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Grasping language – a short story on Embodiment

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Abstract

The new concept of embodied cognition theories has been enthusiastically studied by the cognitive sciences, by as well as such disparate disciplines as philosophy, anthropology, neuroscience, and robotics. Embodiment theory provides the framework for ongoing discussions on the linkage between “low” cognitive processes as perception and “high” cognition as language processing and comprehension, respectively. This review gives an overview along the lines of argumentation in the ongoing debate on the embodiment of language and employs an ALE meta-analysis to illustrate and weigh previous findings. The collected evidence on the somatotopic activation of motor areas, abstract and concrete word processing, as well as from reported patient and timing studies emphasizes the important role of sensorimotor areas in language processing and supports the hypothesis that the motor system is activated during language comprehension.

The idea of embodiment

“Grasp the subject, the words will follow” was advised by Cato the Elder. Grasping an explanation, giving an example, posing a threat – language is full of actions and objects, and the ties between language and motion are under continuous investigation. Embodied cognition theories are becoming more and more popular in cognitive (neuro)science, as well as in philosophy, anthropology, cognitive psychology, and robotics (e.g. Nolfi & Floreano, 2000; Ziemke, 2002). According to the embodied view, there is no separation between the so-called “low” cognitive processes, such as perception and action, and “high” cognitive processes, such as language and thought. Generally, embodiment links the individual sensorimotor experiences with higher cognitive functions such as language processing and comprehension. Connecting motor abilities with cognitive capacities contradicts with the classic amodal view, which assumes a clear-cut separation between low and high level processes and which states that cognition derives from computational processes in separate domains.

When applied to language, embodied cognition views claim that when we understand words, the same sensorimotor areas are recruited as for interacting with the objects and entities the words refer to. Similarly, when we comprehend sentences, we internally simulate the state of the world the sentences describe (Zwaan, 2004). In the past years much behavioural and neural evidence has been collected, showing that the process of language comprehension activates a motor simulation (Gallese, 2008) and involves the motor system (see Barsalou, 2008; Fischer & Zwaan, 2008; Pulvermüller, 2005).

In a neuroscientific context, this perspective also implies that brain areas related to action and language can no be longer be seen as independent, but rather working in concert. Areas traditionally regarded as pure motor areas as e.g. the primary motor or the premotor cortex, as well as areas that have traditionally been assigned to the processing of language, e.g. Broca's or Wernicke's region, are not modularized, but rather provide the linkage of action and language (Pulvermüller 2005). Participation of Broca's region has already been revealed in different motor experiments, such as grasping experiments (Grafton et al., 1996), object manipulation (Binkofski et al., 1999) and action imitation (Rizzolatti & Arbib, 1998). Based on numerous results, it turns out, that Broca’s region is more than just representing a language processing area (Menz & Binkofski, 2008).

In this short story on embodied language we want to review recent literature on language and embodiment – first along the main lines of argumentation in the ongoing debate, and second in an activation likelihood estimation (ALE) meta-analysis on reported neural activity patterns.

Somatotopic activation during processing of action words and sentences

One of the most important issues in the ongoing debate about embodied cognition is the somatotopy of activation. If the hypothesis held true that language recruited the same sensorimotor areas as for action and interaction, motor areas should display the same somatotopy for processing language as for processing actions.

Although the general involvement of premotor and motor cortices has been demonstrated repeatedly, the issue of somatotopy still needs to be clarified.

There is strong evidence for a somatotopic activation of premotor cortices from studies with different techniques (fMRI, MEG, etc.).

Tettamanti et al.(2005) investigated the underlying neural processes while presenting sentences expressing actions performed with the mouth, the hand or the foot.

Specifically, hand action and related words were found activated in the left precentral gyrus, the posterior intraparietal sulcus and the left posterior inferior temporal area. In contrast, leg activity has been identified in the left dorsal premotor and left intraparietal sulcus, but located more dorsally and rostrally in relation to the parietal hand activities. In addition, detection of a bilateral pattern in the posterior cingulate shows clear distinction of activation in processing abstractness.

Activity in Broca's region has been detected detached from any effector-specificity, thus implying a special role in language processing.

Summarized, the fMRI results presented in that study display activity in a frontal-parietal circuit with temporal participation in the left hemisphere.

Furthermore, Pulvermüller (2005) recorded neurophysiological and behavioural responses to verbs referring to actions performed with the face, the arms and the legs. Using a lexical decision task, they found topographical differences in the brain activity patterns generated by the different verbs, starting 250ms after word onset. Consequently, the English verbs 'lick', 'pick', and 'kick' engage different neural sites in a topographical pattern. Moreover, a near-simultaneous activity pattern in the inferior frontal gyrus and the superior temporal gyrus could be identified, which supports both speech production as well as word comprehension. Another study on somatotopic organization of the motor cortex is presented in Hauk et al. (2004). The differentiation of arm-related and leg-related action, respectively action words revealed distinct patterns in the middle frontal and the precentral gyrus for arm actions and, on the contrary, activations in dorsal areas in left and midline of the pre-and postcentral gyrus and dorsal premotor cortex.

Induced by a dissociation on word category processing, the cortical activity found in this study displays effector-dependent processing along the motor strip.

In addition, EEG-recordings showed an activation of the effector specific motor regions occurring quite early, less than 200 ms after word onset (Pulvermüller, 1999). A combined behavioural and TMS study by Buccino et al. (2005) strengthens this suggestion. A decrease in amplitude of MEPs was recorded from hand muscles when listening to hand-action related sentences, and from foot muscles when listening to foot related sentences. In line with this evidence, further results obtained with behavioural tasks (Scorolli & Borghi, 2007; Borghi & Scorolli, 2009) suggest that the simulation activated during combinations of nouns and verbs is sensitive to the congruency between the effector implied by the sentence (e.g. mouth vs. foot) and the effector used to produce the motor response.

Also other studies are able to identify body-part specificity in premotor cortices, but not in other motor areas. In an fMRI study with a lexical decision task Willems, Hagoort and Casasanto (2009) found a preferential activation of the left premotor cortex for right handers, and of the right premotor cortex for left handers, while responding to manual-action verbs (compared to nonmanual action verbs). This suggests that the simulation evoked during language processing is body-specific. However, whereas imagery activated both motor and premotor cortices in a differential way, language comprehension activated only the premotor cortex. In a similar vein, Tomasino et al. (2007; 2008) found activation of the primary motor cortex during explicit mental motor imagery, whereas no activation was found in a letter-detection task.

Although several studies showed evidence towards action word comprehension in connection with somatotopy, a more critical view concerning this topic is dicussed in Postle et al. (2008).

Focussing on different motor areas Postle et al. (2008) used fMRI in cytoarchitectonically regions of interest (primary and premotor cortices) to compare action verbs related to different effectors (hand, foot and mouth) with other concrete nouns unrelated to body parts and actions, as well as to non-words and to strings of hashes. Action and non action words were matched for imageability. Whereas a expected somatotopic organization for observation of simple movements could be identified, i.e. activations of motor areas BA 4 and BA 6 in a ventral-to-dorsal fashion according to the succession mouth, hand and foot. The same applies to a posterior-to-anterior pattern across the lateral surfaces of the mentioned motor areas. Although there was no evidence of a somatotopic organization for action words, the pre-supplementary motor area (pre-SMA) displayed a different activation for foot-related action compared to non-action words, thereby possibly playing a rather cognitive-motor role instead of a pure motor one. A main difference of Postle et al. in comparison to the other studies cited above is the use of cytoarchitectonically defined probability maps. This suggests that studies on somatotopy connected to word meaning extraction should be also related to cytoarchitectural information and functional criteria, in order to correctly interpret activation distibution as somatotopy.

Summarized, several language comprehension studies show evidence on an at least effector-specific activation during language comprehension, though not primarily investigated in all studies introduced above.

In general, but also considering some critical aspects by Postle et al. (2008), it can be stated, that somatotopy can be identified in premotor regions, but not consistently in primary motor cortices. This might be due to the simplicity of tasks, but also to the different roles the motor cortices play in conceptualizing and execution of actions.

Embodiment and the mirror neuron system

Along with a somatotopy in processing language, also the involvement of the mirror neuron system in processing language is based on the theoretical principle, that the processing of language is grounded in the same neural units as the actions the words refer to.

According to embodied theories, canonical and mirror neurons represent the neural basis of the simulation activated during language comprehension (Gallese, 2008). Mirror neurons, which were originally identified in the ventral premotor cortex of monkeys, are not only firing during active motion, but they are also triggered by observing a conspecific performing actions with objects (Rizzolatti and Craighero, 2004). Similar investigations in humans lack the single-neuron resolution, thus it is rather referred to as the mirror neuron system (MNS; Buccino et al, 2001; 2005). The linking element between monkey and man is the area F5 of the monkey ventral premotor cortex which is regarded as a homologue to Broca's region, the inferior frontal region in the human cortex, which is primarily known as a speech processing area (Rizzolatti and Craighero, 2004). This leads to the assumption, that homologue to F5, also Broca's region contains mirror neurons (Buccino et al., 2005) and Broca's region is no longer regarded as a pure language area, but as also as a region linking action and language (Binkofski & Buccino, 2004; Menz & Binkofski, 2008). As Broca's region is the core region of the MNS and implies an additional link between motor processing and speech the whole MNS possibly also has an impact on language processing and comprehension. Glenberg et al. (2008) show mirror neuron activation in an experimental setting by either presenting a typical action sound or a verbal action description. In differential contrasts of typically MNS-activating tasks, as e.g. object observation compared to language processing, the activation of Broca's region to either seems to differ. Aziz-Zadeh et al (2006a,b) and Aziz-Zadeh & Damasio (2008) descibe close but not completely overlapping patterns for action observation and reading phrases. They draw the conclusion that mirror neurons are not directly mediating the understanding of language, but possibly play an important role as a precursor in the development of language (Rizzolatti & Arbib, 1998). However, this does not contradict an integrating role of Broca's region in processing both sounds and actions. In monkey data, Kohler et al. (2002) detected firing of mirror neurons in the presence of action specific noise. Mirror neurons showed a specialization for an action and the sound it produces, e.g. they fire when breaking a peanut and also when only the sound is played. In the human domain, D’Ausilio et al. (2009) reported a facilitation of the perception of a given speech sound when the motor articulator responsible for that sound was stimulated with TMS for motor cortex controlling. Apart from Broca’s region, the left inferior parietal lobe (IPL), also part of the MNS (Buccino et al., 2005) was reported to have an important role in the integration of sounds and actions. McNamara et al. (2008) asked subjects to learn associations between previously unrelated novel sounds and meaningless gestures. Both IPL and Broca's region showed a strong, bilateral, negative correlation of BOLD response with learning of sound-action associations during data acquisition. Together with decrease due to the sharpening of the network, connectivity between the areas increased and the strongest learning related connectivity between regions was found in Broca’s region and left IPL.

Together this leads to the conclusion that the involvement of motor regions in language processing is closely linked to regions of the mirror neuron system, thus possibly relying using mirror neurons to integrate sounds and actions or even to simulate in order to understand action words. However, this claim is strong and will need further evidence.

Abstract and Concrete word processing

A second strong claim of embodied theories relates to the grounding of abstract language. Embodied theories assume that abstract concepts, just like concrete ones, are grounded in the sensorimotor system. Within this general framework, at least three different explanations of abstraction have been proposed (see Glenberg et al., 2008). A key issue in the literature is to what extent concrete and abstract words (e.g., “bottle” vs. “truth”) are represented differently. However, starting from this general assumption different explanations have been proposed, one of the most influential of which is based on metaphors. Lakoff & Johnson (1980) proposed up to fifty metaphor schemes in everyday language. “Cancer finally caught him up” serves as example for personification, whereas “Your claims are indefensible” has yet another categorization. In line with the work, Casasanto & Boroditsky (2008) show connection of metaphorical language processing and experiences built on perception and action. The argumentation of metaphors contributing to access meaning and also appealing to the conceptual system, which is also involved by action experiences and thinking, speaks in favour of the embodiment perspective of language comprehension. According to very recent proposals, abstract words involve more emotional aspects than concrete ones (Vigliocco, 2009); in addition, abstract words rely more on linguistic and social information as their modality of acquisition employs more linguistic information as compared to concrete words (Borghi & Cimatti, 2009). According to the strong version of the embodied framework, both the literal and the more abstract meaning of language (e.g., “grasp” in the context of “grasping an apple” and in the context of “grasping a notion”) are processed in the same neural units. Thus, action words should be represented in the same sensory-motor areas as their simple motor analogue. As an example, Aziz-Zadeh and Damasio (2008) proposed that the verb 'to kick' (literal) and 'kick of the year' (abstract) imply the same 'kick' motor representation. There is TMS evidence supporting this view. Glenberg and collaborators (2008) have shown that abstract transfer sentences (e.g., give some news) activate motor information exactly as concrete transfer sentences (e.g., give a pizza). A more specific description of the processing of abstract and concrete words is given by a study of Rüschemeyer, Brass and Friederici (2007). They performed an fMRI study comparing verbs with motor meaning, such as “to beat”, and verbs with abstract meanings, such as “to guess”**.** Participants had to respond by pressing a key to pseudo-words, while no response for words was required. The authors found enhanced activation of motor verbs compared to abstract verbs in the posterior premotor, primary motor, primary and secondary somatosensory cortex; this activation was bilateral but was higher in the left hemisphere. However, they did not find any difference in the activation of frontal mirror neurons areas, the ventral premotor cortex, and in the parietal module, for processing simple motor verbs and abstract verbs. In addition, no difference was found while comparing German verbs with motor stems and verbs with abstract stems. Tettamanti et al. (2005), however, describe a premotor activation during the processing of action-related sentences as compared to their control condition (e.g. “now I appreciate loyalty”), thus reporting a unique activation of a motor area to concrete sentences containing a manipulable object as opposed to sentences containing abstract objects.

Another recent fMRI study, in turn suggests that the abstract words and sentences activate motor representations (Raposo, Moss, Stamatakis, & Tyler, 2009). The authors compared single verbs and literal and idiomatic sentences in order to verify whether involvement of motor regions is automatic and invariable or whether it is modulated by the sentential context. In the task they used, particularly adequate in case of ambiguous sentences, participants listened to sentences; on half of them they were presented with a visual probe and had to determine by pressing a key whether the visual probe was related or not to the sentence meaning. Listening to leg-related and arm-related action verbs (e.g., grab, kick) activated a fronto-parietal system typically involved in action execution.

This leads to two assumptions. First, verbs and nouns are possibly processed differently regarding their abstractness, and second, that different levels of derivation from a word's literal meaning might lead to different activations. Hence, abstract (“to kick around an idea”), metaphorical (“to kick in the dugout”), idiomatic (“to kick the bucket”), and morphological (rare in English but in German “treten/ to kick” and “eintreten”/ to occur”) should be investigated separately and not be subsumed under the term “abstract” or “non-motor” or even be regarded as homogeneous control conditions.

Altogether we can only conclude that demonstrations of the sensorimotor grounding of abstract words have so far been confined to rather specific domains and further evidence is needed (for further discussion of this issue, see Borghi & Cimatti, 2009).

Are sensorimotor areas essential for language comprehension?

One core issue in discussing embodied language lies in the question whether the involvement of sensorimotor areas is auxiliary, concomitant, or necessary for language processing and comprehension. Even though the majority of studies demonstrate that the motor system is activated during words and sentences processing, there is some controversial evidence, and some issues remain open (see also Willems & Hagoort, 2007). Partly this might be related to the afore mentioned disagreement as to the definition of abstractness and the usage of control conditions. However there are two points of view contributing to an essential role of sensorimotor areas to language processing: evidence from patients and evidence on timing.

The first promising evidence is given by studies on patients with impairments of the motor system. Boulenger et al. (2008) found no priming effect for action verbs for patients affected by Parkinson disease off dopaminergic treatment, i.e. when there is no normal activation level in premotor and motor areas. The priming effect, instead, was present in both controls and Parkinson patients after dopaminergic intake. This study provides strong evidence that the integrity of the motor system is necessary for verb processing. Along with this evidence, Bak et al. (2006) found selective deficits in verb processing in two patients, father and son, with a familial motor disorder; in addition, Bak and Hodges (2004) found a selective difficulty for verb processing in motor neuron disease, a neurodegenerative disease of the motor system. Even if this evidence is not conclusive, a number of studies report action comprehension deficits in patients with premotor and parietal lesions (for a review and discussion, see Aziz-Zadeh & Damasio, 2008). Altogether, it can be claimed that lesions of the motor system selectively impair language processing, and particularly verb comprehension. This evidence can support the argument that an integer motor system might be part of the comprehension process.

The second good argument in favour of the involvement of the motor system as an essential part of language comprehension would be an early activation of the motor system. Papeo et al (2009) recorded TMS-induced motor-evoked potentials from right hand muscles in order to measure M1 activity during comprehension of action verbs. They found an increase of M1-activity only at 500 ms, while no increase was present as they delivered single pulse TMS at 170 and 350 ms after action words appearance. This suggests that M1 is involved during post-conceptual processing of action words, and it is not necessarily implied and does not contribute to words comprehension. However, other studies report an early involvement of motor areas (for a review and a model reproducing results on both early and late activation of motor areas, see Chersi et al., 2010). In a lexical decision task, presenting action-verbs and nouns, Pulvermüller et al. (1999) detected neural activity recorded from EEG less than 200 ms after word onset and in an automatic way. Even in this short time window, the signals highlighted electrocortical differences. As discussed by the authors, the study revealed non-classical language areas involved in language processing, and proposed additional cell assemblies in the motor cortex for action-verbs and neural signals from the visual cortex for nouns, respectively.

Thus, we think that evidence collected so far is promising and that in the near future the issue of the necessity of activation of the motor system concerning semantic processing will be definitively solved.

Embodiment – a meta-analysis

Opposed to narrative reviews or label-based anatomical approaches, the coordinate-based meta-analysis methods statistically aggregate activation foci ('peaks') derived from neuroimaging data and emphasize specific neuronal patterns across multiple studies following a common paradigm or hypothesis. Recent experimental series can be evaluated to a meta-statement. For the meta-analysis included in this review we used the ALE approach as implemented in the Ginger ALE software provided by BrainMap (Laird, 2005).

Literature search and criteria

An exhaustive literature search was conducted on fMRI studies indexed in the Medline database. We focused on studies, which contained the pre-specified keywords “embodiment”, “language”, “motor”, “action”, and “perception”. The filter criteria do not distinguish between concrete and abstract word processing, as the objective of the analysis is to cover the whole range of embodied language. In addition, the selection of experiments took into account both extremities (hand/arm, foot/leg) to increase the variance of particular action-related patterns in literal and abstract meanings. Furthermore, we included studies on words (verbs, nouns) and on sentences or both.

< please include Table 1 about here >

Statistical Procedure

A statistical map was generated by using a collection of 468 foci from the 21 studies reported in Table 1 after transferring them into Talairach space (Talairach & Tournoux, 1988). In order to account for the uncertainty, that is technically inherent to the actual location of the peaks, each coordinate was modelled not as a single point, but by a three-dimensional (3D) Gaussian function with 12mm FWHM. Thus, the localization probability distributions describe the probability that a given focus actually lay within a particular voxel.

Statistical significance is gained via a permutation test of randomly generated foci using the same FWHM and number of foci. The voxel-wise comparison is tested against the null-hypothesis of uniformly distributed peaks, giving a set of ALE-values necessary for thresholding the probability map. Using the False Discovery Rate (FDR) with $q = 0.01$, the test was corrected for multiple comparisons.

Results of the meta-analysis

The activation clusters of the meta-analysis are summarized in Table 2 and Figure 1. All coordinates are in Talairach space and anatomical labels as well as Brodmann areas were obtained with the Talairach Daemon (Lancaster et al., 1997; 2000).

Major activity sites are displayed in the left hemisphere, predominantly in the frontal lobe, comprising the inferior frontal gyrus (cluster 1, BA 44, BA 46) and the precentral gyrus (cluster 1, cluster 3, cluster 9, BA 4, BA 6). In the parietal lobe, distinct clusters could be detected in the left supramarginal gyrus (cluster 1, BA 40), as well as in the right superior parietal lobulus (cluster 5, BA 7) and in the left precuneus (cluster 1, BA 19) area. In the left temporal lobe, activations could be found in the middle temporal gyrus (cluster 2, BA 22, BA 39) and more prominently in the fusiform area (cluster 8, BA 37). Further findings include the insula (cluster 2, BA 13) in the left hemisphere as well as the bilateral cerebellum. Additionally, the analysis reveals two clusters comprising the posterior cingulate (cluster 6, cluster 11, BA 30) in both hemispheres.

< please include Figure 1 about here >

< please include Table 2 about here >

Integrating the meta-analysis into previous findings

The main advantage of the ALE meta-analysis is to give an overview on previously reported findings, to un-weight interpretations, and to re-weight results within, but even more outside of regions of interest. Due to the method, there will be no new evidence, however, the focus on activated areas might change and a more general pattern can be identified.

As described in the first section of this short review, embodied cognition theories propose several ideas. The first important one is the assumption that there is no separation between low and high cognitive processes. This assumption is tightly linked to the second claim, that sensorimotor systems are recruited, when verbal material is processed. Indeed, the main finding from this meta-analysis shows the clear involvement of a variety of regions, including mainly temporal (cluster 1, 2, 8) and frontal (cluster 1, 3), but also cerebellar activity (cluster 4, 10).

Moreover, there is a clear predominance of activations in the (language and motor areas of the) left hemisphere. This could be due to a variety of reasons. First, language processing naturally occurs in the left hemisphere. In addition, the majority of participants in the present studies had right dominant effectors, hand and foot, which are processed contra-laterally. In an fMRI study with a lexical decision task Willems, Hagoort and Casasanto (2009) found a preferential activation of the left premotor cortex for right handers, and of the right premotor cortex for left handers, while responding to manual-action verbs (compared to nonmanual action verbs). However, it should be noted that during the experiments, participants were not performing actions. Rather, they had to read, listen and name actions without concomitant motor activity. Hence, it is important to emphasize that the motor areas such as SMA, the precentral gyrus or the premotor cortex were active when language only was processed.

The meta-analysis also detects neural activations in the right hemisphere, especially in frontal (cluster 9) and parietal (cluster 5) regions. Indeed, there is evidence that the right hemisphere contributes to the processing of semantic components (Canessa et al.,2008; Kemmerer et al., 2008; Gronau et al., 2008).

Another interesting result speaking in favour of motor activation irrespective of a distinction between low and high cognitive processes is the here identified participation of the cerebellum in language processing and, consequently, in language comprehension. This region has not yet been extensively focused on although it is well known that is plays a crucial role in motor learning. However, our results show a significant contribution of the cerebellum in the left hemisphere.

The neural connections in participation with the cerebellum could be another interesting aspect pointing to the neural interoperability of different brain areas in embodied language.

Reallocating this result to the studies in the literature collection (Table 2) it is evident, that the cerebellum activity could be recorded within experiments which investigate action comprehension (Boulenger et al., 2009), action naming (Liljeström et al., 2008) or semantic processing (Saccuman et al., 2006). Therefore, the activation of the cerebellum suggests that language is embodied not only because sensorimotor areas are active, but also because words are processed along a frontal-parietal-temporal network including (cluster 1,2) subcortical activity. An explanation for the distributed character of activity might lie in the distinction between the concepts retrieved from semantic knowledge and the perceptual component of words as hypothesized in Bedny et al. (2008).

The bilateral activity in the temporal lobe, namely the fusiform gyri, suggest that the posterior part of the temporal lobe is an area organizing concepts, rather than visual properties of words, which is in line with findings from Hauk et al. (2004). Also Rüschemeyer and collaborators (2007) highlight the role of the right temporal area processing rather complex verbs with abstract meanings. Although they propose further work on that topic, our work provides supporting results for the implication of temporal areas and conceptualization or categorization.

Only partly reflected in this meta-analysis are the two proposals of embodied cognition theories, namely the somatotopic activation during the processing of action words and sentences, as well as the grounding of abstract concepts in the sensorimotor system. Neither has been investigated per se, as the number of included studies did not allow for a differential contrast between different effectors.

Concluding Remarks

This short review was conceptualized to give an overview along the lines of argumentation in the ongoing debate on the embodiment of language. We further employed an ALE meta-analysis to illustrate and relate previous findings.

Both the narrative review, and the meta-analysis confirm the connection of language and motor areas. Primary motor, supplementary motor and premotor cortices are repeatedly reported to be active during language processing, and they are significantly present in the ALE results.

If the hypothesis held true that the same neural units are responsible for action and simulation of action during language processing, classical characteristics of motor activation should be shared by language comprehension. Namely, language should produce the same somatotopy in activation as real action does. There is growing evidence supporting this view, especially for premotor areas. However, there is not enough data to validate this claim in a meta-analysis, which could theoretically be of immense help clarifying this issue.

The idea, that the mirror neuron system plays an important role in the embodiment of language, is backed by a variety of findings in recent publications. Additionally, a set of peak points in the meta-analysis are very close to the locations reported for the mirror neuron system (Buccino et al., 2001; 2005). However, the strong claim of embodied theories, that mirror neurons represent the neural basis of the simulation activated during language comprehension, needs further thorough investigation. A region of interest in this can be Broca's region, as this seems to have a core role in the integration of motion and sound.

The claim of embodied theories is the grounding of abstract language in sensorimotor areas. Currently the findings on abstract words and sentence processing provide inconsistent results which are possibly due to the varieties in the definition of abstractness, but also to the variety of stimuli used in control conditions. Although our meta-analysis is not able to further enlighten this debate, the regions identified would be well suitable as regions of interest for further analyses on the processing of abstract language.

The strongest results in all lines of argumentation are provided by the findings from patients and timing, both of which argue in favour of a necessary instead of an auxiliary role of sensorimotor areas in language processing.

This very fast activation, its automaticity, taken together with the likely somatotopic organization render the hypothesis advanced among others by Mahon and Caramazza (2008), that information is first transduced in an abstract format and then influences the motor system rather unlikely. The hypothesis that the motor system is activated in a direct and straightforward way is much more plausible and economical, even if evidence on timing and somatotopy still leave some unsolved issues.

Finally, it should be noted that the discussion on embodiment should take into account in a sufficient way the strong plasticity and distributed character of the human brain. Consider some of the results we discussed. Even if abstract words are not represented in the same motor areas as concrete words, this would not necessarily be a problem. For example, it is possible that abstract words, due to the fact that they do not have a concrete referent, activate more language areas (for a discussion, see Borghi & Cimatti, **2009;** submitted). Even if the activation during language processing pertains the pre-motor cortices and not the motor ones, this would not undermine the embodied hypotheses. If we found that the activation of explicit imagery differs from that elicited by language comprehension, this result would even strengthen the embodied hypothesis. If some patients preserve their ability to comprehend language despite their motor disabilities, as it might happen with apractic patients, this might suggest that the brain is distributed and plastic enough.

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Legends to Figure and Tables

Figure 1

ALE results of the meta-analysis. Images display maximum ALE-values thresholded at p<0.01 (FDR corrected).

Left column displays 3D surface renderings from posterior-left, left, frontal, and right viewpoints. Lightbox images illustrate sections at x,y,z= -38, -42, -20, x,y,z= -38, 10, 26, x,y,z= -4, 5, 56, and x, y, z= 42, -16, 36 (from top to bottom).

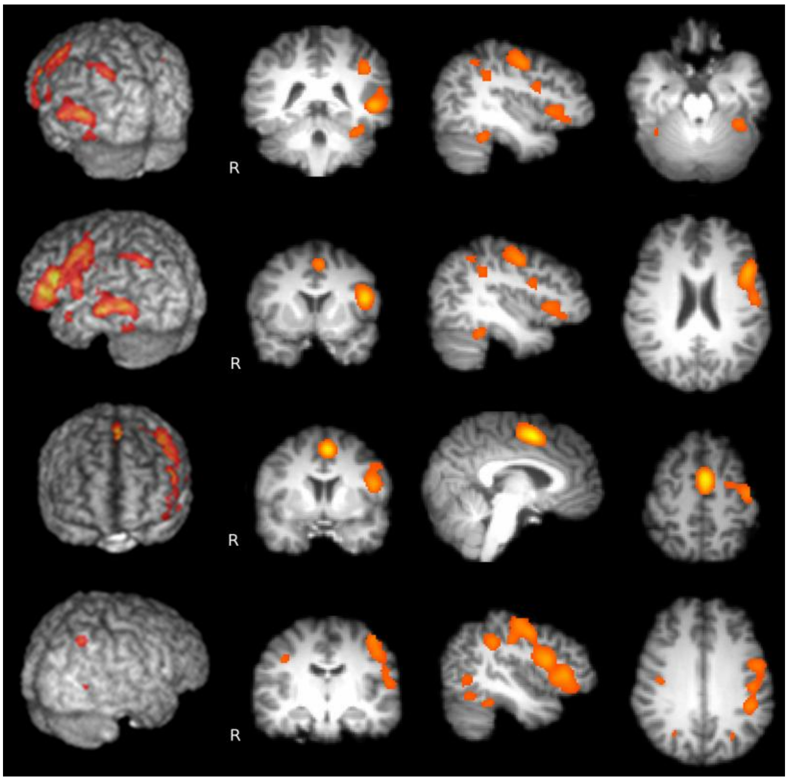

Table 1

Publications included in the meta-analysis, task they employed, number of subjects that were investigated and number of selected foci for the ALE meta-analysis.

Study	**task**	**N**	**Foci**
Bedny et al., 2008	action verb comprehension	12	6
Boulenger et al., 2008	arm- and leg-related action verbs	18	43
Canessa et al., 2007	semantic decisions on picture pairs of (non-)manipulable objects (e.g. tools)	15	35
Gennari et al., 2007	nouns (objects), verbs (action)	17	5
Gronau et al., 2008	classification of real (e.g. tools) and nonense objects (e.g.artificial shapes)	20	48
Hauk et al., 2004	arm- and leg-relates action words	14	15
Kemmerer et al., 2008	hand-and leg-related action verbs	16	45
Liljeström et al., 2007	action-/ object-naming , verbs or nouns	15	62
Meister & Iacoboni, 2007	responses on hand manipulation and phonological word decisions	14	25
Postle, 2008	hand- and foot- related action verbs	18	6
Raposo et al., 2008	arm-and leg-related action verbs	22	5
Rüschemeyer, 2009	lexical decision between functional and	15	5

	volumetric manipulability (by hand)		
Rüschemeyer, 2009	Go/NoGo tasks to words stimuli	19	7
Rüschemeyer, 2007	motor- and abstract verbs/wordstems	20	19
Saccuman et al., 2006	action- and object naming (verbs,nouns),hand- and leg-related	13	25
Siri et al., 2008	action- and object naming (verbs,nouns)	12	6
Tremblay & Gracco, 2006	word reading and generation from semantic categories	12	18
Tettamanti, 2005	hand- and foot related sentences	17	14
Tettamanti, 2008	action-related and abstract sentences, supplemental data to Tettamanti, 2005	18	10
Tomasino, 2007	motor and non-motor verbs, hand related	15	29
Willems, 2009	word decision on concrete hand actions	20	40

Table 2

Results from the ALE meta-analysis. Clusters of activation connected above threshold, activation sites, Talairach-Coordinates (x,y,z) of maximum ALE-value, and maximum ALE-value of this cluster.

Cluster	Area	X	Y	Z	Cluster size	ALE_{MAX}
1	L. Inferior Frontal Gyrus (BA 44)	-46	12	20	32144	0.0310
	L. Inferior Frontal Gyrus (BA 45)	-46	26	8		0.0239
	L. Precentral Gyrus (BA 6)	-40	-6	48		0.0199
	L. Supramarginal Gyrus (BA 40)	-44	-38	36		0.0187
	L. Postcentral (BA 3)	-46	-20	40		0.0186
	L. Precuneus (BA 19)	-28	-66	42		0.0168
	L. Precentral Gyrus (BA 4)	-52	-10	24		0.0165
	L. Insula (BA13)	-32	22	4		0.0148
	L. Middle Frontal Gyrus (BA 6)	-26	-6	58		0.0127
2	L. Middle Temporal Gyrus (BA 22)	-52	-40	2	8856	0.0268
	L. Middle Temporal Gyrus (BA 39)	-50	-58	6		0.0204
	L. Insula (BA 13)	-54	-32	18		0.0120
3	L Medial Frontal Gyrus (BA 6)	-4	0	54	5760	0.0341
4	L. Cerebellum Anterior Lobe	-36	-42	-22	1224	0.0515

5	R. Superior Parietal Lobe (BA 7)	26	-64	42	1072	0.0165
6	L. Posterior Cingulate (BA 30)	-20	-62	4	848	0.0145
7	L. Middle Temporal Gyrus (BA 30)	-52	-4	-10	816	0.0162
8	L Fusiform Gyrus (BA 37)	-46	-56	-14	736	0.0143
9	R. Precentral Gyrus (BA 4)	40	-16	36	312	0.0140
10	R. Fusiform Gyrus (BA 37)	38	-48	-18	136	0.0112
11	R. Posterior Cingulate (BA 30)	16	-64	10	136	0.0123