 2008). Even though the analogy with abstract language captures only a few aspects of figurative language processing, this is indeed an interesting hypothesis to be explored by future studies. This may also be consistent with the fact that a separate group of subjects than those participating in the fMRI study rated the figurative sentences as less concrete than the literal sentences (see Stimuli section).

A further relevant finding concerns the direct comparison of idiomatic, metaphorical, and fictive-motion sentences within the same design, thus highlighting the specific neural contribution of each sentence type. Fictive motion has been compared with literal motion and static sentences (Saygin et al., 2010; Wallentin et al., 2005), but never, as far as we know, with other types of figurative language with the exception of our TMS study (Cacciari et al., 2011). Comparing together all these types of figurative sentences, we found that fictive motion activated a more posterior region, involving primary visual areas and motion sensitive visual areas, such as the left posterior middle temporal gyrus (as in Wallentin et al., 2005, 2011), but also the left middle frontal gyrus (BA9). While the activation of motion sensitive visual areas can be explained by suggesting that the readers mentally scan the space described by fictive sentences, the interpretation of the left middle frontal gyrus activation is more challenging. The middle frontal gyrus is activated bilaterally when the reasoning demands increase (Hampshire et al., 2011), but also when there is a need for greater phonological encoding in reading (see Jamal et al., 2012): since fictive motion sentences were apparently the most difficult

type of stimuli, this activation can reflect the need for additional cognitive resources. Indeed, we can speculate that the presence of an inanimate agent in fictive motion sentences "conflicts" with the motion verb: indeed, for fictive motion sentences RTs were slower than RTs for literal motion sentences, and accuracy was lower. Alternatively, since it has been demonstrated that this frontal area plays a monitoring role over the visual areas (Danielmeier et al., 2011), we can assume that it has a monitoring role also over mental scene scanning.

Conclusions

In summary, we studied whether the activation of the motor system was sensitive or not to the literal vs. figurative nature of the motion conveyed by sentences. We found activation with a somatotopic distribution for literal sentences, confirming the results of previous studies. For fictive motion, we found a lower limb-related somatotopic effect, in addition to the well-known activation of motion sensitive visual areas. For metaphorical sentences, we found a somatotopic upper limb-related effect, but no significant effects for lower limb-related sentences, similar to Boulenger et al.'s (2012) results with idioms. So, while for literal and fictive motion all data seem to converge on the same structures involved in their processing, the evidence for metaphorical sentences was less strong. Finally, for upper limb-related ambiguous idiomatic sentences, the level of somatotopic activation in the precentral gyrus only approached significance.

We have suggested that differences in the rating of concrete motion between upper and lower limb verbs and, within lower limb verbs, among idiomatic and other sentence types might account for the variance of the somatotopic effect. However the results suggest that the motion component of the verb is preserved in fictive motion sentences, and possibly in metaphorical sentences (in line with a previous TMS study), but the evidence is poorer for idiomatic sentences. Indeed, idioms do have a unique meaning that cannot be changed by context and that is retrieved from semantic memory, while constituent words have lost their original meaning. In contrast, metaphors require categorization and the original meaning of the constituent words is maintained (Cacciari and Glucksberg, 1995; Cacciari et al., 2011). Therefore, the literal versus figurative specific context in which the motion verbs appear determines at least in part how concrete the motion is perceived and, consequently, the degree of involvement of the motor cortex. Moreover, our data suggest that the motor cortex involvement takes place when an explicit demand on semantic processing is required. Finally, we argue that they support weak embodied views suggesting that the motor system enhances the comprehension of linguistically encoded actions (Tettamanti and Moro, 2012; van Dam et al., 2012).

Conflict of interest

The authors declare no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.06.050.

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