

Semantic domain-specific functional integration for action-related vs. abstract concepts

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ABSTRACT

A central topic in cognitive neuroscience concerns the representation of concepts and the specific neural mechanisms that mediate conceptual knowledge. Recently proposed modal theories assert that concepts are grounded on the integration of multimodal, distributed representations. The aim of the present work is to complement the available neuropsychological and neuroimaging evidence suggesting partially segregated anatomo-functional correlates for concrete vs. abstract concepts, by directly testing the semantic domain-specific patterns of functional integration between language and modal semantic brain regions. We report evidence from a functional Magnetic Resonance Imaging study, in which healthy participants listened to sentences with either an action-related (actions involving physical entities) or an abstract (no physical entities involved) content. We measured functional integration using Dynamic Causal Modeling, and found that the left superior temporal gyrus was more strongly connected: 1) for action-related vs. abstract sentences, with the left-hemispheric action representation system, including sensorimotor areas; 2) for abstract vs. action-related sentences, with left infero-ventral frontal, temporal, and retrosplenial cingulate areas. A selective directionality effect was observed, with causal modulatory effects exerted by perisylvian language regions on peripheral modal areas, and not vice versa. The observed condition-specific modulatory effects are consistent with embodied and situated language processing theories, and indicate that linguistic areas promote a semantic content-specific reactivation of modal simulations by top-down mechanisms.

INTRODUCTION

The debate on the nature of concepts has been feeding philosophic discussion for centuries, mainly focusing on the ontological status of concepts and on the well-known referential problem. In cognitive neuroscience, in turn, the debate hinges on the specific structure, format, and content of concepts. Two main types of theories about conceptual knowledge have been proposed. The so called amodal theories claim that knowledge is represented in semantic memory by amodal and arbitrary symbols governed by syntactic combinatorial rules (e.g. Fodor, 1975; Newell & Simon, 1972; Pylyshyn, 1984). According to this view, all concepts are symbolic and abstract and are represented in systems separated from the modal neural systems underlying perception and action. However, there is little empirical evidence supporting amodal theories (Machery, 2007). An unresolved challenge for this type of hypothesis is specifying where amodal symbols are stored in the brain and whether the proposed neural representations are compatible with neural principles of computation (Barsalou, 1999; 2008; Pulvermüller, 1999). An alternative point of view is represented by modal theories asserting that concepts are grounded on multiple, distributed representations. Some of these theories focus on simulation, such as the perceptual symbol system proposed by Barsalou (1999); others focus on situated action (Glenberg & Robertson, 2000; Glenberg & Kaschak, 2002) or on bodily states (Gallese & Lakoff 2005; Gallese, 2007). Within modal theories, concepts are interpreted as the mental simulation of specific things or events, i.e. implicit and automatic concept-driven reactivations of the very same schematic simulations engaged during primary processes (Barsalou, 1999; 2008; Barsalou, Kyle Simmons, Barbey & Wilson, 2003). Evidence from neuropsychology and functional neuroimaging show that information about the relevant features of an object – such as visual, auditory, and olfactory, the manner in which it moves, and its name – is partially stored in the same sensory and motor systems activated during the acquisition of that information (Boronat et al., 2005;

Gainotti, 2004; Gonzalez et al., 2006; Martin, 2007; Patterson, Nestor & Rogers, 2007; Perani et al., 1995; Simmons, Martin & Barsalou, 2005).

At a purely theoretical level, a theory about conceptual knowledge can only be considered valid if it is able to account for the processing of virtually any kind of concepts. An important implication of modal theories is that they take into account both concrete and abstract meanings, and therefore possess a degree of explanatory power comparable to amodal theories. Perceptual and motor simulations are thought to mediate the representation of concrete concepts and words. Abstract concepts are thought to be represented via simulation of internal states and/or simulation of factual and contextual situations (Barsalou, 1999; 2008; Barsalou & Wiemer-Hastings, 2005). Here we propose to test modal vs. amodal theories by using the concrete vs. abstract distinction as a paradigmatic model.

Convergent evidence from behavioral, physiological and neuroimaging studies have demonstrated the role of perceptual simulations (Gonzalez et al., 2006; Kaschak et al., 2005; Kaschak, Zwaan, Aveyard & Yaxley, 2006; Meteyard, Bahrami & Vigliocco, 2007; Pulvermueller & Hauk, 2006) and of motor simulations (see Pulvermueller, 2005 for a review) in processing the concrete content of linguistic utterances. For example, Tettamanti and colleagues (2005) showed in a fMRI study that listening to sentences describing actions performed with different body parts (mouth, hand, or leg) activates a left fronto-parieto-temporal circuit with somatotopic organization in the premotor cortex. This evidence, together with results obtained in similar experiments on action words (Hauk, Johnsrude & Pulvermueller, 2004) and action-related phrases (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006), indicates that the somatotopic activation of motor circuits reflects some aspects of linguistic meaning. However, due to its poor temporal resolution, fMRI does not permit to determine whether the processing of action-related items immediately activates motor circuits – during lexical processing – or if these activations are

elicited by subsidiary processes, such as imagining the actions verbally described. Neurophysiological techniques with high temporal resolution offer a source of complementary evidence. Early and automatic involvement of motor areas was demonstrated not only for the recognition of action-related sounds (Hauk, Shtyrov, Pulvermueller, 2006) but also for the processing of action-related words. The results of ERPs experiments on silent reading of face-, hand-, leg-related words, showing category-specific activations at 200ms after words onset, indicate that the processing of action words immediately triggers the activation of action-related neural networks (Hauk & Pulvermueller, 2004; Pulvermueller, Harle & Hummel, 2000). Similar results were obtained in an EEG study on action words (Shtyrov, Hauk & Pulvermueller, 2004) and in a MEG study investigating the time course of cortical activity during action-related word processing (Pulvermueller, Shtyrov & Ilmoniemi, 2005). Behavioral measures have shown interaction effects between linguistic and motor-perception tasks, supporting the claim that the same mechanisms involved in the perception of events or in action execution are used during the comprehension of language describing the corresponding events or actions. This involvement was interpreted as a necessary requisite to understand language (Boulenger et al., 2006; Buccino et al., 2005; Kaschak et al., 2005; Sato, Mengarelli, Riggio, Gallese & Buccino, 2008). The results of TMS studies show a specific influence on motor system activity in response to action-related word processing (Buccino et al., 2005; Pulvermueller, Hauk, Nikulin & Ilmoniemi, 2005). In sum, these results indicate that action simulation is specific, automatic and presents temporal dynamics compatible with its role in language comprehension. These data suggest the existence of shared neural substrates for action and language. A plausible hypothesis is that the mirror-neuron system (premotor and parietal brain regions that respond both to action execution and observation) represents the key neural substrate for action-related language processing (Aziz-Zadeh et al., 2006; Gallese & Lakoff, 2005; Gallese, 2007; Rizzolatti & Craighero,

2004).

While there is a growing body of literature on the neural mechanisms underlying the representation of concrete concepts, there is presently little evidence about the neural mechanisms underlying the perceptual simulation of internal states, such as emotions, and the simulation of factual and contextual information. As proposed by Barsalou (1999; 2008; Barsalou & Wiemer-Hastings, 2005), this type of simulation could provide much of the semantic representations that are central to abstract concepts. Some tentative lines of support to this perspective came from two fMRI studies that investigated the auditory processing of action-related and abstract sentences (Tettamanti et al., 2005; Tettamanti et al., 2008). In the former study (Tettamanti et al., 2005) – discussed above with respect to action-related sentences – sentences with an abstract content, such as “I appreciate sincerity”, activated the retrosplenial cingulate cortex. A similar finding was previously reported by Tyler, Russell, Fadili and Moss (2001). This result was subsequently replicated by a study (Tettamanti et al., 2008), consisting in a factorial combination of concreteness and polarity (i.e. affirmative or negative sentences with either an action-related or an abstract content). The main effect of concreteness, irrespective of the level of polarity, again revealed a higher BOLD signal in the retrosplenial cingulate cortex for the processing of abstract vs. action-related sentences. Advances in the experimental design and in the methods of fMRI data analysis in the second study compared to the first study, allowed us to conclude that the higher BOLD signal in the retrosplenial cingulate cortex for abstract sentences was actually due to a stronger deactivation by action-related than by abstract sentences (Tettamanti et al., 2008). The observation of a relative deactivation in the retrosplenial cingulate cortex prompted a possible interpretation of the findings. The retrosplenial cingulate cortex is a component of the default mode brain system, a system that gathers information about the world around and within us, and that becomes deactivated during goal-directed actions (Greicius & Menon, 2004; Gusnard & Raichle,

2001; McKiernan, Kaufman, Kucera-Thompson & Binder, 2003; Raichle et al., 2001). A relative absence of goal-directed action plans may be associated to abstract vs. action-related sentences, explaining why abstract sentences deactivated the retrosplenial cingulate cortex less than action-related sentences. In addition to its association with introspective/proprioceptive functions, a distinct line of evidence suggests that the retrosplenial cingulate cortex may hold abstract representations of contextual information (Bar & Aminoff, 2003; Canessa et al., 2008; Simmons, Hamann, Harenski, Hu & Barsalou, 2008). Context representations may be crucial for the simulation of affective and introspective states, as expressed by abstract sentences. In sum, these studies highlighted the importance of the retrosplenial cingulate cortex for the processing of abstract sentences, in relation to introspective state monitoring and contextual representations.

A specific prediction of embodied language theories is that language comprehension is mediated by the fast and automatic cross-talk between speech parsing networks, extracting phonological, morphological, syntactic and semantic information, and modal representations (Barsalou, 1999; Glenberg & Kaschak, 2002). If this view is correct, measures of functional integration (Friston, Harrison & Penny, 2003; Lee, Friston & Horwitz, 2006), such as Dynamic Causal Modeling (DCM), should reveal modulations of this cross-talk that are dependent on the semantic content expressed by linguistic utterances. The aim of the present study was to verify this hypothesis, by testing with DCM whether left-hemispheric auditory language processing regions displayed a relatively stronger coupling with the left fronto-parieto-temporal action representation system when processing action-related sentences, and a relatively stronger coupling with retrosplenial areas coding for abstractness and contextual information when processing abstract sentences. To this aim, we re-analyzed the data of our fMRI study (Tettamanti et al., 2008), using DCM to define two dynamic causal models linking perisylvian regions, in the first

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case with the left action representation system (Action-DCM), and in the second case with the retrosplenial cingulate cortex (Abstract-DCM).

MATERIALS AND METHODS

Subjects

Eighteen right-handed volunteer subjects (12 females, mean age 24.7 years, range 20-34 years), matched on education level (range 14-18 years of education), took part in the experiment. Participants were all native monolingual speakers of Italian, with no history of neurological or psychiatric disorders and no structural brain abnormalities. They gave written consent to participate in the study after receiving an explanation of the procedures. The study was approved by the Ethics Committee of the San Raffaele Scientific Institute, Milano, Italy. As outlined below in more details (see the “Dynamic Causal Modeling” section), the data of 3 subjects were excluded, as they did not meet the required criteria for the DCM analysis.

Stimuli and experimental design

Comprehensive details on the experimental procedures can be found in Tettamanti and colleagues (2008). Here, we provide details relevant to the present data reanalysis, hinging on the concreteness factor (Action vs. Abstract). Stimuli consisted of 60 action-related sentences (e.g. “Adesso io premo il bottone”, “Now I push_{first person singular (1ps)} the button”) and 60 abstract sentences (e.g. “Ora io apprezzo la fedeltà”, “Now I appreciate_{1ps} the loyalty”). Sentences began with an adverb followed by a transitive verb in the first person singular, and a syntactically and semantically congruent object complement. Both transitive verbs and object complements had a univocal action-related (Action sentences) or abstract (Abstract sentences) meaning. Semantic ambiguities were carefully avoided. Each sentence was presented twice to all subjects, with minimal variations reflecting a second factor not considered in the present reanalysis (i.e. polarity: affirmative vs. negative). Thus, all subjects were presented with 120 Action sentences and with 120

Abstract sentences.

The frequency of adverbs, verbs, and object complements were balanced between the Action and Abstract conditions, based on frequency norms of Italian (De Mauro, Mancini, Vedovelli & Voghera, 1993). We also balanced the total number of syllables for each sentence between the Action and Abstract conditions. The choice of stimuli was based on a norm for comprehensibility on 20 normal adults, to avoid interference with lexical difficulty. Sentences were digitally recorded by a native Italian speaker. Average sentence length was 2293 ms (st. dev. 192 ms), (Action: 2314 ms (st. dev. 190 ms); Abstract: 2272 ms (st. dev. 192 ms)). Sentence duration was not significantly different between Action and Abstract sentences (Two sample t-Student, $P=0.09$). A varying period of silence was added to the end of each sentence, so that the global stimulus duration was 4000 ms for all sentences. Subjects heard all auditory stimuli via MRI-compatible headphones connected to a personal computer. Stimuli were presented with Presentation 9.90 (Neurobehavioral Systems, Albany, CA, USA) in 9 separate sessions (26/27 stimuli each) in pseudo-randomized order. The number of sentences of each condition was counter-balanced across sessions. Sentences were presented in an event-related mode. Within sessions, sentences were spaced by variable interstimulus intervals, i.e. 1873 ms, 3558 ms, and 4964 ms (randomly ordered, in the proportion 4:2:1). Intervals of varying durations were used to maximise haemodynamic signal sensitivity (Dale, 1999).

The participants were instructed to listen to the auditorily presented sentences with maximal attention to the meaning of each sentence. The task did not require on-line responses. Once the fMRI data acquisition was completed, the participants were submitted to an informal interview on the experimental stimuli. All participants reported of being unaware of the grouping of sentences into the Action vs. Abstract condition.

fMRI data acquisition

MRI scans were acquired on a 3T Intera Philips body scanner (Philips Medical Systems, Best, NL) using an 8 channels-sense head coil (sense reduction factor = 2). Whole-brain functional images were obtained with an echo-planar T2*-weighted gradient-echo, echo-planar sequence, using blood-oxygenation-level-dependent contrast. Functional image comprised 30 contiguous axial slices (4 mm thick), acquired in interleaved mode, and with a repetition time of 2100 ms (TE: 30 ms; FOV: 240 mm x 240 mm; matrix: 128 x 128). Each participant underwent 9 functional scanning sessions. The duration of each session was 136 scans, preceded by 10 dummy scans that were discarded prior to data analysis.

For anatomical localization and visualization of brain activations, we acquired 2 high-resolution whole-brain structural T1 weighted scans (resolution 1mm x 1mm x 1mm) of each participant. The normalized structural images of all participants were then averaged in one single image. This average structural image was automatically segmented with Caret 5.4 to obtain a cortical surface reconstruction with tissue specific image values for sulcal vs. gyral cortex (Van Essen et al., 2001). Caret 5.4 was also used to map brain activations obtained with SPM2 onto cortical surface maps.

Image pre-processing

Statistical parametric mapping (SPM2, Wellcome Department of Imaging Neuroscience, London, UK) was used for slice timing, image realignment and unwarping (Andersson, Hutton, Ashburner, Turner & Friston, 2001), normalization to the Montreal Neurological Institute (MNI) standard space, smoothing by a 6 mm FWHM Gaussian kernel, and General Linear Model statistical analysis (Friston et al., 2002).

Dynamic Causal Modeling

A complementary but independent approach to the investigation of functional

specialization is the analysis of functional integration, by means of methods which estimate effective connectivity, i.e. causal coupling of brain areas and the modulatory influence of experimental manipulations on the strength of that coupling. One of these methods is DCM, which derives connectivity parameters for the direct driving influence of the experimental conditions on brain states, for the strength of intrinsic connections between brain areas independently of the experimental conditions, and for the modulations of connectivity strength that reflect changes in the coupling between areas induced by experimental conditions (Friston et al., 2003). Within DCM, the brain is regarded as a dynamic input-state-output system, in which the input is represented by experimentally controlled perturbations, the neuronal states are hidden variables representing an index of neuronal population activity in each region, and the outputs are the measured regional haemodynamic responses. DCM parameters are estimated within a Bayesian framework, with an iterative expectation-maximisation (EM) algorithm that takes into account the temporal and inter-regional covariances (Friston et al., 2003). DCM is not an exploratory technique, but rather a confirmatory technique that relies on a priori hypotheses, based on independent evidence, to infer inter-regional causality effects. Such evidence may inform the choice of brain regions included in the dynamic causal model, the hypothesized anatomical and/or functional connections between these regions, and the direction of the inter-regional effects.

Here we used DCM (Friston et al., 2003), as implemented in SPM5 (Wellcome Department of Imaging Neuroscience, London, UK), to test the hypothesis that left-hemispheric auditory language processing regions, including the superior temporal gyrus, showed a positive increase of coupling with distinct modal semantic brain networks, reflecting the semantic content of the stimuli. For Action sentences, we expected a relatively stronger coupling with the left-hemispheric action representation system; for Abstract sentences, we expected relatively stronger coupling with semantic regions coding

for abstractness and contextual information.

In order to assess these condition-specific modulations, we specified two dynamic causal models that were characterized by a common auditory input brain region, namely the left anterior superior temporal gyrus (LSTG), but differed with respect to the other regions included in the systems: 1) Action-DCM was used to test the hypothesis of a stronger coupling within the left-hemispheric fronto-parieto-temporal system for Action vs. Abstract, and included the *pars triangularis* of the inferior frontal gyrus (LIFG-PT), the dorsal precentral gyrus (LdPCG), the supramarginal gyrus (LSMG), and the posterior inferior temporal gyrus (LpITG); 2) Abstract-DCM was used to test the hypothesis of a stronger coupling within semantic regions coding for abstractness and contextual information for Abstract vs. Action, and included the *pars orbitalis* of the left inferior frontal gyrus (LIFG-PB), the left middle temporal gyrus (LMTG), the left anterior inferior temporal gyrus (LaITG), and the bilateral retrosplenial cingulate cortex (LRpCC).

Definition of volumes of interest

First, we defined for each participant a General Linear Model that was specifically designed to encompass the requirements of the intended DCM analysis. The time series of each participant were high-pass filtered at 67 s and pre-whitened by means of an autoregressive model AR(1). Evoked responses were modeled with the canonical haemodynamic response function, time-locked to the onset of auditory sentence presentation. We modeled the 9 functional scanning sessions as one single concatenated session and we included 9 additional constant regressors, each with values of 1 for the scans of one session and 0 for the other scans, to account for the separate functional scanning sessions. Global normalization was included to reduce spike amplitude corresponding to transitions between sessions in the concatenated time series. The model included a separate regressor representing all stimuli of all conditions (ALL) and additional

regressors for Action and Abstract stimuli considered separately. For each participant, we computed three t-Student contrasts: 1) main effect of all conditions (Action + Abstract); 2) Action > Abstract; 3) Abstract > Action. These contrasts were used to identify subject-specific volumes of interest from the brain regions included in the two dynamic causal models. Contrast 1 was used to identify the LSTG input region for both dynamic causal models. Contrast 2 was used to identify the four brain regions constituting the left-hemispheric fronto-parieto-temporal system, namely LIFG-PT, LdPCG, LSMG, and LpITG. Contrast 3 was used to identify the brain regions coding for abstractness and contextual information, namely LIFG-PB, LMTG, LaITG, and LRpCC.

Subject-specific volumes of interest were defined through a small volume correction procedure: the stereotactic coordinates of the group-level activations in the standard GLM analysis (Table 1) were chosen as the center of spherical volumes for small volume correction ($P < 0.05$). The radius of the spherical correction was enlarged step-wise from 6 to 12 to 20 mm, until a significant subject-specific coordinate was found. Subject-specific coordinates identified through this procedure were excluded if they did not correspond to the same anatomical location represented by group-level coordinates. Three subjects were excluded from the DCM analysis because one or several brain regions of interest were not significantly activated at the specified threshold. Consequently, the DCM analysis included the data of 15 out of 18 participants. We then extracted the first eigenvector signal from spherical volumes of interest of 6-mm radius centered on the identified subject-specific coordinates. This signal was adjusted for all effects of interest, such that it was not biased toward any particular experimental conditions, but instead included the information relative to the stimuli of both conditions as represented by the ALL regressor.

First-level model specification

We adopted a two-stage random-effects approach for the DCM analysis. At the

single-subject level, we implemented Action-DCM and Abstract-DCM to assess the degree of stimulus-bound activity conveyed from the LSTG to other regions for each experimental condition. In both Action-DCM and Abstract-DCM, the ALL regressor provided direct input to LSTG. The resulting perturbation was then allowed to propagate throughout the network via interconnections between LSTG and the remaining regions of the two systems (Figure 2). For Action-DCM, the specified connections were chosen based on known neuroanatomical and functional connectivity (Petrides & Pandya, 2008; Rizzolatti & Craighero, 2004), and were as follows (\rightarrow : unidirectional; \leftrightarrow : bidirectional): LSTG \rightarrow LIFG-PT; LSTG \rightarrow LpITG; LIFG-PT \leftrightarrow LdPCG; LIFG-PT \leftrightarrow LSMG; LIFG-PT \leftrightarrow LpITG; LdPCG \leftrightarrow LSMG; LSMG \leftrightarrow LpITG. For Abstract-DCM, we adopted a fully connected and modulated model, with the exception of the two connections departing from the LSTG: LSTG \rightarrow LIFG-PB; LSTG \rightarrow LpMTG; LIFG-PB \leftrightarrow LaITG; LIFG-PB \leftrightarrow LpMTG; LIFG-PB \leftrightarrow LpCC; LaITG \leftrightarrow LpMTG; LaITG \leftrightarrow LpCC; LpMTG \leftrightarrow LpCC. In both models, all connections in the system were allowed to be modulated separately by each condition (i.e., Action vs. Abstract).

Second-level group analysis

At the second-level, the SPM5-DCM average function was used to obtain fixed-effects group-level parameters, i.e. average Bayesian weighted connection strengths and Bayesian posterior probabilities, for both dynamic causal models. We report Bayesian weighted connection strengths (Hz) and posterior probabilities for the direct effects on the input region and for the intrinsic connections. For both models and for each connection, we also computed a two-tailed Action vs. Abstract contrast for the condition-specific modulatory effects, and obtained the corresponding posterior densities.

We also performed classical statistical analyses outside SPM –corresponding to

second-level random-effects analyses – on the arithmetic (non-Bayesian) means of the first-level intrinsic and modulatory connection-strengths of both Action-DCM and Abstract-DCM. For both the intrinsic and modulatory connection strengths, we first used a Shapiro-Wilk normality test to check the normality of the distribution of the values pertaining to each connection. Given a high proportion of connection strength values with a non-normal distribution, we then applied throughout non-parametric paired tests of means (Wilcoxon signed-rank). For the intrinsic connections, we tested the alternative hypothesis that each connection strength was significantly greater than zero. For the modulatory effects, we directly compared the two conditions, by testing the alternative hypothesis of a stronger effect for Action vs. Abstract (within Action-DCM), and vice versa (within Abstract-DCM). We also tested, for each condition taken alone, the alternative hypothesis that each connection strength was significantly greater than zero. To account for the number of tested connections (12 connections in Action-DCM and 14 connections in Abstract-DCM), we calculated False Discovery Rate (FDR) (Benjamini & Hochberg, 1995) corrected alpha values (Tables 2, 3).

In order to increase confidence in the reported results, we only discuss intrinsic and modulatory effects that survived both a fixed-effects $P > 0.95$ posterior probability/density threshold, and a random-effects $P < 0.05$ (FDR corrected) significance threshold (see Stephan et al., 2007).

RESULTS

Based on the anatomical distribution of the condition-specific activations for Action vs. Abstract identified by a standard General Linear Model analysis (Table 1, Figure 1), we specified two distinct dynamic causal models, one representing the left-hemispheric action representation system (Action-DCM), and one representing a system for the representation of abstract concepts (Abstract-DCM). For both models, the DCM analysis allowed us to assess the condition-independent intrinsic connection strengths between the areas included in the connectivity systems, which can be interpreted as a measure of baseline-state functional integration. Most importantly, DCM allowed us to assess the condition-specific modulatory effects upon these connections, i.e. increases of functional coupling between the brain regions for the two experimental conditions.

For Action-DCM, the intrinsic, condition-independent connection strengths (Table 2A) were of significant magnitude for all connections included in the system (thin, solid arrows in Figure 2a), with the exception of the connection from LSTG to LpITG (thin, dashed arrow in Figure 2a). For Abstract-DCM, we also found significant intrinsic connection strength values for most connections included in the system (Table 2B), but five connections did not reach the significance level either in the random-effects and/or in the Bayesian fixed-effects group analysis (thin, dashed arrows in Figure 2b). Significant intrinsic connection strengths (thin, solid arrows in Figure 2b) were found from LSTG to LpMTG, from LpMTG to LaITG, from LpMTG to LIFG-PB and backward, from LaITG to LIFG-PB and backward, from LaITG to LRpCC, and from LRpCC to both LpMTG and LIFG-PB.

As for the condition-specific modulatory effects, for Action-DCM we found, by directly comparing the two conditions, that in 5 out of 12 connections there were stronger modulatory effects for Action vs. Abstract, both in the random-effects and in the Bayesian fixed-effect group analyses (Table 3A and Figure 2c). These connections were from LSTG

to both LIFG-PT and LpITG, and, crucially, from LIFG-PT to all the other three brain regions of the action representation system, i.e. LdPCG, LSMG, and LpITG. Vice versa, the three backward connections from LdPCG, LSMG, and LpITG to LIFG-PT did not show any condition-specific modulatory effects. This suggests a strictly top-down, as opposed to bottom-up, causal modulation exerted by LIFG-PT onto the three action-related semantic regions. No significant modulatory effects were found in the reciprocal connections between LdPCG, LSMG, and LpITG, in either directions. No connections within Action-DCM showed a stronger increase of coupling for Abstract vs. Action.

The significant modulatory differences in five connections of Action-DCM may in principle be attributed to: either i) an increase of functional coupling for Action vs. Abstract; or ii) a relative decrease of functional coupling for Abstract vs. Action. In order to discriminate between these two possibilities, we tested, for each condition taken alone, whether each connection strength was significantly greater or less than zero. For Action, the mean connection strength values were significantly greater than zero, indicating an increase of functional integration (see Table 3A, significant effects marked by §). For Abstract, all values were negative, with the values of the two connections from LSTG to LIFG-PT and to LpITG that were significantly less than zero, suggesting a functional decoupling (Table 3A).

Notably, in the remaining 7 out of 12 connections of Action-DCM in which the modulatory effects did not differ between the two experimental conditions, the mean connection strength values were not significantly different from zero for either Action or Abstract. This reinforces the view that the modulatory effects within Action-DCM were driven by a selective increase of functional coupling in a subset of connections in the context of action-related sentence processing.

For Abstract-DCM, in turn, we found, by directly comparing the two conditions, that in 6 out of 14 connections there were stronger modulatory effects when processing Abstract

than when processing Action sentences (Table 3B and Figure 2d). These connections were from LSTG to LpMTG, from LaITG to LpMTG, from LpMTG to LIFG-PB, and, crucially, all connections projecting to LRpCC, i.e. LIFG-PB to LRpCC, LaITG to LRpCC, and LpMTG to LRpCC. Vice versa, the three connections projecting back from LRpCC to LIFG-PB, LaITG, and LpMTG did not show any condition-specific modulatory effects. By analogy to the result obtained for Action-DCM, this suggests a top-down causal modulation exerted by perisylvian areas on peripheral modal areas. No connections within Abstract-DCM showed stronger modulatory effects for Action vs. Abstract.

In order to discriminate between either i) relative increases of functional coupling for Abstract vs. Action; or ii) relative decreases for Action vs. Abstract, we tested, for each condition taken alone, whether each connection strength was significantly greater or less than zero. The six Abstract-DCM connections with significantly different modulatory effects for Action vs Abstract presented, for the Abstract condition, mean connection strength values that were significantly greater than zero, and, for the Action condition, negative values that did not differ significantly from zero (Table 3B). In the remaining 8 out of 12 connections of Abstract-DCM, which did not present any modulatory differences between the two conditions, the mean strength values for either Abstract or Action did not significantly differ from zero. These results suggest a strictly selective increase of functional integration for the Abstract condition within Abstract-DCM.

In sum, we found a stronger increase of functional integration: 1) within the left-hemispheric action representation system, when processing Action sentences than when processing Abstract sentences; 2) within the system including semantic regions coding for abstractness and contextual information, when processing Abstract sentences. Within both systems, the directionality of causal modulatory effects was selectively from perisylvian language regions onto peripheral modal areas.

DISCUSSION

Models of distributed conceptual and semantic representation imply some compositional operations that link together specific configurations of representational units to produce a particular meaning. This general idea applies to distinct, though complementary, fields of research, including: i) psycholinguistics, where individual words, or lemmas, are assembled from sets of intrinsic parameters, such as thematic roles, syntactic categories, and diacritics (Levelt, 1999); ii) connectionist language accounts, where meaning results from the co-activation of distributed conceptual nodes (Dell, 1986); iii) implicit memory, where conceptual priming occurs based on associations within the semantic network (Hutchison, 2003; Lucas, 2000); iv) cognitive neuropsychology, where concepts are thought to be represented in multiple, distributed brain regions (Barsalou et al., 2003; Pulvermüller, 1999). Conceptual knowledge can be considered as a higher-order system that intervenes in virtually all higher cognitive functions, including memory, language, and thought. A crucial aspect of distributed representation accounts is that conceptual representations are not merely the result of multiple focal activations, each working in isolation, but very much the result of the connections that mediate the integration of the information provided by the contributing foci. Classical functional localization as employed in neuropsychology or neuroimaging studies is of limited usefulness for the falsification of specific theories. The identification of relevant brain regions participating in concept formation, processing, and retrieval needs to be complemented by some measures of the integration processes and information exchanges occurring between these brain regions. Although not strictly reflecting the type of microscopical interactions occurring between representational units, such as for instance synaptic communication between neuronal populations, measures of functional integration such as DCM, may provide an important step forward in clarifying how the activity of a particular brain area is influenced by the activity of other areas under specific experimental

conditions.

The main objective of the present study was to use DCM to test modal theories of distributed conceptual representations, by focusing on the semantic domain-specific modulatory effects exerted on inter-regional connections by the processing of sentences with either an action-related or an abstract content. We specifically postulated that the input activity elicited in LSTG, within the auditory cortex, would propagate: 1) more strongly to the left-hemispheric action representation system for Action vs. Abstract sentences; 2) more strongly to semantic regions coding for abstractness and contextual information for Abstract vs. Action sentences. The results clearly demonstrated a relatively stronger functional coupling between auditory language processing areas and the left action representation system for Action sentences, and a relatively stronger coupling between auditory language processing areas and the retrosplenial cingulate cortex for Abstract sentences. In the following paragraphs, we will first concentrate on the discussion of these two neural systems, and then discuss some general properties regarding the connections between perisylvian language regions and modal areas.

Action-DCM

The analysis of modulatory effects within Action-DCM showed that all modeled areas displayed a synergistic increase of activity specifically for Action vs. Abstract sentences. Action-DCM consists of the LSTG (a region receiving auditory sentence input) and four interconnected left fronto-parietal-temporal areas subserving action representation. Of the twelve modeled modulatory effects representing reciprocal causal influences, five effects were significantly more positive for Action vs. Abstract, and no effects showed the opposite tendency. All five regions included in Action-DCM were involved by at least one significant modulatory effect. In other words, the Action-DCM neural system as a whole was functionally more integrated when processing Action sentences than when processing

Abstract sentences. This type of evidence is directly compatible with the view that the semantic computation of concepts expressed by sentences with a concrete, action-related content is driven by the coupling of perisylvian language areas and modal, perceptuo-motor areas that are engaged during the corresponding primary perceptuo-motor processes. Our results support embodied simulation theories of distributed conceptual representation, and complement the evidence of classical functional localization studies demonstrating the activation of left inferior frontal, premotor, motor, anterior parietal, and posterior temporal areas in action-related word/sentence processing (see Pulvermueller, 2005, for a review). Measures of functional and effective connectivity have been previously applied by a limited number of studies on the semantic processing of concrete, action-related words. In an fMRI study on semantic verbal fluency, Vitali and colleagues (2005) asked subjects to generate nouns, alternating between tools and animals. Psychophysiological interaction analysis and structural equation modeling were used to assess category-specific increases of functional integration during lexical retrieval. Both connectivity measures demonstrated stronger activation coupling in left inferior frontal, premotor, anterior parietal, and posterior occipito-temporal areas for tools vs. animals. Noppeney, Price, Penny and Friston (2006) performed an fMRI study on category-specific responses for tools vs. animals that was characterized by the manipulation of stimulus modality (pictures vs. words) and semantic task (implicit: judgment on word form; vs. explicit: judgment on meaning). Using DCM, the authors showed that the tool-category-specific functional integration was characterized by modality-driven modulation of forward connections from the occipital cortex to the fusiform gyrus and to the anterior parietal cortex, and by task-driven modulation increases from the left inferior frontal gyrus to the anterior parietal cortex and to the fusiform gyrus. Finally, Mahon and colleagues (2007), found functional connectivity interactions between the left fusiform gyrus and both the left posterior middle temporal gyrus and the left inferior parietal lobule that were specific for

the processing of pictures representing tools. Altogether, these studies and the present study converge in showing that the processing of action-related concepts implies a functional cross-talk between modal brain regions involved in perceptuo-motor action representation.

Abstract-DCM

The results of the analysis on the model specific for Abstract sentences, Abstract-DCM, are also in agreement with our predictions. Within Abstract-DCM, the induced auditory perturbation in LSTG was allowed to propagate to four other fully inter-connected areas, namely LIFG-PB, LaITG, LpMTG, and LRpCC. Of the fourteen modeled modulatory connections, six connections presented a stronger causal coupling for Abstract vs. Action, and no effects showed the opposite tendency. All five regions included in Abstract-DCM were involved by at least one significant modulatory effect. In particular, all three regions projecting to LRpCC, i.e. LIFG-PB, LaITG, and LpMTG positively modulated the activity of the retrosplenial cingulate cortex (LRpCC). Although predicted based on evidence from previous studies (Tettamanti et al., 2005; 2008), this remains, to the best of our knowledge, a largely novel finding. Conclusive remarks are therefore difficult to draw. In what follows, we will attempt to situate the Abstract-DCM findings within the available psycholinguistic and neuroimaging literature on abstract words/concepts.

Abstract words are cognitively more difficult than concrete words: more difficult to learn, to understand, to remember, and to define, as shown by a series of classical studies. Normal adult subjects process words representing abstract concepts more slowly and less accurately than words representing concrete concepts (Binder, Westbury, McKiernan, Possing & Medler, 2005; Holcomb, Kounios, Anderson & West, 1999; Kounios & Holcomb, 1994; Schwanenflugel, Harnishfeger & Stowe, 1988). Abstract words are also remembered less than concrete words (Paivio, 1991). These effects in favor of concrete

words have been traditionally interpreted by two competing models. The first model, the dual-coding theory (Paivio, 1991), postulates that abstract words are only represented verbally in the left hemisphere, whereas concrete words rely on additional imagery-based representations in the right hemisphere. The second model, context availability theory (Schwanenflugel et al., 1988), postulates that there is only one single semantic system located in the left hemisphere that processes both abstract and concrete words, with concrete words relying on larger contextual information than abstract words. The specific predictions on the neural representation of abstract words provided by these two models are that concrete words should be associated with additional activations compared to abstract words, and that no specifically dedicated extra-linguistic brain regions should be found for abstract words, not even in terms of a relatively stronger activation than for concrete words. However, these predictions have not turned out to be consistent with the large majority of the neuroimaging studies. These studies showed either that (contrary to both the dual-coding and the context availability theories), i) there is a set of brain regions that are more activated by abstract than concrete words, and no brain regions showing the opposite tendency (Grossman et al., 2002; Kiehl et al., 1999; Noppeney & Price, 2004; Perani et al., 1999; Pexman, Hargreaves, Edwards, Henry & Goodyear, 2007); or that (again contrary to both theories) ii) abstract words activate distinct extralinguistic brain regions not activated by concrete words (D'Esposito et al., 1997; Jessen et al., 2000; Tyler et al., 2001); or that (contrary to the context availability theory), iii) abstract words activate distinct linguistic brain areas not activated by concrete words (Binder et al., 2005; Jessen et al., 2000; Mellet, Tzourio, Denis & Mazoyer, 1998; Sabsevitz, Medler, Seidenberg & Binder, 2005).

An alternative account that is more compatible with a wide host of neuropsychological and neuroimaging findings is represented by modal theories described in the Introduction (Barsalou, 1999; 2008; Barsalou et al., 2003; Gallese, 2007; Gallese &

Lakoff, 2005, Glenberg & Kaschak, 2002). According to modal theories of conceptual knowledge, the processing of abstract words/concepts relies not only on left-hemispheric language brain regions, but also on semantic content-specific modal brain regions. In agreement with modal theories, we found that the processing of Abstract sentences was associated with an increase of functional integration between left-hemispheric language processing areas and the retrosplenial cingulate cortex, as a semantic region for contextual information coding and introspective state monitoring. With respect to functional localization of left-hemispheric language processing areas, the recruitment of LIFG-PB, LaITG, and LpMTG in the pattern of Abstract-specific, synergistic increase of activity is consistent with the results of previous functional localization studies (Binder et al., 2005; Noppeney et al., 2004; Perani et al., 1999; Sabsevitz et al., 2005). Each of these studies found some or all of these perisylvian regions to be activated more by abstract than by concrete words, and interpreted this finding as a correlate of non-perceptually based semantic association and comprehension processes. With respect to the retrosplenial cingulate cortex, as already specified in the Introduction, previous neuroimaging studies (Tettamanti et al., 2005; 2008; Tyler et al., 2001) have found this region to be associated with the processing of abstract vs. concrete words/sentences. Tettamanti and colleagues (2008) interpreted this finding as being due to a higher activation of the default mode brain network for abstract vs. concrete items, reflecting a relative absence of goal-directed action plans in the content expressed by abstract vs. concrete sentences. An alternative interpretation is that modulations of the default mode brain network are related to the complexity of the task (e.g. McKiernan et al., 2003). This, however, does not seem to offer a plausible explanation in the context of this study, which consisted of a passive listening task with minimal cognitive demands that, most importantly, did not differ between the Action and the Abstract conditions.

In relation to the role of the default mode brain network for abstract concepts,

D'Esposito and colleagues (1997) found stronger activation for abstract vs. concrete words in the precuneus, i.e. a region that is functionally associated with the retrosplenial cingulate cortex within the default mode brain network (Raichle et al., 2001).

However, it must also be noted that at least two neuroimaging studies have found the reverse activation pattern in the retrosplenial cingulate cortex, namely a stronger activation for concrete vs. abstract words (Binder et al., 2005; Sabsevitz et al., 2005). The interpretation of these controversial findings remains to be clarified. One possibility is that distinct portions of the retrosplenial cingulate cortex may participate in the representation of abstract and concrete words/concepts, an hypothesis that could be tested with a localization meta-analysis, once more studies become available. It is also possible that the stimuli used in these latter studies required contextual cue retrieval for concrete words, whereas abstract words engaged other associative representations, such as emotions.

Directionality of modulatory connections

An interesting feature emerging from the results of both Action-DCM and Abstract-DCM concerns the direction of the modulatory effects exerted on the specified inter-regional connections. Although both experimental conditions were allowed to modulate bidirectional connection strengths (forward and backward connections from one region to another) within the condition-specific neural systems, significant effects were unidirectional within both Action-DCM and Abstract-DCM. For Action-DCM, unidirectional forward connections were found from LIFG-PT – i.e. the component of the auditory action representation system with the most genuinely linguistic properties (Tettamanti et al., 2005) – to LdPCG, LSMG, and LpITG – i.e. the perceptuo-motor components of the action representation system. The attribution of a more cognitive, linguistic function to LIFG-PT as opposed to LdPCG, LSMG, or LpITG is supported by the fact that the LIFG-PT, which has been found to be activated in neuroimaging studies investigating the comprehension

of action related sentences (Aziz-Zadeh et al., 2006; Tettamanti et al., 2005; 2008), is anatomically and functionally distinct from the posterior portion of the IFG (*pars opercularis*) that is typically considered to be part of the human mirror-neuron system (Rizzolatti & Craighero, 2004). For Abstract-DCM, unidirectional connections were found from all three Abstract-specific linguistic areas, i.e. LIFG-PB, LaITG, and LpMTG, to the retrosplenial cingulate cortex.

This overall pattern of directionality may indicate that language parsing brain regions operate on modal areas to promote content-specific semantic retrieval and integration. This is consistent with the view that during language processing, there is no bottom-up access from primary sensory to perceptuo-motor/contextual brain areas, but rather a reactivation of the corresponding schematic simulations driven by top-down regulations from linguistic areas. This view is compatible with the evidence collected by MEG studies, showing that the auditory processing of action words is associated with a temporal spread of activation from perisylvian temporal and inferior frontal areas to body part-specific motor areas (Pulvermueller et al., 2005).

Conclusions

Recently proposed modal theories of conceptual knowledge suggest that concepts are grounded on distributed neural representations that subserve concept-specific simulation of primary processes. While there is abundant evidence on the simulation processes that mediate the reactivation of concrete, action-related concepts, there is a lack of evidence on the postulated simulation of internal states and of factual and contextual information that may be crucial to abstract semantic representations. The present study provides information compatible with modal theories' predictions for both concrete and abstract semantic domains, by showing that left auditory language areas are functionally more integrated with left-hemispheric areas subserving action representation

in the case of Action sentences, and with the retrosplenial cingulate cortex in the case of Abstract sentences. The reported effective connectivity analysis takes into account inter-regional modulatory effects that are particularly relevant for distributed conceptual representation theories. The observed condition-specific modulatory effects are consistent with top-down mechanisms by which linguistic areas promote a semantic content-specific reactivation of modal simulations.

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Table 1. Brain regions included in the DCM analysis

Subject-specific volumes of interest for the analyzed brain regions were defined for each subject around the individual local maxima that corresponded anatomically and functionally to the group-level activations in the standard GLM analysis (for details on, and for results of the standard GLM analysis, see Tettamanti et al., 2008). In this table, we list the group-level stereotactic coordinates of the standard GLM analysis. L, left; R, right; a- (prefix), anterior; p- (prefix), posterior; d- (prefix), dorsal; IFG, inferior frontal gyrus; PB, *pars orbitalis*; PT, *pars triangularis*; PCG, precentral gyrus; SMG, supra-marginal gyrus; STG, superior temporal gyrus; ITG, inferior temporal gyrus; MTG, middle temporal gyrus; CC, cingulate cortex.

Brain region	x,y,z
<i>Auditory language processing input region</i>	
LSTG	-54,-16,0
<i>Left-hemispheric action representation system</i>	
LIFG-PT	-48,36,12
LdPCG	-36,-12,56
LSMG	-60,-32,40
LpITG	-52,-60,-12
<i>Semantic regions coding for abstractness and contextual information</i>	
LIFG-PB	-48,24,-8
LpMTG	-52,-36,-8
LalTG	-50,8,-36
LRpCC	0,-52,32

Table 2. Intrinsic, condition-independent connection strengths

Arithmetic (non-Bayesian) values and random-effects statistics for the intrinsic connections. M.Str., Mean Strength (Hz); St.Dev., Standard Deviation. Significant effects ($P < 0.05$, corrected for multiple comparisons) are shown in bold. An asterisk denotes the connections also showing a significant effect in the Bayesian fixed-effects analysis: these connections are indicated with thin, solid arrows in Figure 2.

Connection	M.Str.	St.Dev.	Wilcoxon
<i>(A) Action-DCM</i>			
LIFG-PT → LdPCG	0.2031	0.1690	P=0.0007 *
LIFG-PT → LSMG	0.1874	0.1474	P=0.0008 *
LIFG-PT → LpITG	0.1838	0.1558	P=0.0012 *
LdPCG → LIFG-PT	0.0314	0.0609	P=0.0025 *
LdPCG → LSMG	0.0539	0.0541	P=0.0005 *
LSMG → LIFG-PT	0.0604	0.0947	P=0.0092 *
LSMG → LdPCG	0.0477	0.0657	P=0.0092 *
LSMG → LpITG	0.1047	0.1130	P=0.0012 *
LpITG → LIFG-PT	0.0801	0.1062	P=0.0035 *
LpITG → LSMG	0.1657	0.1454	P=0.0014 *
LSTG → LIFG-PT	0.1434	0.1316	P=0.0027 *
LSTG → LpITG	0.0321	0.1365	P=0.2216
<i>(B) Abstract-DCM</i>			
LIFG-PB → LaiTG	0.2397	0.2929	P=0.0004 *
LIFG-PB → LpMTG	0.1675	0.2106	P=0.0012 *
LIFG-PB → LRpCC	0.0705	0.1122	P=0.0191
LaiTG → LIFG-PB	0.0768	0.0984	P=0.0049 *
LaiTG → LpMTG	0.0809	0.0906	P=0.0012
LaiTG → LRpCC	0.0435	0.0837	P=0.0285 *
LpMTG → LIFG-PB	0.1818	0.2324	P=0.0041 *
LpMTG → LaiTG	0.1103	0.1150	P=0.0004 *
LpMTG → LRpCC	0.0113	0.1283	P=0.2947
LSTG → LIFG-PB	0.0605	0.1586	P=0.0661
LSTG → LpMTG	0.1226	0.1529	P=0.0079 *
LRpCC → LIFG-PB	0.0698	0.0623	P=0.0005 *
LRpCC → LaiTG	0.0446	0.0756	P=0.0124
LRpCC → LpMTG	0.0546	0.0636	P=0.0029 *

Table 3. Connection strength modulations by level of concreteness

Arithmetic (non-Bayesian) values representing modulatory effects for the Action and Abstract conditions and their significances. Significant effects ($P < 0.05$, corrected for multiple comparisons) are marked by § for the Wilcoxon tests with respect to the mean of zero, and marked in bold for the paired Wilcoxon comparisons between the two conditions. An asterisk denotes the connections also showing a significant effect in the Bayesian fixed-effects analysis: only these connections are illustrated in Figure 2.

Connection	<i>Action</i>		<i>Abstract</i>		Wilcoxon
	M.Str.	St.Dev.	M.Str.	St.Dev.	
<i>(A) Action-DCM</i>					<i>Action>Abstract</i>
LIFG-PT → LdPCG	0.0424	0.0744 §	-0.0202	0.0668	P=0.0015 *
LIFG-PT → LSMG	0.0322	0.0643 §	-0.0221	0.0705	P=0.0036 *
LIFG-PT → LpITG	0.0122	0.0217 §	-0.0015	0.0256	P=0.0253 *
LdPCG → LIFG-PT	0.0068	0.0199	-0.0067	0.0195	P=0.0214
LdPCG → LSMG	0.0015	0.0213	-0.0057	0.0251	P=0.0149
LSMG → LIFG-PT	0.0062	0.0239	-0.0055	0.0267	P=0.4185
LSMG → LdPCG	0.0052	0.0304	-0.0146	0.0290	P=0.0101
LSMG → LpITG	0.0043	0.0232	-0.0008	0.0269	P=0.2026
LpITG → LIFG-PT	0.0060	0.0248	0.0032	0.0258	P=0.5491
LpITG → LSMG	-0.0002	0.0511	0.0077	0.0624	P=0.8432
LSTG → LIFG-PT	0.0906	0.0766 §	-0.0710	0.0808 §	P=9.121x10⁻⁷ *
LSTG → LpITG	0.0220	0.0618 §	-0.0732	0.0645 §	P=3.665x10⁻⁶ *
<i>(B) Abstract-DCM</i>					<i>Abstract>Action</i>
LIFG-PB → LaITG	-0.0097	0.0471	0.0105	0.0469	P=0.0458
LIFG-PB → LpMTG	0.0054	0.0407	0.0301	0.0410 §	P=0.0031
LIFG-PB → LRpCC	-0.0110	0.0487	0.0256	0.0465 §	P=0.0170 *
LaITG → LIFG-PB	0.0089	0.0524	0.0168	0.0529	P=0.1333
LaITG → LpMTG	-0.0039	0.0173	0.0153	0.0341 §	P=0.0045 *
LaITG → LRpCC	-0.0035	0.0154	0.0112	0.0280 §	P=0.0080 *
LpMTG → LIFG-PB	-0.0115	0.0549	0.0373	0.0671 §	P=0.0162 *
LpMTG → LaITG	-0.0161	0.0445	0.0150	0.0397	P=0.0128
LpMTG → LRpCC	-0.0267	0.0721	0.0198	0.0554 §	P=0.0008 *
LSTG → LIFG-PB	-0.0021	0.0382	0.0130	0.0461 §	P=0.0179
LSTG → LpMTG	-0.0024	0.0283	0.0158	0.0473 §	P=0.0040 *
LRpCC → LIFG-PB	0.0041	0.0131	0.0010	0.0118	P=0.7000
LRpCC → LaITG	0.0018	0.0137	0.0020	0.0110	P=0.5164
LRpCC → LpMTG	0.0012	0.0109	0.0024	0.0132	P=0.2619

Figure legends

Figure 1. Distinct activation patterns for Action vs. Abstract sentence processing

The results of the standard General Linear Model statistical analysis are illustrated here just for reference (for details, see Tettamanti et al., 2008). Activations (orange color scale) or deactivations (magenta color scale, black arrow) elicited by action-related sentences, or activations elicited by abstract sentences (blue color scale). Significant effects ($P < 0.05$, False Discovery Rate correction) are displayed on fiducial cortical renderings of the participants' average anatomical image.

Figure 2. Distinct anatomo-functional effective connectivity patterns for Action vs. Abstract sentence processing

(a, b) The Action-DCM model (a), consisting in the left-hemispheric system for action representation, included the *pars triangularis* of the inferior frontal gyrus (LIFG-PT), the dorsal precentral gyrus (LdPCG), the supramarginal gyrus (LSMG), and the posterior inferior temporal gyrus (LpITG). The Abstract-DCM model (b), involving semantic regions coding for abstractness and contextual information, included the *pars orbitalis* of the left inferior frontal gyrus (LIFG-PB), the left middle temporal gyrus (LMTG), the left anterior inferior temporal gyrus (LaITG), and the bilateral posterior cingulate cortex (LRpCC). The left superior temporal gyrus (LSTG) was chosen as the stimulus-independent input region for both the Action-DCM and the Abstract-DCM models (thick, black arrows). Significant (thin, solid arrows; both fixed- and random-effects analyses) and non-significant (thin, dashed arrows; either fixed- and/or random-effects analyses) intrinsic connection strengths between areas of the two brain systems (see also Table 2). Average, Bayesian weighted intrinsic connection strengths (Hz) and associated posterior probabilities (in brackets) are indicated close to the corresponding connection arrows.

(c, d) Significantly different modulations of connection strengths for Action vs. Abstract sentence processing. The Action-DCM model (c) only showed stronger modulatory effects for Action vs Abstract sentences (orange arrows), and not vice versa. The Abstract-DCM model (d) only showed stronger modulatory effects for Abstract vs Action sentences (blue arrows), and not vice versa. Posterior densities for the contrasts between experimental conditions are indicated close to the corresponding connection arrows. Only the connections displaying both fixed-effects $P > 0.95$ posterior densities and random-effects $P < 0.05$ corrected alpha levels (see Table 3) are shown.

Figure 1

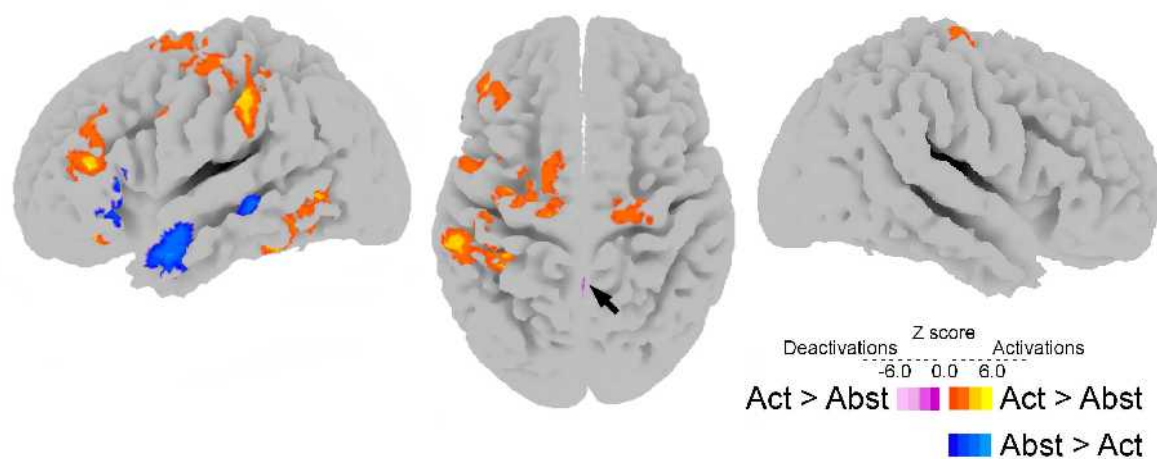


Figure 2

