

## Beyond the word and image: characteristics of a common meaning system for language and vision revealed by functional and structural imaging



A.L. Jouen<sup>a</sup>, T.M. Ellmore<sup>b</sup>, C.J. Madden<sup>a</sup>, C. Pallier<sup>c</sup>, P.F. Dominey<sup>a</sup>, J. Ventre-Dominey<sup>a,\*</sup>

<sup>a</sup> INSERM Stem Cell and Brain Research Institute U846, Bron, France

<sup>b</sup> Department of Psychology and Program in Cognitive Neuroscience, The City College and Graduate Center of the City, University of New York, New York, NY, USA

<sup>c</sup> Cognitive Neuroimaging Unit, INSERM-CEA, Gif-sur-Yvette, France

### ARTICLE INFO

#### Article history:

Accepted 11 November 2014

Available online 15 November 2014

#### Keywords:

Semantic  
Language  
Vision  
DTI  
fMRI  
Human

### ABSTRACT

This research tests the hypothesis that comprehension of human events will engage an extended semantic representation system, independent of the input modality (sentence vs. picture). To investigate this, we examined brain activation and connectivity in 19 subjects who read sentences and viewed pictures depicting everyday events, in a combined fMRI and DTI study. Conjunction of activity in understanding sentences and pictures revealed a common fronto-temporo-parietal network that included the middle and inferior frontal gyri, the parahippocampal-retrosplenial complex, the anterior and middle temporal gyri, the inferior parietal lobe in particular the temporo-parietal cortex. DTI tractography seeded from this temporo-parietal cortex hub revealed a multi-component network reaching into the temporal pole, the ventral frontal pole and premotor cortex. A significant correlation was found between the relative pathway density issued from the temporo-parietal cortex and the imageability of sentences for individual subjects, suggesting a potential functional link between comprehension and the temporo-parietal connectivity strength. These data help to define a “meaning” network that includes components of recently characterized systems for semantic memory, embodied simulation, and visuo-spatial scene representation. The network substantially overlaps with the “default mode” network implicated as part of a core network of semantic representation, along with brain systems related to the formation of mental models, and reasoning. These data are consistent with a model of real-world situational understanding that is highly embodied. Crucially, the neural basis of this embodied understanding is not limited to sensorimotor systems, but extends to the highest levels of cognition, including autobiographical memory, scene analysis, mental model formation, reasoning and theory of mind.

© 2014 Elsevier Inc. All rights reserved.

### Introduction

A significant portion of human mental life is built upon the construction of perceptually and socially rich internal scene representations, or mental models (Johnson-Laird, 2010). These models can be used for reasoning, exploring specific memories of the past, planning for the future, or understanding current situations that may be presented in real-time through immersion in an actual life-activity scene, or more passively, through reading, watching a movie or viewing a photograph. It is possible that these mental models play an intricate role in generating predictions as part of perception (Friston, 2005), and that they are at the core of meaning. In this context, embodied theories of meaning argue that the human conceptual system is implemented in distributed brain networks whose mechanisms are shared by perceptual and action

processing (Barsalou, 1999; Barsalou et al., 2003). In a review of the neurophysiology of meaning, and the continuum from symbolic to embodied models, Binder and Desai (2011) argue that the semantic system consists of both modality specific and supra-modal representations. They advocate a semantic system which consists of multiple levels of abstraction, grounded on sensori-motor and affective representations. At the more abstract level, they highlight the important role of the angular gyrus, in the inferior parietal cortex near the temporo-parietal junction, as an abstract supramodal convergence zone (Damasio, 1989) participating in the semantics of event concepts.

Such representations of meaning should be accessible by different perceptual routes, including language and vision. Indeed, one of the most basic problems of cognition is “understanding” or generating a coherent mental model from an image or sentence. This problem was at the core of cognitive science in the 1980s (Jackendoff, 1987; Johnson-Laird, 1981, 1987, 1988; Kintsch, 1988), with the challenge to find the unified representation of meaning common to language and vision. Behavioral research suggests indeed that language and vision

\* Corresponding author at: INSERM Stem Cell and Brain Research Institute, U846, 18 Avenue Doyen Lepine, 69500-Bron, France.

E-mail address: [Jocelyne.ventre-dominey@inserm.fr](mailto:Jocelyne.ventre-dominey@inserm.fr) (J. Ventre-Dominey).

interact thus in a common representation, as cross modal priming can occur between pictures and words (Bajo, 1988).

Examining the possible neurophysiological bases of this relation between language and vision, Vandenberghe et al. (1996) observed significant overlap in brain activation when subjects read single words and saw pictures of simple objects in semantic matching tasks. The common activation was seen in areas including the temporal parietal junction, left middle temporal gyrus and inferior frontal gyrus. Recent studies have examined the commonality between cognitive processing of words and pictures in variety of tasks including priming (Kircher et al., 2009), and brief masked presentation at the threshold of consciousness (Van Doren et al., 2010). Because of their relatively restricted nature of word and object stimuli, such tasks may not tap into the more elaborated processes of comprehension that would be elicited by richer stimuli. For example, in the linguistic domain, as the structural complexity of the input stimulus increases, so does the extent of activation. Xu et al. (2005) thus demonstrated that as stimulus complexity increases over words, sentences and narratives, there is an expansion of activity from perisylvian language areas, to frontal operculum and temporal pole for words and sentences respectively. Processing in a narrative sense extended this recruitment to areas including precuneus, medial prefrontal and dorsal temporo-parietal-occipital cortices. One could imagine a similar expansion in the representation of meaning as image stimuli increase in complexity from simple objects, to richer spatial scenes (Harel et al., 2013).

From Vandenberghe's early work on words and images (Vandenberghe et al., 1996) to recent studies and meta-analyses of the semantic system (Binder and Desai, 2011; Binder et al., 2009; Graves et al., 2010; Vandenberghe et al., 2013) the cortex in the temporal-parietal junction including the angular gyrus appears to play the role of an integrating convergence zone in a distributed semantic network.

If such a network exists, allowing these brain regions to encode meaning representations that may be extended in space and time, it is likely that dedicated anatomical white matter pathways contribute to the infrastructure for this distributed network. Diffusion tensor imaging (DTI) provides a method for analysis of white matter pathways in the living brain based on diffusion properties of water molecules within these pathways (Makris et al., 1997). DTI has proven to be a potent tool for examination of language-related white matter pathways (Anwander et al., 2007; Frey et al., 2008; Friederici, 2009; Friederici et al., 2006; Glasser and Rilling, 2008; Makris et al., 2005; Makris and Pandya, 2009; Menjot de Champfleury et al., 2013; Sarubbo et al., 2013; Saur et al., 2008, 2010; Turken and Dronkers, 2011). Catani and colleagues (Catani et al., 2005) used DTI to examine the organization of one of the principal language-related pathways, the arcuate fasciculus (AF) of the left hemisphere. They identified the classical pathway connecting Broca's region (in the territory of the inferior frontal gyrus) and Wernicke's region (in the territory of middle temporal gyrus), and an additional previously undescribed indirect pathway passing through inferior parietal cortex. They suggest that the indirect pathway, which passes via parietal cortex, is involved in semantically based language functions, while the direct pathway is involved in phonological language functions. Their dissection of the indirect pathway highlights the importance of this parietal area, characterized as Geschwind's territory in BA39/40, which Lichtheim (Lichtheim, 1885) referred to as a concept center (Catani et al., 2005). Glasser and Rilling (2008) subsequently demonstrated distinct components of the AF with a superior temporal gyrus (STG) pathway for phonological content and middle temporal gyrus (MTG) pathway for lexical semantic content in accord with Hickok and Poeppel (2004). Further investigating this connectivity, Frey et al. (2008) identified the link between BA45 and STG via extreme capsule system, and BA44 with rostral inferior parietal lobe (IPL) via the third branch of the superior longitudinal fasciculus (SLF3). Additional pathways from this parietal territory that contribute to language include the middle longitudinal fasciculus (MdLF) linking STG and inferior parietal cortex/angular gyrus (Makris et al., 2009;

Menjot de Champfleury et al., 2013; Saur et al., 2010; Turken and Dronkers, 2011), and the inferior fronto-occipital fasciculus (IFOF) (Sarubbo et al., 2013; Turken and Dronkers, 2011). Indeed, frontal terminations of IFOF reveal a multifunction pathway with a superficial part that distributes information from posterior cortex (superior parietal, TPJ, occipital extrastriate cortex) to pars triangularis and opercularis in inferior frontal gyrus, and the deep component that projects to orbito-frontal, middle frontal cortex and dorso-lateral prefrontal cortex (DLPFC) (Sarubbo et al., 2013). This TPJ/MTG area in the proximity of the semantic convergence zone of Binder (Binder and Desai, 2011) is at the crossroads of multiple language related pathways including the AF/SLF, the IFOF and the MdLF (Sarubbo et al., 2013; Turken and Dronkers, 2011) that could contribute to its semantic integration function.

The current research tests the hypothesis that comprehension of human events will engage an extended semantic representation system, independent of the input modality. In particular, if the temporo-parietal cortex in the region of the angular gyrus is an integrating convergence zone for event representation as suggested by Binder and Desai (2011), then this area should be activated when subjects understand sentences or images depicting events. Likewise, if this region plays a privileged role in comprehension, then one would expect that structural connectivity to this area would relate to comprehension. In order to assess this we first characterize the fMRI response to the semantic processing of visual scenes and sentences and then, by using DTI tractography we investigate specific pathways within the activated semantic network.

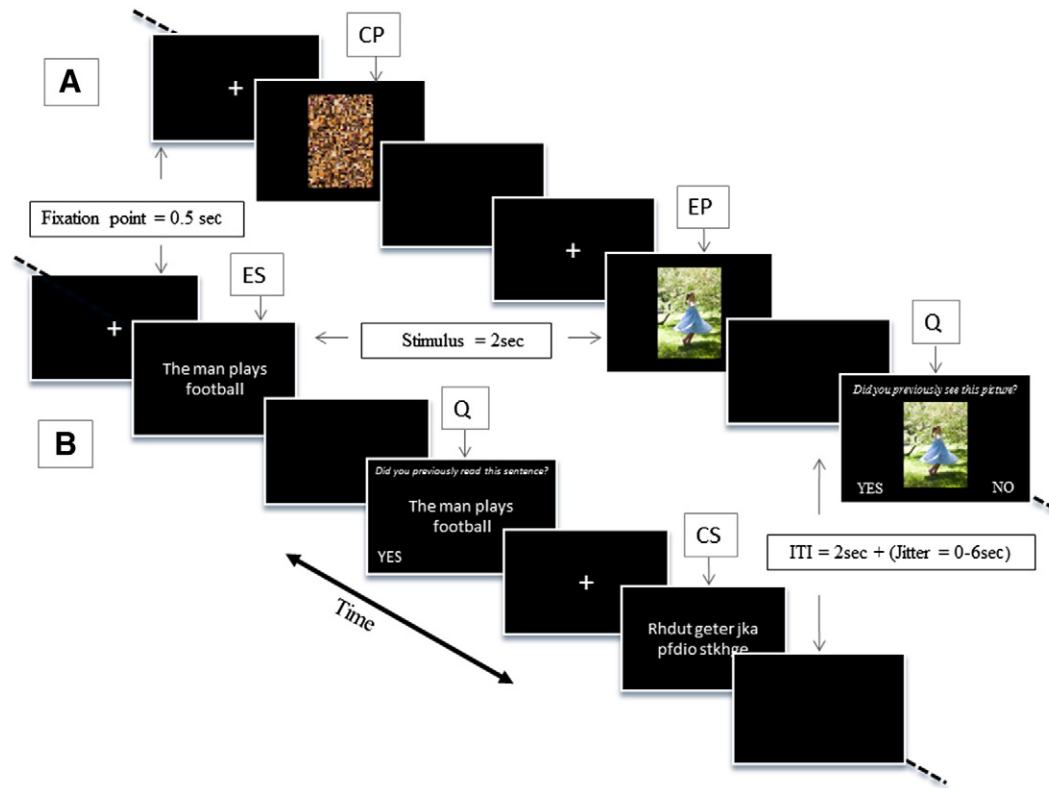
Previous functional imaging studies comparing linguistic and visual input stimuli have tended to use relatively constrained stimuli (Van Doren et al., 2010; Vandenberghe et al., 1996), rather than richer visual scenes and sentences that would potentially tap more heavily into the semantic system. In the current study, we make a compromise, by using relatively complex stimuli. Most importantly, we use stimuli that engage the semantic system by two separate input modalities – scene vision vs. language. We combine functional and anatomical imaging to identify a neural system for the representation of meaning at the sentence and scene level, independent of the input modality.

The resulting event related fMRI experiment allows us to examine the representation of meaning in two processing modes, corresponding to reading sentences, and seeing pictures (see Fig. 1). In both cases, the stimuli (sentences or pictures) depicted rich human events or scenes. In the sentence condition, example sentences include “The man climbs the ladder”, and “The little girl rakes the leaves.” In the picture condition, the pictures were photographs depicting these same kinds of events. For both the sentences and pictures, a protocol was employed which ensured that subjects processed the sentence or picture stimuli. We examined fMRI results for sentence and picture comprehension, and the conjunction of these modality dependent activations, in order to identify the common network. After the fMRI, while subjects were still in the scanner we obtained DTI data that allowed us to characterize the anatomical connectivity within the network, and establish the link between such measures of connectivity and a behavioral measure of comprehension.

## Materials and methods

### Subjects

Nineteen healthy, right-handed, native-French speakers with normal or corrected to normal vision participated in the study (11 male; mean age: 23 years; SD: 5.36 years). No participant had a history of neurological, major medical, or psychiatric disorder. The protocol was approved by the regional ethic committee (Comité de Protection des Personnes Ile-de-France VII. Protocole de Recherche Biomedicale #2008-A00241-54/1) and all participants gave their written informed consent before the scanning session.



**Fig. 1.** Illustration of the paradigm showing the control (CP: Control Picture; CS: Control Sentence) and event (EP: Event Picture; ES: Event Sentence) stimuli and the timing of their presentation over 2 examples of pictures (A) and sentences (B) sessions. Questions (Q) are presented in 10% of the trials. One trial = One event or control stimulus with or without question.

### Stimuli

The paradigm used in the study is illustrated in Fig. 1. 200 pictures (Event pictures) of single persons (no negative emotional valence) performing a common daily activity (e.g. reading, running, raking leaves, eating) were collected from the Getty photo database (<http://www.gettyimages.fr/>). 200 sentences (Event sentences) describing the same actions were generated such that the sentences corresponded to an equivalent set of events as the pictures. Two sets of stimuli (A and B) were generated, each composed of 100 pictures and 100 sentences. In order to avoid subjects seeing both a given sentence and its corresponding picture, stimuli were crossed, such that the 100 sentences in stimulus set A corresponded to the 100 pictures from stimulus set B and vice versa. The everyday events described/depicted by the stimuli were balanced across static (reading, relaxing, watching) and dynamic situations (climbing, sweeping, getting dressed), and this was counterbalanced across the two stimulus sets.

### Stimuli norming prior to scanning

During a pretest session, the 200 pictures were shown to 20 pilot subjects who were instructed to produce a sentence describing the action represented in the images. This yielded a 96% correspondence between produced sentences and actual sentence stimuli. Subjects also evaluated the imageability of the sentences, from 1 (very difficult) to 5 (very easy). Subjects were instructed to rate how well they were able to visualize the sentence, or how vivid their representation was. This yielded a measure of 99% of sentences judged as easily imageable (mean rating of 4 or higher). In addition to controlling the number of static and dynamic events across the two stimulus sets, pictures and their corresponding sentences were matched in terms of age and gender of the protagonists (equal numbers of adults/children and males/females). Furthermore, sentences from the two sets were also matched in terms

of number of words and letters, grammatical construction (number and type of verbs; transitive, intransitive, reflexive; number of prepositions, adverbs, and adjectives), and word frequency within the Lexique 3.55 database, using both book frequency and film frequency corpora. A sample of images from one run (including 25 control and 50 test images) and the 200 sentences are presented in Supplementary Materials 1 and 2. As pictures were in either portrait or landscape orientation, sentences were presented so as to have a similar vertical (text on 4 or 5 narrow lines) or horizontal orientation (text on 2 longer lines) so as to reduce the differences in eye movements between pictures and sentences. In order to subtract low-level (non-semantic) processing in subsequent analyses, scrambled images of the original pictures were generated as Control pictures (with no identifiable semantic content), and scrambled strings of letters were generated from the original sentences as Control sentences. Thus, in both cases, comparable visual information was retained but without the semantic component.

### Procedure

During the fMRI scanning session, 10 subjects were exposed to set A, and 9 to set B. Each stimulus set was divided and presented in 4 blocks or runs, two runs of 50 event pictures each, and two runs of 50 event sentences each. Each of the four experimental runs (two runs of pictures and two runs of sentences, random order) contained 50 event trials, 25 control trials and 8 probe questions, and lasted about 10 minutes. During a trial, a white fixation cross appeared on a black screen for 500 ms, followed by a picture or sentence on a black background for 2 seconds, and finally a blank black screen was presented for 2 seconds plus jitter time (0–6 sec) before the next trial (Fig. 1). The subjects' task was to process sentences and pictures in order to be able to respond to a further possible question. In order to maintain subjects' alertness, on 10% of trials subjects were asked if the current stimulus had previously been seen and they had to respond with their right hand by pressing on a button. If the response was positive, the previous occurrence

was always one-back, and if not, the stimulus had not been previously presented at any time during the experiment. The number of correct responses to these questions exceeded 95% indicating that the subjects were attending to the stimuli.

Following the scanning, the subjects performed a behavioral test similar to the pretest described above. In this test, the subjects' imageability capability was assessed on a subset of 50 sentences: 25 from the list that they had just seen in the scanner, and 25 from the list that the other half of subjects saw. As in the stimuli norming test with separate subjects, the subjects provided judgments of imageability on a scale of 1–5. Sentences were designed to be highly imageable, as verified by the aforementioned pretest norming study. The lowest rated sentences (The man dives in the sand. The little girl spies through the fence.) and the highest rated sentences (The young woman throws a snowball. The woman is waiting for the bus.) both seem to evoke relatively vivid representations. Thus, subjects' mean ratings during the post-scanner test were generally high, ranging from 3.46 to 5, with 4 of 19 participants rating all 50 sentences as 5. Nonetheless, these mean imageability ratings yielded enough variability to be subsequently used as an individual difference regressor in correlation with DTI tract strength (see Supplementary Material Table 3 for full set of sentences and subject ratings).

#### *fMRI and DTI scanning*

Functional and structural MRI data were acquired on a 3 T Siemens Magnetom TrioTim scanner at Neurospin (CEA Saclay, Gif-sur-Yvette, France). Blood oxygen level dependent (BOLD) fMRI signal was recorded during the four experimental runs. Whole brain coverage was obtained with 38 transversal gradient echo-planar imaging (EPI) images (repetition time: 2000 ms, echo time: 30 ms, flip angle: 76 degrees, bandwidth: 2694 Hz per pixel, FOV: 192 mm<sup>2</sup>; voxel size: 3.0 mm<sup>3</sup>, 300 repetitions). A high resolution T1 weighted image of the whole brain was acquired for later spatial coregistration (TR/TE: 2300/2.98 ms; flip angle: 9 degrees; FOV: 256 mm<sup>2</sup>; 1.10 mm thick sagittal slices). During the same session, 3 scans of 60 (19, 20 and 21) direction diffusion images were acquired to allow reconstruction of white matter pathways (TR/TE: 13000/93 ms; flip angle: 90 degrees; matrix size: 128 × 128; FOV: 220 mm<sup>2</sup>; 1.70 mm thick axial slices, max. b-value: 1500 s/mm<sup>2</sup>).

#### *Data analysis*

##### *fMRI data*

fMRI analysis was performed with the Statistical Parametric Mapping software (SPM 5) running in the Matlab environment. The functional images were realigned with respect to the first functional image and corrected for slice acquisition timing referenced to the first slice in each scan. The resulting volumes were spatially normalized to fit to an echo planar imaging template in MNI (Montreal Neurological Institute) space. The normalized images were then spatially smoothed using an isotropic Gaussian kernel with a 8x8x8mm full width at half maximum. For each participant, a design matrix was made with all the stimuli onsets and separate regressors for the sentence and picture modalities (Event and Control) and for the 6 estimated head movements rotation and translation that never exceeded 2 mm. By using the general linear model (GLM) (Friston et al., 1994), the individual BOLD impulse responses were modeled with the hemodynamic response function (HRF) and its derivative convolved with a delta (event-related) function.

Task related BOLD changes were estimated as linear combinations of the individual regressors: ES: event sentences, CS: control sentences, EP: event pictures, and CP: control pictures. In order to extract the BOLD changes due to semantic processing of sentences and pictures, we conducted contrasts between each modality and its respective control i.e. ES > CS, EP > CP.

For the statistical group analysis, the individual contrast images were then processed in a second-level random effects model by using a one-sample t test in a group analysis of all the 19 subjects. The task related BOLD changes were extracted for each ES > CS and EP > CP for the group at a voxel-based false discovery rate (FDR) threshold of  $p < .05$  and with a minimum cluster size of 15 voxels ( $Ke = 15$ ). To determine the neural structures activated in common during the processing of pictures and sentences, we performed a conjunction analysis based on the Nichols' procedure (Nichols et al., 2005) for the ES > CS and EP > CP contrasts at  $p < .005$  uncorrected. By using the Brett transformation (<http://www.brainmap.org/icbm2tal/>), MNI coordinates of the cerebral activation foci were transformed into Talairach stereotaxic atlas coordinates (Talairach and Tournoux, 1988). In a supplementary analysis, in order to differentiate the effect of the category of actions on the Event stimuli, we conducted a second-level analysis using a 2x2 factorial model in the 19 subjects (see Supplementary Material 4).

##### *DTI data*

Image processing, alignment, and visualization were performed with AFNI (Cox, 1996). Each diffusion-weighted image was aligned to the skull-stripped T1 MRI, followed by correction of gradient orientations by the angular motion parameters (Leemans and Jones, 2009) and computation of a diffusion tensor. Separately, the T1 MRI was spatially normalized to a template (Montreal Neurological Institute N27 brain) and the resulting 12-parameter affine transformation matrix was saved. A set of whole-brain deterministic pathways was saved in a pathway database for further interrogation.

The native-space resolution of the output realigned diffusion-weighted volumes (1.72 × 1.72 × 1.70 mm) was preserved for the purposes of computing the set of whole-brain tractography pathways (no Talairach transformation). Deterministic fiber tracking was used to compute a native-space tensor in DTIQuery v1.1 software (Sherbondy et al., 2005) with the streamline tracking algorithm (STT) and optimal parameters (Basser et al., 2000), which included path step size of 1.0 mm, seed point spacing at 2.0 mm, fractional anisotropy termination threshold of 0.15, angular termination threshold at 45 degrees, maximum pathway length at 300 mm, and Euler's method for STT numerical integration.

The seed regions for the deterministic fiber tracking were extracted from the t-maps of the fMRI random effects (conjunction analysis on the group) where peak voxels in the major clusters of activation were identified. Sets of tractography pathways were objectively isolated using the following steps: 1) backward transformation of the fMRI group map local maxima coordinates was performed for each subject to obtain a native image space coordinate; 2) these coordinates were used to place volumes of interest in DTI Query (VOI, radius = 5 or 10 mm depending on the anatomy and the size of the functional seed regions); 3) pathways intersecting the VOI were saved as a native space binary image volume for each subject. For each subject, the native space binary image volume representing the set of tractography pathways intersecting the VOI around the fMRI local maxima was transformed to MNI space using the 12-parameter transformation matrix derived from the T1 MRI spatial normalization procedure. This resulted in 19 single-subject image volume masks in the same standard coordinate space. These volumes were then summed to create a single volume map where the integer value at each voxel represents the number of subjects who have tractography pathways passing through the given voxel. A threshold was applied to this volume to visualize voxels where at least 10 of the 19 subjects exhibited common tractography connections.

DTI tract fiber density was calculated as the percentage of fibers (ratio of the number of fibers for one tract to the number of the whole brain fibers for one subject) for each determined pathway. The fiber density was correlated with imageability ratings by using a regression analysis on the 3 main identified pathways issued from the tempo-

parietal cortex. The significant value was established at  $p < 0.017$  with Bonferroni corrections for multiple comparisons.

## Results

### FMRI results

Here we describe a voxel based analysis of the whole brain activation that was performed for (1) sentence processing and (2) picture processing, and then (3) by a conjunction analysis of the sentence and picture processing in order to identify a shared network (Nichols et al., 2005).

### Event Sentences vs Control Sentences (ES > CS)

As expected, a large predominantly left-hemisphere network distributed across frontal and temporal cortices showed more activity to sentences than to the control non-word sequences, at FDR  $p$  corrected  $< 0.05$  (Table 1 and Fig. 2). A large cluster of activated voxels was observed bilaterally in the middle and superior temporal gyri, spreading medially in the para-hippocampal gyrus (BA36) and dorsally in the angular gyrus (BA39). In each hemisphere the peaks of temporo-parietal activation were two-fold and were localized in BA 22 and 39 (Table 1 and Fig. 2). Rostrally, a small focus of activation included the left inferior frontal lobe (BA46–45) of the classic perisylvian network involved in sentence processing. This contrast also activated the premotor region in the left middle frontal gyrus (BA6) forming a small cluster (cluster extent  $Ke = 43$ ) peaking at TAL  $-39, 3, 52$ . A slight activation ( $Ke < 15$ ) was also found bilaterally in the medial frontal gyrus (BA11). In addition, subcortically, the right caudate nucleus showed significant increased activity in a large area extending ventro-dorsally ( $Ke = 131$ ).

### Event pictures vs control pictures (EP > CP)

Contrasting EP > CP activation at FDR  $p$  corrected  $< 0.05$  revealed an extended occipito-frontal network partially overlapping with sentence processing regions (Table 2 and Fig. 2). Significant activity was found in the right associative visual cortex including the fusiform and middle occipital gyri (BA19 and BA37) spreading bilaterally and anteriorly in the precuneus, the temporo-parietal cortex (BA39 and BA40) and the para-hippocampal (BA35,36) and retro-splenial (BA 29,30) cortical regions. Activity was also found in a small region of the anterior cingulate cortex localized in BA 24 and 31 ( $Ke = 70$ ). Finally, the level of prefrontal cortex activity was also increased forming three distinct clusters of substantial sizes in the left middle prefrontal gyrus (BA6) and bilaterally in the medial orbitofrontal cortex (BA11–10) and

smaller ( $Ke < 15$ ) in the inferior prefrontal gyrus (BA45–46) (Table 2 and Fig. 2).

### Global conjunction of sentences and pictures: ES > CS $\cap$ EP > CP

Conjunction analysis of the sentence (ES > CS) and picture (EP > CP) contrasts (Nichols et al., 2005) revealed a rich distributed fronto-temporo-parietal network (Table 3 and Figs. 2 and 5). Common activation was identified in the left frontal cortex forming three small clusters (Figs. 3 and 4A): (1) a two-fold cluster in the ventro-medial prefrontal cortex (BA11) with a bilateral activation in the medial orbital cortex ( $Ke = 27$ ) spreading rostrally and dorsally in the left dorsal prefrontal gyrus ( $Ke = 19$ ), and (2) a more lateral activation ( $Ke = 21$ ) was localized in the left inferior frontal gyrus including BA46 and BA45 at the limit with BA47. Interestingly, voxels activated in common for sentences and images were observed in the premotor cortex with activity peaking at Tal  $-42, 0, 53$  in the middle prefrontal gyrus BA6 (Fig. 3).

In the more posterior temporal and parietal lobes, the conjunction analysis revealed large volumes of activation ( $Ke > 100$ ). As illustrated in Figs. 3 and 5, an extended volume of the retrosplenial region ( $Ke = 1019$ ) was significantly activated and was sub-divided into 2 main clusters: (1) one concerned the left parahippocampal region with a peak of activation at TAL  $-33, -39, -12$  (BA35–36) spreading ventrally to the fusiform gyrus to include BA37 and (2) the other cluster was large and medial, overlapping the 2 hemispheres with an activation peaking at TAL  $-9, -57, 15$  on the left and TAL  $12, -51, 15$  on the right. This bilateral retrosplenial activity extended from the hippocampus and cingulate gyri (BA 23,30) dorsally to the lingual gyrus (BA19) ventrally (Figs. 5C–D).

The ES > CS and EP > CP conjunction analysis revealed several clusters of activation in the lateral temporal lobe (Fig. 3): a small focus ( $Ke = 19$ ) at TAL  $-45, 16, -21$  in the anterior temporal pole (BA38), only in the left hemisphere and two bilateral foci localized in the middle temporal gyri (BA21). In the posterior part of the temporal lobe a bilateral, symmetrical pattern of activation was centered in the middle temporal gyrus (BA39) peaking at TAL  $-42, -66, 23$  on the left and TAL  $53, -69, 26$  on the right. While the peak of activation was in the middle temporal gyrus on both sides (BA39), a substantial activation expanded dorsally in the adjacent postero-ventral angular gyrus and ventrally in the inferior temporal sulcus, including the posterior part of BA21. In the most antero-posterior extension, this cluster reached the middle occipital gyrus including BA37 posteriorly and the superior temporal gyrus including BA22. As shown in Figs. 3 and 5, this large cluster activated in common between sentences and images involved the temporo-parietal cortex with a larger extent in the left ( $Ke = 651$ ) relative to the right ( $Ke = 76$ ) hemisphere. Interestingly, the right medio-ventral caudate nucleus was significantly activated with a peak of activation at TAL  $3, 12, -6$  (Fig. 4).

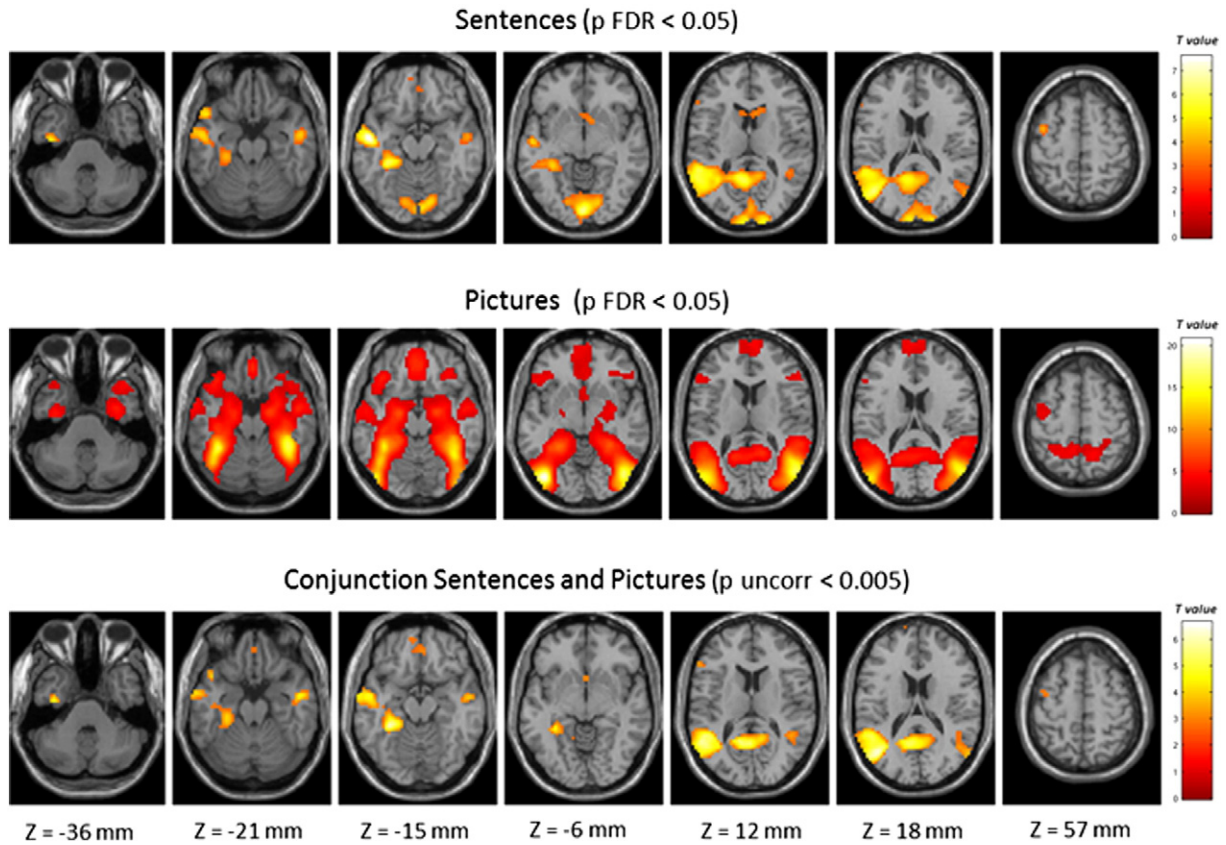
**Table 1**

Anatomical regions displaying significant activation revealed when sentences of event are contrasted with the sequence of scrambled word control sentences.

Anatomical area	BA	x, y, z	t-stat	Ke
(ES > CS) $P < 0.05$ (FDR)				
L middle temporal gyrus	21	-53 -9 -10	7.60	3442
L middle temporal gyrus	39	-42 -66 23	6.64	
L parahippocampal gyrus	36	-33 -38 -8	6.63	
R middle temporal gyrus	39	53 -69 26	3.89	132
R superior temporal gyrus	22	45 -46 11	3.34	
R middle temporal gyrus	21	33 -40 8	2.89	
R middle temporal gyrus	21	53 -7 -17	4.39	82
R middle temporal gyrus	21	50 -15 -7	3.03	
L superior temporal gyrus	38	-50 14 -18	4.79	45
L middle frontal gyrus	6	-39 3 52	4.05	43
L inferior frontal gyrus	46	-56 29 7	3.41	21
L inferior frontal gyrus	45	-56 27 18	3.23	
L medial frontal gyrus	11	-9 52 -13	3.16	11
R medial frontal gyrus	11	3 40 -17	3.13	12
R caudate		6 15 8	3.93	131
R caudate		9 9 -3	3.56	

### Diffusion tensor imaging and tracking results

In order to characterize the anatomical connectivity of this temporo-parietal area that is activated during sentence and picture processing, we placed a seed volume in this region, and performed a deterministic tractography analysis. Fig. 6 illustrates a group map of white matter tracts that reveals a multi-component network emanating from this area. As illustrated, the multi-component network included a ventro-lateral component, a medial component, and a dorsal component. Fig. 6A illustrates the dorsal component reaching into the premotor cortex, by way of the superior longitudinal fasciculus/arcuate fasciculus (SLF/AF). Fig. 6B illustrates the medial component that reaches into the ventral frontal pole, by way of the inferior fronto-occipital fasciculus (IFOF). The ventro-lateral component illustrated in Fig. 6C reaches into the temporal pole, by way of the inferior longitudinal fasciculus (ILF) and middle longitudinal fasciculus (MdLF). What is remarkable about the connectivity of this region is that it is at the crossroads of these



**Fig. 2.** Comparison of sentence (ES > CS), picture (EP > CP) and conjunction (ES > CS) ∩ (EP > CP) contrasts. Activations are displayed on serial transverse sections in the stereotaxic space of Talairach and Tournoux (1988) with slices location indicated at the lower side of each image. On the right: scale of the t values.

major white matter pathways. This can be further seen in Fig. 6D illustrating deterministic tractography in an example subject.

*Correlation between pathway density and comprehension*

The white matter pathways linked to the temporo-parietal area involve an extended network, linking areas that are known to play functional roles that could contribute to the processing of comprehension. In order to establish the potential functional link between comprehension and the density of this pathway, we analyzed the correlation between the relative pathway density (number of fibers in the temporo-parietal pathway/total number of fibers) for individual subjects, and their sentence imageability described above. As illustrated in Fig. 6E, this analysis reveals a significant correlation between this

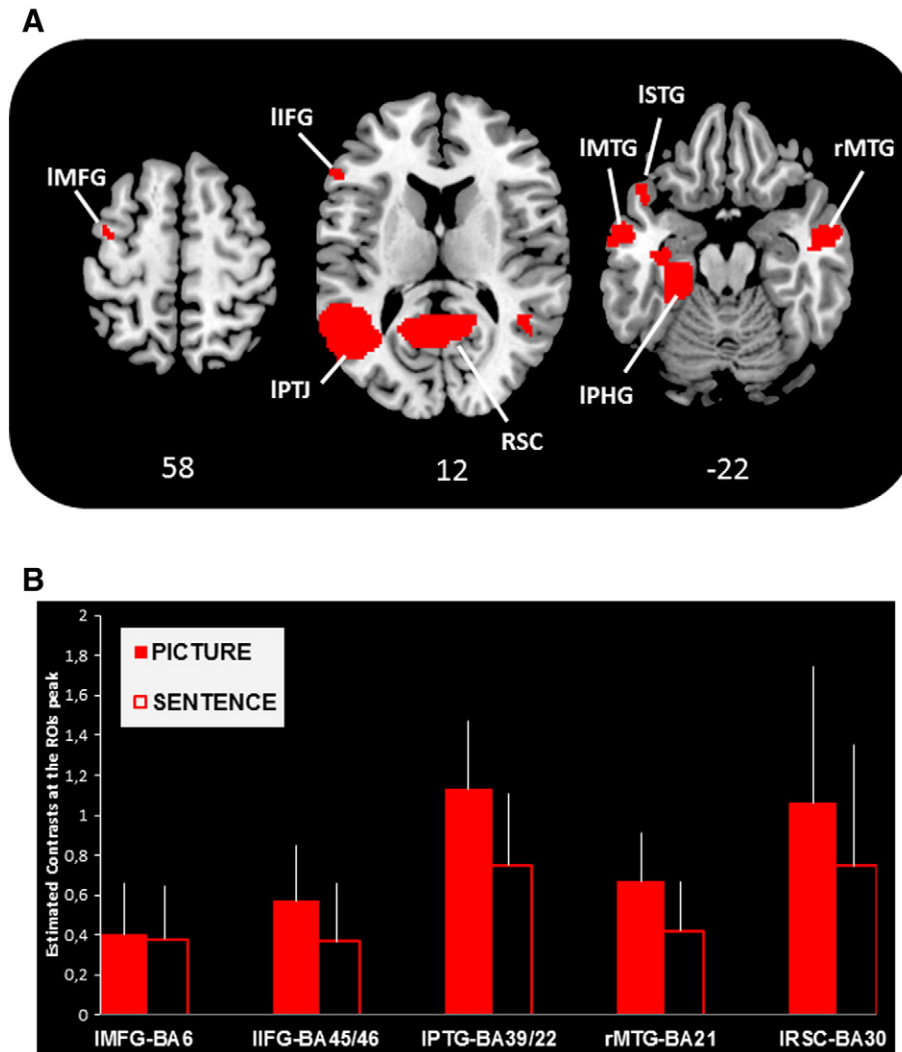
measure of the connectivity, and subject’s imageability ( $r = 0.57$ ,  $F = 8.34$ ,  $p = 0.010$ ). Looking in more detail, we dissected pathways originating at the temporo-parietal cortex (TPC) observed in at least 15/19 subjects, including a subdivision of the ventrolateral branch into the ILF terminating in BA38 and the MdLF terminating in BA21 (Menjot de Champfleury et al., 2013), and IFOF terminating in BA45–46. Dissection was performed by a two ROI method, with one ROI at the original TPC site, and the second at 3 sites corresponding to our fMRI ROIs at BA21, BA38 and BA45–46.

**Table 2**  
Anatomical regions displaying significant activation revealed when pictures of event scenes are contrasted with the scrambled picture control images.

Anatomical area	BA	x, y, z	t-stat	Ke
(EP > CP) P < 0.05 (FDR)				
L inferior temporal gyrus	19	-42 -76 -1	20.86	11670
R middle occipital gyrus	39/19	50 -72 9	18.38	
R middle temporal gyrus	39	50 -69 17	16.55	
R medial frontal gyrus	11	0 40 -17	6.08	1050
L medial frontal gyrus	10	-6 62 19	4.91	
R medial frontal gyrus	10	9 61 5	4.29	
L inferior frontal gyrus	45	39 19 21	2.73	12
L precentral	4	-42 -6 53	3.46	77
L precentral	6/4	-50 -10 39	2.55	
L cingulum	24	-3 -4 39	3.21	70
L cingulum	31	-12 -27 40	2.79	

**Table 3**  
Anatomical regions displaying significant activation revealed by conjunction analysis of sentences vs control sentences (ES > CS) and pictures vs control pictures (EP > CP) contrasts. Anatomical localization and coordinates are based on Talairach and Tournoux’s stereotaxic atlas (1988).

Anatomical area	BA	x, y, z	t-stat	Ke
(ES > CS) ∩ (EP > CP) P < 0.005 (unc.)				
L parahippocampal gyrus	35/36	-33 -38 -8	6.63	1019
L Cingulum post (RSC)	30/23	-9 -55 17	5.52	
L Cingulum post (RSC)	29/30	-15 -49 8	5.06	
L uncus	20	-36 -13 -30	4.7	
L middle temporal gyrus	21	-63 -4 -15	4.43	
L middle temporal gyrus	39	-42 -66 23	6.64	651
L superior temporal gyrus	22	-53 -52 14	5.72	
R middle temporal gyrus	39	53 -69 26	3.89	166
R middle/superior temporal gyrus	22	45 -46 11	3.34	
R middle temporal gyrus	21	53 -7 -17	4.39	76
L superior temporal gyrus	38	-45 16 -21	3.84	19
R medial frontal gyrus	11	3 40 -17	3.13	27
L medial frontal gyrus	11	-9 52 -13	3.16	19
L inferior frontal gyrus	45/46	-56 29 7	3.41	21
L middle frontal gyrus	6	-42 0 53	3.00	10
R caudate		3 11 -6	3.04	13



**Fig. 3.** (A) Clusters of activation for the conjunction contrasts  $(ES > CS) \cap (EP > CP)$  represented on transverse sections at  $p_{\text{uncorr}} < 0.005$  and (B) estimated contrasts (mean beta values and error bars) at the activation peak for each ROI. Note the significant ROIs activation for both picture and sentence: left inferior and middle prefrontal (IIFG, IMFG), in left parahippocampal gyrus (IPHG), bilaterally in retrosplenial cortex (RSC), in temporo-parietal junction (PTJ) and middle temporal gyrus (MTG). Activations are displayed on serial transverse sections in the stereotaxic space of Talairach and Tournoux (1988) with slices location indicated at the lower side of each image.

We then performed the correlation analysis on these individual components. The only pathway whose density correlated with the behavioural imageability scores was the parieto-temporal-BA21 pathway corresponding to the MdLF ( $r = 0.57$ ,  $p = 0.011$ , significant with Bonferroni correction for multiple comparisons). The correlation between pathway density and imageability thus appears at two levels: first, when taking into consideration all fibers identified using the TPC ROI, and then again selectively for the TPC-BA21 pathway identified as the MdLF. Details on the statistical analysis and tract identification are provided in the Supplementary Material 5.

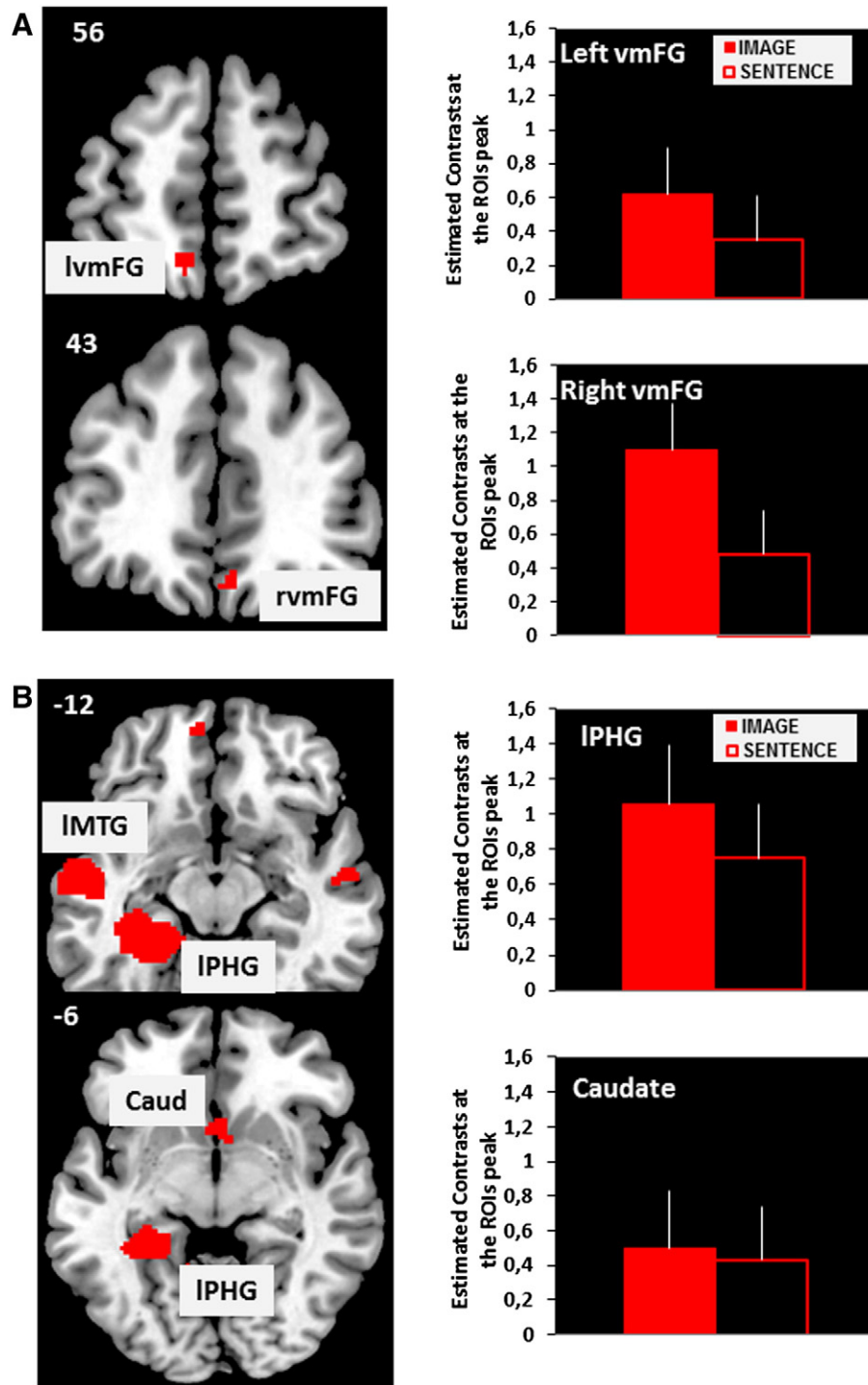
## Discussion

In a task of semantic analysis of pictures and sentences describing daily events, we found bilateral activation in neural structures distributed in the prefrontal cortex, in the temporal and parietal lobes as well as in the basal ganglia. Interestingly, this neural network was strikingly overlapping with the previously described semantic network involved in language comprehension ((Binder et al., 2009), for Review). If the existence of common processes in semantic extraction of verbal and non-verbal events is indubitable, the neural correlates of such a common system remain a matter of investigation. After assessing alternative

interpretations, we then discuss the mental processes and anatomical substrates potentially implicated in our results.

### Possible caveats and other considerations

Our findings of a distributed neural network commonly activated during our verbal and non-verbal tasks could be related to cognitive processes other than the semantic or conceptual knowledge system. First, one can argue that the subject might have explored the pictures displayed in our experiment by a mentally evoked verbal description, which would thus activate the same neural structures as in the verbal task. Such a strategy in the picture exploration, while it cannot be totally excluded, would have triggered activity in numerous neural structures linked to language function, including syntactic, phonologic related prefrontal structures. Indeed, when we analysed the pictures/control contrasts, we observed a pattern of activation which encompasses a number of neural structures not activated with the sentences/control contrasts. More specifically, as observed in Fig. (2) the picture related pattern is distinct from the sentence related activation, and does not include the regions involved in language processing including the perisylvian region of the inferior frontal cortex (Keller et al., 2009; Price et al., 1996). Second, another cognitive alternative to the activation of a common semantic system could be that our experimental tasks in

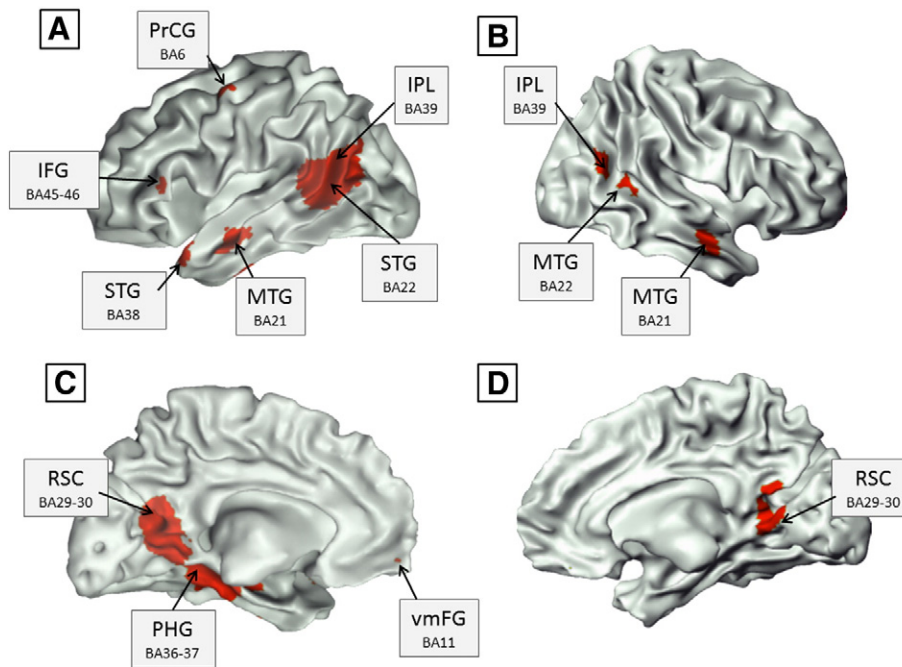


**Fig. 4.** Clusters of activation for the conjunction contrasts  $(ES > CS) \cap (EP > CP)$  represented on coronal (A) and transverse (B) sections at  $p_{\text{uncorr}} < 0.005$  and estimated contrasts (mean beta values and error bars) at the activation peak for each ROI. Note the significant ROIs activation for both picture and sentence: in left parahippocampal gyrus (IPHG), bilaterally in ventro-medial frontal (lvmFG, rvmFG) and middle temporal gyrus (MTG) and in the caudate nucleus. Activations are displayed on serial transverse sections in the stereotaxic space of Talairach and Tournoux (1988) with slices location indicated at the lower side of each image.

both conditions triggered attentional processes and recruited the corresponding structures. However, attention related networks typically implicate more dorsal neural pathways than those described in the current study, i.e. the associative visual cortex with the intraparietal sulcus and adjacent parietal areas, the executive function related structures including the dorsolateral prefrontal cortex and the FEF involved in re-orienting behaviour (Corbetta et al., 2008) for review). Another argument in favour of a neural network common to language and picture semantic processing is the partial left hemispheric lateralization.

Even though the common semantic neural network was largely bilateral in the medial and temporo-parietal regions, the prefrontal and anterior temporal clusters were found only in the left hemisphere. In previous studies (Nielsen et al., 2013; Paivio, 1986; Stephan et al., 2003), it has been shown that while attention to external stimuli require more right parieto-frontal activation, attending to internal stimuli, narrative or self-reflection tend to recruit a left lateralized network including hubs in parieto-temporal and temporal cortex as well as the lateral and inferior prefrontal cortex. Thus, based on the overall literature





**Fig. 5.** Lateral and medial views of the brain representing the identified semantic network shared by pictures and sentences processes. Lateral left (A) and right (B) sides: inferior prefrontal gyrus (IFG)- precentral gyrus (PrCG)-Superior and middle temporal gyri (STG, MTG)- Inferior parietal lobe (IPL). Medial left (C) and right (D) sides: retrosplenial gyrus (RSC), parahippocampal gyrus (PHG) and ventro-medial frontal gyrus (vmFG). Each ROI is identified with the corresponding Brodman's area.

observations (Gainotti, 2014; Nielsen et al., 2013; Paivio, 1986; Stephan et al., 2003) left dominant connections associated to language and perception of internal stimuli are in accordance with our findings and interpretation of a prime involvement of our common network in conceptualization rather than in sensory-motor processing. Thus based on the topography of the activated neural structures it seems unlikely that the shared neural system might be the result of either a purely linguistic computation or an attentional driven activity. Moreover, in favour of this assessment, the distribution of the neural structures with shared activity was clearly comparable to previously described semantic system triggered during word and object stimuli (Binder and Desai, 2011; Bright et al., 2004; Vandenberghe et al., 1996).

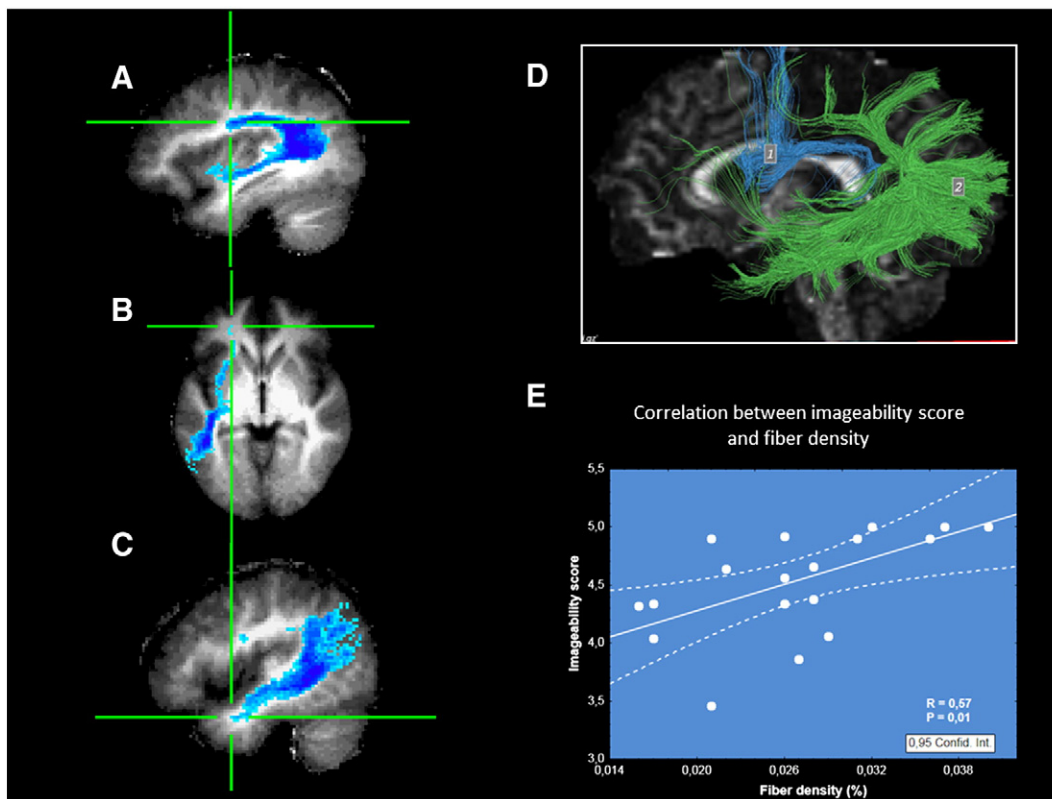
Previous studies have diverging views concerning the neural representation of the conceptual knowledge and several theories have been proposed. Indeed, some authors (Barsalou, 1999, 2008; Hauk et al., 2004; Hauk and Pulvermuller, 2004, 2011; Pulvermuller, 2005; Tettamanti et al., 2005; van Dam et al., 2010) defend the “embodied” theory based on a simulation of experiential perception-action traces underlying semantic representation, and at the extreme other authors defend symbolic disembodied models based on an amodal representation of concepts (Fodor, 1983; Mahon and Caramazza, 2009). Between these two extremes theories, hybrid models yield the idea of an embodied abstraction characterised by variable sensory-motor simulation that progressively converges to a common heteromodal semantic network (Binder and Desai, 2011; Damasio, 1989; Jefferies, 2013; Man et al., 2012, 2013; Meyer et al., 2010; Patterson et al., 2007; Regev et al., 2013). Interestingly our findings provide compelling evidence for such relationships between perception/action and conceptual processing as our common multiple level meaning system reveals the implication of (1) modality-specific cortical areas localised in the premotor cortex, the parahippocampus-retrosplenial areas, and the medio-ventral prefrontal cortex (2) high level convergence zones in the temporo-parietal and middle temporal cortices and finally (3) a possible semantic control region represented by the inferior prefrontal cortex and the basal ganglia. In the following sections, we will address each of these different processes and their anatomical correlates, in the context of the literature on competing theories.

#### *From grounded-based to introspective inference-based processes*

The cortical network commonly activated during sentences and pictures implicated sensory-motor, introspective memory and emotion related cortical regions including the premotor cortex in the middle prefrontal cortex, the inferior parietal cortex, the posterior cingulate areas in the retro-splenial gyrus extending to the parahippocampus and the medio-ventral prefrontal region (BA11). This is consistent with the embodied theories of sentence comprehension, e.g. (Barsalou, 1999, 2009) which suggest that a process referred to as “simulation” underlies not only language understanding, but the deepest aspects of conceptual processing, social cognition and natural intelligence. Indeed, evidence has been provided that language comprehension arises from activation of supplementary areas, in addition to the core language regions, in the inferior frontal and superior temporal lobes (Binder et al., 2009; Jefferies, 2013; Kiefer and Pulvermuller, 2012). In addition, the embodiment theory has also been extended to concept representation implicating modality specific areas typically encoding visual and motor information (Hauk et al., 2004; Hauk and Pulvermuller, 2004, 2011; Pulvermuller, 2005; Tettamanti et al., 2005; van Dam et al., 2010).

#### *Sensory-motor simulation*

In our current study, the displayed pictures and sentences described action-related events involving a person engaged in an event. The analysis of such events induced activation in both premotor cortex BA6 and visual extrastriate cortex, including parietal regions respectively implicated in action word and visual scene comprehension. Extended work has demonstrated the relevance of the motor system in concept representation (Boulenger et al., 2009; Desai et al., 2010; Hauk et al., 2004; Hauk and Pulvermuller, 2004, 2011; Pulvermuller, 2005; Tettamanti et al., 2005). More specifically, the comprehension of action words triggers an activation pattern in motor areas in an effector specific fashion (Hauk et al., 2004; Hauk and Pulvermuller, 2011). Likewise, Tettamanti et al. (2005) found a similar category-specific organisation of motor cortex during comprehension of action related sentences. Our results showing an activation in premotor area (TAL,  $-42, 0, 53$ ) closely correspond



**Fig. 6.** Population and individual subject images of multi-component network from temporo-parietal cortex, and correlation of this pathway density and comprehension behavior. A–C. Population hit maps. Light to dark blue indicates number of subjects displaying a streamline at that location, with a minimum threshold of 10/19 subjects. A. Dorsal pathway via a pathway adjacent to the superior longitudinal fasciculus and arcuate fasciculus. B. Medial route to the mediofrontal pole via the inferior front-occipital fasciculus. C. Temporal route to the temporal pole via the inferior longitudinal fasciculus. D. Individual subject rendering of AF and the temporo-parietal pathway ensemble. Blue stained pathways from a seed value in BA44 (1) to isolate the AF. Green stained pathways from the temporo-parietal seed (2) value (MNI:  $-42, -66, 23$ ). E. Correlation between the imageability score and the relative number of fibers leaving the temporo-parietal cortex.

to those of Tettamanti et al. (2005) in the left premotor area BA 6 (hand-specific area:  $-30, -2, 56$ ) as observed during listening to hand-related action sentences. In our semantic network we found that the left inferior parietal lobe was significantly active during our verbal and nonverbal tasks similarly to previously described semantic circuit common to words and pictures (Vandenberghe et al., 1996). Electrophysiological recording in the monkey (Gallese et al., 1996; Rizzolatti et al., 1996) has shown that the observation of another individual's action could trigger neuronal discharge in premotor and parietal cortex as part of an observation/action matching “mirror-neuron” system (Rizzolatti et al., 1996, 2001). Such a mirror-neuron system further described in human could sustain the comprehension of others' actions (Rizzolatti and Craighero, 2004). Interestingly, by comparing cortical activation during Theory of Mind (TOM) vs. exogenous Attention tasks in normal and autistic subjects, Scholz et al. (2009) have located a specific TOM related region in the parieto-temporal cortical regions whose ventral part overlaps bilaterally with our parieto-temporal clusters (Dufour et al., 2013; Scholz et al., 2009). Recently, evidence has been provided that action related knowledge can be provided not only by action observation but also by hearing action or even by understanding sentences describing actions (Desai et al., 2010; Kohler et al., 2002; Tettamanti et al., 2005). Based on these observations, it is likely that our visuo-motor activations in the precentral gyrus and visual associative parietal cortex reflect the implication of such an observation-execution mirror system involved in the understanding of actions evoked during either verbal or non-verbal tasks.

#### Introspective-based processes

Another interesting finding concerns the activation pattern in visual extrastriate areas including bilaterally the retrosplenial cortex (RSC)

implicated in high-level vision. The greatest responses obtained during our verbal and non-verbal tasks were found in the ventral part of the retrosplenial cortex (BA29-30) that is involved in hippocampus-dependent processes (Vann et al., 2009) for Review). Interestingly, this retrosplenial region formed a ventrally extended cluster of activation in continuum with the activation of the parahippocampal gyrus in the left hemisphere (Huth et al., 2012; Johnson and Johnson, 2014; Vann et al., 2009). Along with a range of cognitive functions, the RSC has been associated to episodic memory and spatial navigation and more precisely in translating information between allocentric (world-centred) and egocentric (self-centred) reference frames (Spreng et al., 2009; Vann et al., 2009). Similarly, the parahippocampal gyrus localised in the left hemisphere is associated with semantic operations and episodic retrieval (Levine et al., 2004; Vargha-Khadem et al., 1997). These two cortical structures are richly interconnected and thus could play a critical role in scene-relevant relationships between objects and context as well as in episodic memory encoding and recall. The RSC along with the hippocampus cortical region have been proposed as a core network that might support scene construction as a process of mentally generating and maintaining a complex scene or event (Spreng et al., 2009; Vann et al., 2009). More recently, by using fMRI multi-voxel pattern analysis, Johnson and Johnson (2014) have shown that during mental imagery, item-specific information about perceived scenes is re-instantiated in parahippocampal and retrosplenial cortex. In the same vein, in our study the RSC and parahippocampus gyrus could have been responsible respectively for the reconstruction and transformation of visuo-spatial information related to the events and scenes evoked in our tasks.

Previous studies have reported the role of the ventro-medial prefrontal cortex in subserving different aspects of pro-social sentiments,

mood and emotional regulation as well as self-reference information processing (Feldmanhall et al., 2014; Lewis et al., 2005, 2011; Moll et al., 2011). In our study we found significant bilateral activation in the ventro-medial prefrontal region BA 11 in semantic analysis of verbal and non-verbal events. Little is known about the functional relation between the medial prefrontal cortex and the conceptual system. In a recent work, Burin et al. (2014) have shown that ventro-medial prefrontal cortex contributes to narrative comprehension by supporting inferences about socio-emotional aspects of verbally described situations. Furthermore, with the temporo-parietal junction this medial prefrontal region could work in coordination to regulate moral cognition (FeldmanHall et al., 2012, 2014). Likewise, it is possible that these two cortical regions through dynamic interactions integrate emotional attributes of events evoked in our verbal and non-verbal tasks. Another alternative interpretation of the medio-ventral prefrontal activity relies on self-processing and self-knowledge involving the default mode network (Molnar-Szakacs and Uddin, 2013). Activation of the default mode network including medial prefrontal cortex, posterior cingulate, lateral parietal and medial temporal cortices has been associated with “tasks that encourage subjects toward internal mentation, including autobiographical memory, thinking about one’s future, theory of mind, self-referential and affective decision making...” (Andrews-Hanna et al., 2010 p. 550). Our results indicate that understanding scenes depicting human activities, communicated via sentences or pictures, also recruits part of the default mode network, especially the medial cerebral structures in the prefrontal cortex in addition to the posterior cingulate cortex and the temporal region. Such a medial network might be preferentially implicated in mentalizing about the self and others. Using functional connectivity, Lombardo et al. (2010) described shared neural representations for mentalizing and physical representation of self and other. These authors hypothesize “that high level inference-based mentalising systems (a.g. ventro-medial prefrontal cortex, posterior cingulate cortex, right TPJ) are integrating their signal with lower level embodied/simulation based systems” (e.g. sensorimotor cortices: pre-SMA, premotor, frontal operculum, intraparietal cortices). This extends the notion of embodied comprehension. Bar (2009) suggests then that recognition (which we can extend to comprehension) consists in determining ‘what is this like?’ which requires a proactive link to existing situations in memory. This proposal on understanding implies the integration of the understood into one’s predictive, proactive memory/prediction system. In our study, the presented sentences and pictures act as triggers for the initiation of such processes, as part of understanding.

Combined with the literature findings our results are consistent with the idea that the understanding of both verbal and non-verbal event descriptions recruits a distributed network whose activity results in the integration of low-level embodied processes (premotor and visual associative parietal activity) within higher level inference-based mentalizing (parahippocampal-cingulate-ventro-medial prefrontal circuit activity) as suggested in the verbal domain by Lombardo et al. (2010).

#### *Heteromodal representations*

In addition to grounded simulation processing, there is compelling evidence that conceptual processing (i.e. generalized processing that can occur without reference to specific experience, such as social cognition, language) can occur through supramodal representations involving the parieto-temporal and the lateral temporal cortex, (for review (Binder and Desai, 2011; Binder et al., 2009; Jefferies, 2013)). Interestingly, these two parietal and temporal sites were found to be quite responsive during our tasks, suggesting an action in computing the meaning of both verbally- and visually-driven events. Evidence for a semantic integration in temporal lobe is provided in semantic dementia patients with brain atrophy specifically in the lateral temporal cortex (Hodges et al., 1992, 1995; Jefferies and Lambon Ralph, 2006; Lambon Ralph et al., 2007). These patients are characterised by advancing

degradation in multimodal semantic memory with no category-specific impairment suggestive of more general or amodal form of semantic representation.

In our study we observed two separate sites of activation in the temporal lobe: one located in the middle part (BA21) and the other in the anterior pole (BA38). There is a longstanding view for the temporal lobe to be the highpoint of a caudo-rostral convergence of high-level multimodal information involved in conceptual knowledge. While there is evidence for such a proposal of the temporal cortex as a centre of conceptual representation, controversy remains about the distributed aspects in the parietal and temporal lobes of the conceptual construction. Indeed, while some authors defend the idea of distributed networks with multiple specialized convergent regions (Damasio, 1989; Man et al., 2013), others argue for a distributed network + hub organisation that could achieve the higher-order generalizations of conceptual processes (Jefferies, 2013). In the same vein as the convergence zone theory, it has been suggested that semantic representations would be combined in a central “hub” in the anterior temporal lobe (ATL) in addition to a distributed presemantic network (Jefferies, 2013; Patterson et al., 2007; Visser et al., 2010). The idea of a central amodal store in the anterior temporal lobe accounts for semantic disorders affecting several modalities described in semantic dementia. These different theories on the underpinnings of conceptual representation in the brain have in common the idea of a distributed sensorimotor pre-semantic signals converging towards one or several central and modality invariant region of conceptual representation either in an anterior temporal “hub” (Patterson et al., 2007) or in the postero-lateral temporal convergence-divergence zone (CDZ) (Meyer and Damasio, 2009). However, while the ATL hub would constitute a unique central store of semantic representation, the CDZs establish meaning through multiregional dynamic interactions. While our present fMRI data cannot speak for the current issue related to these two possible mechanisms subserving semantic analysis, our DTI findings on connections density from the parieto-temporal cortex tend to support the idea of a heteromodal semantic posterior temporal zone as defined by Meyer and Damasio (2009). Indeed, the activation clusters identified in our current study, in the lateral temporal cortex (TAL: 45, –46, 11 and –53, –52, 14) encompassed the posterior temporal site (TAL: 64, –42, 12 and –60, –42, 12) previously described by Man et al. (2012) as a supramodal conceptual zone. Our DTI analysis revealed that the temporo-parietal area that was significantly activated in comprehension participates in a number of white matter pathways that have been associated with language processing including the SLF/AF, the IFOF, the ILF and the MdLF. These connections could provide the anatomical basis for the hub status attributed to this area (Vandenberghe et al., 2013). Of those that were observed in at least 15/19 subjects (MdLF, ILF, IFOF), the pathway density of the MdLF was correlated with subjects behavioural imageability scores. This is consistent with recent connectivity analyses that identified the role of the MdLF between STS/BA39 (corresponding to our temporo-parietal region) and anterior STG/BA22 in the neural architecture of the language comprehension network (Turken and Dronkers, 2011). By combining neuroimaging activation with tractography measurements from the parieto-temporal ROI, our results are in favour of interactive parietal and temporal regions acting as convergence zones for heteromodal conceptualization.

#### *Prefronto-striatal system involved in a semantic control*

Recent evidence supports the view that while the posterior part of the inferior frontal cortex including the pars opercularis is preferentially recruited for low level phonological processing of language, the anterior part including pars triangularis part is preferentially involved in semantic processing of language (Keller et al., 2009; Nixon et al., 2004). The fact that this latter region was activated during both verbal and nonverbal tasks in our study is suggestive of a role of this prefrontal region including BA45–46 in integration of a semantic representation shared between language and images. Compelling evidence of this claim has

been provided by neuroimaging and EEG explorations by Van Doren et al. (2010, 2012) who studied whether there are similar brain regions involved in word and picture identification when the stimuli became conscious. The authors described two zones, in the left inferior frontal cortex and occipito-temporal cortices activated in an amodal manner with conscious perception of word and picture stimuli. While we did not find a similar activity in the occipito-temporal cortex, our activated site in the left inferior frontal lobe (TAL:  $-57,30,9$ ) was near the one (TAL:  $-42,36,15$ ) described by Van Doren et al. (2010) to be implicated in semantic processing of word and pictures and possibly mediating access to short-term memory enhancing cognitive control. While these 2 sites are at 6 mm apart in the antero-posterior and dorso-ventral planes, Van Doren's site is localized deeper (about 1.6 mm) in the inferior prefrontal sulcus. Based on Gabrieli's findings (Gabrieli et al., 1998) activation in left inferior prefrontal cortex might reflect a semantic working memory independently of the stimulus modality. Accordingly, through neuroimaging and neuropsychological studies in aphasia, the inferior frontal cortex has been implicated in semantic control acting preferentially in semantic selection when several representations are active (Jefferies, 2013; Thompson-Schill, 2003). Furthermore, by rTMS stimulation in inferior frontal cortex or posterior middle temporal cortex in normal subjects, Jefferies' group suggests a strong coupling between inferior prefrontal and posterior middle temporal regions forming a distributed network underpinning a semantic control (Jefferies, 2013; Whitney et al., 2011, 2012). Such a functional fronto-temporal linkage has also been reported by Van Doren et al. (2012) who demonstrated a long distance inferior frontal- occipito-temporal network subserving conscious identification associated to memory retrieval of semantic attributes common to words and pictures. Furthermore, we know that the inferior prefrontal cortex as well as the lateral temporal cortex are connected to the striatum forming cortico-striatal loops involved in executive function, including working memory, planning and selection processes (Alexander et al., 1986; Monchi et al., 2007; Nakano et al., 2000; Redgrave et al., 2010). As found in our study the caudate nuclei were activated during our sentence and picture comprehension tasks suggesting a role of this structure in semantic function. Accordingly Crosson et al. (Crosson et al., 2007) provide compelling evidence of a caudate implication in semantically related operations. Thus, the striatum including the caudate nucleus being the core of cortico-thalamo-cortical pathways could regulate semantic processing by the interplay of enhancing/suppressing the transmission inside the thalamo-cortical circuit (Hart et al., 2013). Taken together, these findings combined with our data are consistent with the hypothesis of a distributed cortico-striatal network including the inferior prefrontal (BA45–46) and middle temporal cortices and the caudate nucleus activated in our study, as a candidate for amodal representation or control of conceptual knowledge common to language and visual systems.

## Conclusions

In this research we have attempted to further characterize the fronto-temporo-parietal semantic network. Previous research has focused largely on semantics in language, and those studies that combine language and visual scenes used relatively simple stimuli. In order to tap more deeply into the semantic system, here we used sentences and images that depicted rich human activity. The resulting conjunction analysis revealed a broadly distributed system that included sensorimotor and associative areas evoked in embodied models of semantics, and more heteromodal areas including the lateral temporal cortex that have been evoked as semantic centers, along with a major activation in the temporoparietal cortex. The strong activation of the temporoparietal region argues for the role of this area as a core region in the semantic system, with a potential role as an abstract convergence-divergence zone, as suggested by Binder and Desai (2011). The DTI results stress that this area is anatomically well-situated, at the crossroads of the principal white matter pathways that have been

implicated in comprehension. Furthermore, the correlation between subjects' ability to represent sentences and the structural density of the pathway between the temporo-parietal cortex and the middle temporal lobe support arguments for the functional role of these areas in comprehension.

The extended activation in areas supporting the most diverse higher cognitive functions, semantic processing, spatial perspective taking, mentalizing, suggest that comprehension is a profound process that involves the projection of the individual into the understood scene.

## Acknowledgments

This research was supported by funding from the French ANR Comprendre, and from the European Community through grants FP7-ICT 231267 Project Organic, FP7-ICT-270490 Project EFAA, and FP7-ICT-612139 Project WYSIWYD.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2014.11.024>.

## References

- Alexander, G.E., DeLong, M.R., Strick, P.L., 1986. Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annu. Rev. Neurosci.* 9, 357–381.
- Andrews-Hanna, J.R., Reidler, J.S., Sepulcre, J., Poulin, R., Buckner, R.L., 2010. Functional-anatomic fractionation of the brain's default network. *Neuron* 65, 550–562.
- Anwander, A., Tittgemeyer, M., von Cramon, D.Y., Friederici, A.D., Knosche, T.R., 2007. Connectivity-based parcellation of Broca's area. *Cereb. Cortex* 17, 816–825.
- Bajo, M.T., 1988. Semantic facilitation with pictures and words. *J. Exp. Psychol. Learn. Mem. Cogn.* 14, 579–589.
- Bar, M., 2009. The proactive brain: memory for predictions. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 364, 1235–1243.
- Barsalou, L.W., 1999. Perceptual symbol systems. *Behav. Brain Sci.* 22, 577–609 (discussion 10–60).
- Barsalou, L.W., 2008. Grounded cognition. *Annu. Rev. Psychol.* 59, 617–645.
- Barsalou, L.W., 2009. Simulation, situated conceptualization, and prediction. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 364, 1281–1289.
- Barsalou, L.W., Kyle Simmons, W., Barbey, A.K., Wilson, C.D., 2003. Grounding conceptual knowledge in modality-specific systems. *Trends Cogn. Sci.* 7, 84–91.
- Basser, P.J., Pajevic, S., Pierpaoli, C., Duda, J., Aldroubi, A., 2000. In vivo fiber tractography using DT-MRI data. *Magn. Reson. Med.* 44, 625–632.
- Binder, J.R., Desai, R.H., 2011. The neurobiology of semantic memory. *Trends Cogn. Sci.* 15, 527–536.
- Binder, J.R., Desai, R.H., Graves, W.W., Conant, L.L., 2009. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* 19, 2767–2796.
- Boulenger, V., Hauk, O., Pulvermüller, F., 2009. Grasping ideas with the motor system: semantic somatotopy in idiom comprehension. *Cereb. Cortex* 19, 1905–1914.
- Bright, P., Moss, H., Tyler, L.K., 2004. Unitary vs multiple semantics: PET studies of word and picture processing. *Brain Lang.* 89, 417–432.
- Burin, D.I., Acion, L., Kurczek, J., Duff, M.C., Tranel, D., Jorge, R.E., 2014. The role of ventromedial prefrontal cortex in text comprehension inferences: Semantic coherence or socio-emotional perspective? *Brain Lang.* 129, 58–64.
- Catani, M., Jones, D.K., ffytche, D.H., 2005. Perisylvian language networks of the human brain. *Ann. Neurol.* 57, 8–16.
- Corbetta, M., Patel, G., Shulman, G.L., 2008. The reorienting system of the human brain: from environment to theory of mind. *Neuron* 58, 306–324.
- Cox, R.W., 1996. AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Comput. Biomed. Res.* 29, 162–173.
- Crosson, B., Benjamin, M., Levy, I., 2007. Role of the basal ganglia in language and semantics: Supporting cast. Cambridge University Press, Cambridge (UK).
- Damasio, A.R., 1989. Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. *Cognition* 33, 25–62.
- Desai, R.H., Binder, J.R., Conant, L.L., Seidenberg, M.S., 2010. Activation of sensory-motor areas in sentence comprehension. *Cereb. Cortex* 20, 468–478.
- Dufour, N., Redcay, E., Young, L., Mavros, P.L., Moran, J.M., et al., 2013. Similar brain activation during false belief tasks in a large sample of adults with and without autism. *PLoS ONE* 8, e75468.
- FeldmanHall, O., Dalgleish, T., Thompson, R., Evans, D., Schweizer, S., Mobbs, D., 2012. Differential neural circuitry and self-interest in real vs hypothetical moral decisions. *Soc. Cogn. Affect. Neurosci.* 7, 743–751.
- Feldmanhall, O., Mobbs, D., Dalgleish, T., 2014. Deconstructing the brain's moral network: dissociable functionality between the temporoparietal junction and ventro-medial prefrontal cortex. *Soc. Cogn. Affect. Neurosci.* 9, 297–306.
- Fodor, J.A., 1983. *The modularity of mind: an essay on faculty psychology*. MIT Press, Cambridge (MA).

- Frey, S., Campbell, J.S., Pike, G.B., Petrides, M., 2008. Dissociating the human language pathways with high angular resolution diffusion fiber tractography. *J. Neurosci.* 28, 11435–11444.
- Friederici, A.D., 2009. Pathways to language: fiber tracts in the human brain. *Trends Cogn. Sci.* 13, 175–181.
- Friederici, A.D., Bahlmann, J., Heim, S., Schubotz, R.I., Anwander, A., 2006. The brain differentiates human and non-human grammars: functional localization and structural connectivity. *Proc. Natl. Acad. Sci. U. S. A.* 103, 2458–2463.
- Friston, K., 2005. A theory of cortical responses. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 360, 815–836.
- Friston, K.J., Worsley, K.J., Frackowiak, R.S., Mazziotta, J.C., Evans, A.C., 1994. Assessing the significance of focal activations using their spatial extent. *Hum. Brain Mapp.* 1, 210–220.
- Gabrieli, J.D., Poldrack, R.A., Desmond, J.E., 1998. The role of left prefrontal cortex in language and memory. *Proc. Natl. Acad. Sci. U. S. A.* 95, 906–913.
- Gainotti, G., 2014. Why are the right and left hemisphere conceptual representations different? *Behav. Neurol.* 2014, 603134.
- Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition in the premotor cortex. *Brain* 119 (Pt 2), 593–609.
- Glasser, M.F., Killing, J.K., 2008. DTI tractography of the human brain's language pathways. *Cereb. Cortex* 18, 2471–2482.
- Graves, W.W., Binder, J.R., Desai, R.H., Conant, L.L., Seidenberg, M.S., 2010. Neural correlates of implicit and explicit combinatorial semantic processing. *NeuroImage* 53, 638–646.
- Harel, A., Kravitz, D.J., Baker, C.I., 2013. Deconstructing visual scenes in cortex: gradients of object and spatial layout information. *Cereb. Cortex* 23, 947–957.
- Hart Jr., J., Maguire, M.J., Motes, M., Mudar, R.A., Chiang, H.S., et al., 2013. Semantic memory retrieval circuit: role of pre-SMA, caudate, and thalamus. *Brain Lang.* 126, 89–98.
- Hauk, O., Pulvermüller, F., 2004. Neurophysiological distinction of action words in the fronto-central cortex. *Hum. Brain Mapp.* 21, 191–201.
- Hauk, O., Pulvermüller, F., 2011. The lateralization of motor cortex activation to action-words. *Front. Hum. Neurosci.* 5, 149.
- Hauk, O., Johnsrude, I., Pulvermüller, F., 2004. Somatotopic representation of action words in human motor and premotor cortex. *Neuron* 41, 301–307.
- Hickok, G., Poeppel, D., 2004. Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition* 92, 67–99.
- Hodges, J.R., Patterson, K., Oxbury, S., Funnell, E., 1992. Semantic dementia. Progressive fluent aphasia with temporal lobe atrophy. *Brain* 115 (Pt 6), 1783–1806.
- Hodges, J.R., Graham, N., Patterson, K., 1995. Charting the progression in semantic dementia: implications for the organisation of semantic memory. *Memory* 3, 463–495.
- Huth, A.G., Nishimoto, S., Vu, A.T., Gallant, J.L., 2012. A continuous semantic space describes the representation of thousands of object and action categories across the human brain. *Neuron* 76, 1210–1224.
- Jackendoff, R., 1987. On beyond zebra: the relation of linguistic and visual information. *Cognition* 26, 89–114.
- Jefferies, E., 2013. The neural basis of semantic cognition: converging evidence from neuropsychology, neuroimaging and TMS. *Cortex* 49, 611–625.
- Jefferies, E., Lambon Ralph, M.A., 2006. Semantic impairment in stroke aphasia versus semantic dementia: a case-series comparison. *Brain* 129, 2132–2147.
- Johnson, M.R., Johnson, M.K., 2014. Decoding individual natural scene representations during perception and imagery. *Front. Hum. Neurosci.* 8, 59.
- Johnson-Laird, P.N., 1981. Cognition, computers, and mental models. *Cognition* 10, 139–143.
- Johnson-Laird, P.N., 1987. The mental representation of the meaning of words. *Cognition* 25, 189–211.
- Johnson-Laird, P.N., 1988. Levels of representation: consciousness and the computational mind. *Science* 239, 1546–1547.
- Johnson-Laird, P.N., 2010. Mental models and human reasoning. *Proc. Natl. Acad. Sci. U. S. A.* 107, 18243–18250.
- Keller, S.S., Crow, T., Foundas, A., Amunts, K., Roberts, N., 2009. Broca's area: nomenclature, anatomy, typology and asymmetry. *Brain Lang.* 109, 29–48.
- Kiefer, M., Pulvermüller, F., 2012. Conceptual representations in mind and brain: theoretical developments, current evidence and future directions. *Cortex* 48, 805–825.
- Kintsch, W., 1988. The role of knowledge in discourse comprehension: a construction-integration model. *Psychol. Rev.* 95, 163–182.
- Kircher, T., Sass, K., Sachs, O., Krach, S., 2009. Priming words with pictures: neural correlates of semantic associations in a cross-modal priming task using fMRI. *Hum. Brain Mapp.* 30, 4116–4128.
- Kohler, E., Keysers, C., Umiltà, M.A., Fogassi, L., Gallese, V., Rizzolatti, G., 2002. Hearing sounds, understanding actions: action representation in mirror neurons. *Science* 297, 846–848.
- Lambon Ralph, M.A., Lowe, C., Rogers, T.T., 2007. Neural basis of category-specific semantic deficits for living things: evidence from semantic dementia, HSVE and a neural network model. *Brain* 130, 1127–1137.
- Leemans, A., Jones, D.K., 2009. The B-matrix must be rotated when correcting for subject motion in DTI data. *Magn. Reson. Med.* 61, 1336–1349.
- Levine, B., Turner, G.R., Tisserand, D., Hevenor, S.J., Graham, S.J., McIntosh, A.R., 2004. The functional neuroanatomy of episodic and semantic autobiographical remembering: a prospective functional MRI study. *J. Cogn. Neurosci.* 16, 1633–1646.
- Lewis, P.A., Critchley, H.D., Smith, A.P., Dolan, R.J., 2005. Brain mechanisms for mood congruent memory facilitation. *NeuroImage* 25, 1214–1223.
- Lewis, P.A., Rezaie, R., Brown, R., Roberts, N., Dunbar, R.I., 2011. Ventromedial prefrontal volume predicts understanding of others and social network size. *NeuroImage* 57, 1624–1629.
- Lichtheim, L., 1885. On aphasia. 2006, English translation In: Grodzinsky, Y., Amunts, K. (Eds.), *Broca's Region*. Oxford University Press, Oxford, pp. 318–347.
- Lombardo, M.V., Chakrabarti, B., Bullmore, E.T., Wheelwright, S.J., Sadek, S.A., et al., 2010. Shared neural circuits for mentalizing about the self and others. *J. Cogn. Neurosci.* 22, 1623–1635.
- Mahon, B.Z., Caramazza, A., 2009. Concepts and categories: a cognitive neuropsychological perspective. *Annu. Rev. Psychol.* 60, 27–51.
- Makris, N., Pandya, D.N., 2009. The extreme capsule in humans and rethinking of the language circuitry. *Brain Struct. Funct.* 213, 343–358.
- Makris, N., Worth, A.J., Sorensen, A.G., Papadimitriou, G.M., Wu, O., et al., 1997. Morphometry of in vivo human white matter association pathways with diffusion-weighted magnetic resonance imaging. *Ann. Neurol.* 42, 951–962.
- Makris, N., Kennedy, D.N., McInerney, S., Sorensen, A.G., Wang, R., et al., 2005. Segmentation of subcomponents within the superior longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. *Cereb. Cortex* 15, 854–869.
- Makris, N., Papadimitriou, G.M., Kaiser, J.R., Sorg, S., Kennedy, D.N., Pandya, D.N., 2009. Delineation of the middle longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. *Cereb. Cortex* 19, 777–785.
- Man, K., Kaplan, J.T., Damasio, A., Meyer, K., 2012. Sight and sound converge to form modality-invariant representations in temporoparietal cortex. *J. Neurosci.* 32, 16629–16636.
- Man, K., Kaplan, J., Damasio, H., Damasio, A., 2013. Neural convergence and divergence in the mammalian cerebral cortex: from experimental neuroanatomy to functional neuroimaging. *J. Comp. Neurol.* 521, 4097–4111.
- Menjot de Champfleury, N., Lima Maldonado, I., Moritz-Gasser, S., Machi, P., Le Bars, E., et al., 2013. Middle longitudinal fasciculus delineation within language pathways: a diffusion tensor imaging study in human. *Eur. J. Radiol.* 82, 151–157.
- Meyer, K., Damasio, A., 2009. Convergence and divergence in a neural architecture for recognition and memory. *Trends Neurosci.* 32, 376–382.
- Meyer, K., Kaplan, J.T., Essex, R., Webber, C., Damasio, H., Damasio, A., 2010. Predicting visual stimuli on the basis of activity in auditory cortices. *Nat. Neurosci.* 13, 667–668.
- Moll, J., Zahn, R., de Oliveira-Souza, R., Bramati, I.E., Krueger, F., et al., 2011. Impairment of prosocial sentiments is associated with frontopolar and septal damage in frontotemporal dementia. *NeuroImage* 54, 1735–1742.
- Molnar-Szakacs, I., Uddin, L.Q., 2013. Self-processing and the default mode network: interactions with the mirror neuron system. *Front. Hum. Neurosci.* 7, 571.
- Monchi, O., Petrides, M., Mejia-Constain, B., Strafella, A.P., 2007. Cortical activity in Parkinson's disease during executive processing depends on striatal involvement. *Brain* 130, 233–244.
- Nakano, K., Kayahara, T., Tsutsumi, T., Ushiro, H., 2000. Neural circuits and functional organization of the striatum. *J. Neurol.* 247 (Suppl. 5), V1–V15.
- Nichols, T., Brett, M., Andersson, J., Wager, T., Poline, J.B., 2005. Valid conjunction inference with the minimum statistic. *NeuroImage* 25, 653–660.
- Nielsen, J.A., Zielinski, B.A., Ferguson, M.A., Lainhart, J.E., Anderson, J.S., 2013. An evaluation of the left-brain vs. right-brain hypothesis with resting state functional connectivity magnetic resonance imaging. *PLoS ONE* 8, e71275.
- Nixon, P., Lazarova, J., Hodinott-Hill, I., Gough, P., Passingham, R., 2004. The inferior frontal gyrus and phonological processing: an investigation using rTMS. *J. Cogn. Neurosci.* 16, 289–300.
- Paivio, A., 1986. *Mental representations: a dual coding approach*. Oxford University Press, Oxford, UK.
- Patterson, K., Nestor, P.J., Rogers, T.T., 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* 8, 976–987.
- Price, C.J., Wise, R.J., Warburton, E.A., Moore, C.J., Howard, D., et al., 1996. Hearing and saying. The functional neuro-anatomy of auditory word processing. *Brain* 119 (Pt 3), 919–931.
- Pulvermüller, F., 2005. Brain mechanisms linking language and action. *Nat. Rev. Neurosci.* 6, 576–582.
- Redgrave, P., Rodriguez, M., Smith, Y., Rodriguez-Oroz, M.C., Lehericy, S., et al., 2010. Goal-directed and habitual control in the basal ganglia: implications for Parkinson's disease. *Nat. Rev. Neurosci.* 11, 760–772.
- Regev, M., Honey, C.J., Simony, E., Hasson, U., 2013. Selective and invariant neural responses to spoken and written narratives. *J. Neurosci.* 33, 15978–15988.
- Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192.
- Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Premotor cortex and the recognition of motor actions. *Brain Res. Cogn. Brain Res.* 3, 131–141.
- Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2, 661–670.
- Sarubbo, S., De Benedictis, A., Maldonado, I.L., Basso, G., Duffau, H., 2013. Frontal terminations for the inferior fronto-occipital fascicle: anatomical dissection, DTI study and functional considerations on a multi-component bundle. *Brain Struct. Funct.* 218, 21–37.
- Saur, D., Kreher, B.W., Schnell, S., Kümmerer, D., Kellmeyer, P., et al., 2008. Ventral and dorsal pathways for language. *Proc. Natl. Acad. Sci.* 105, 18035–18040.
- Saur, D., Schelter, B., Schnell, S., Kratochvil, D., Küpper, H., et al., 2010. Combining functional and anatomical connectivity reveals brain networks for auditory language comprehension. *NeuroImage* 49, 3187–3197.
- Scholz, J., Triantafyllou, C., Whitfield-Gabrieli, S., Brown, E.N., Saxe, R., 2009. Distinct regions of right temporo-parietal junction are selective for theory of mind and exogenous attention. *PLoS ONE* 4, e4869.
- Sherbondy, A., Akers, D., Mackenzie, R., Dougherty, R., Wandell, B., 2005. Exploring connectivity of the brain's white matter with dynamic queries. *IEEE Trans. Vis. Comput. Graph.* 11, 419–430.

- Spreng, R.N., Mar, R.A., Kim, A.S., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J. Cogn. Neurosci.* 21, 489–510.
- Stephan, K.E., Marshall, J.C., Friston, K.J., Rowe, J.B., Ritzl, A., et al., 2003. Lateralized cognitive processes and lateralized task control in the human brain. *Science* 301, 384–386.
- Talairach, J., Tournoux, P., 1988. *Co-planar stereotaxic atlas of the human brain*. Thieme Medical, New York.
- Tettamanti, M., Buccino, G., Saccuman, M.C., Gallese, V., Danna, M., et al., 2005. Listening to action-related sentences activates fronto-parietal motor circuits. *J. Cogn. Neurosci.* 17, 273–281.
- Thompson-Schill, S.L., 2003. Neuroimaging studies of semantic memory: inferring "how" from "where". *Neuropsychologia* 41, 280–292.
- Turken, U., Dronkers, N.F., 2011. The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Front. Syst. Neurosci.* 5.
- van Dam, W.O., Rueschemeyer, S.A., Bekkering, H., 2010. How specifically are action verbs represented in the neural motor system: an fMRI study. *NeuroImage* 53, 1318–1325.
- Van Doren, L., Dupont, P., De Grauwe, S., Peeters, R., Vandenberghe, R., 2010. The amodal system for conscious word and picture identification in the absence of a semantic task. *NeuroImage* 49, 3295–3307.
- Van Doren, L., Schrooten, M., Adamczuk, K., Dupont, P., Vandenberghe, R., 2012. Chronometry of word and picture identification: common and modality-specific effects. *NeuroImage* 59, 3701–3712.
- Vandenberghe, R., Price, C., Wise, R., Josephs, O., Frackowiak, R.S., 1996. Functional anatomy of a common semantic system for words and pictures. *Nature* 383, 254–256.
- Vandenberghe, R., Wang, Y., Nelissen, N., Vandenbulcke, M., Dhollander, T., et al., 2013. The associative-semantic network for words and pictures: effective connectivity and graph analysis. *Brain Lang.* 127, 264–272.
- Vann, S.D., Aggleton, J.P., Maguire, E.A., 2009. What does the retrosplenial cortex do? *Nat. Rev. Neurosci.* 10, 792–802.
- Vargha-Khadem, F., Gadian, D.G., Watkins, K.E., Connelly, A., Van Paesschen, W., Mishkin, M., 1997. Differential effects of early hippocampal pathology on episodic and semantic memory. *Science* 277, 376–380.
- Visser, M., Jefferies, E., Lambon Ralph, M.A., 2010. Semantic processing in the anterior temporal lobes: a meta-analysis of the functional neuroimaging literature. *J. Cogn. Neurosci.* 22, 1083–1094.
- Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M.A., Jefferies, E., 2011. The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus. *Cereb. Cortex* 21, 1066–1075.
- Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M.A., Jefferies, E., 2012. Executive semantic processing is underpinned by a large-scale neural network: revealing the contribution of left prefrontal, posterior temporal, and parietal cortex to controlled retrieval and selection using TMS. *J. Cogn. Neurosci.* 24, 133–147.
- Xu, J., Kemeny, S., Park, G., Frattali, C., Braun, A., 2005. Language in context: emergent features of word, sentence, and narrative comprehension. *NeuroImage* 25, 1002–1015.