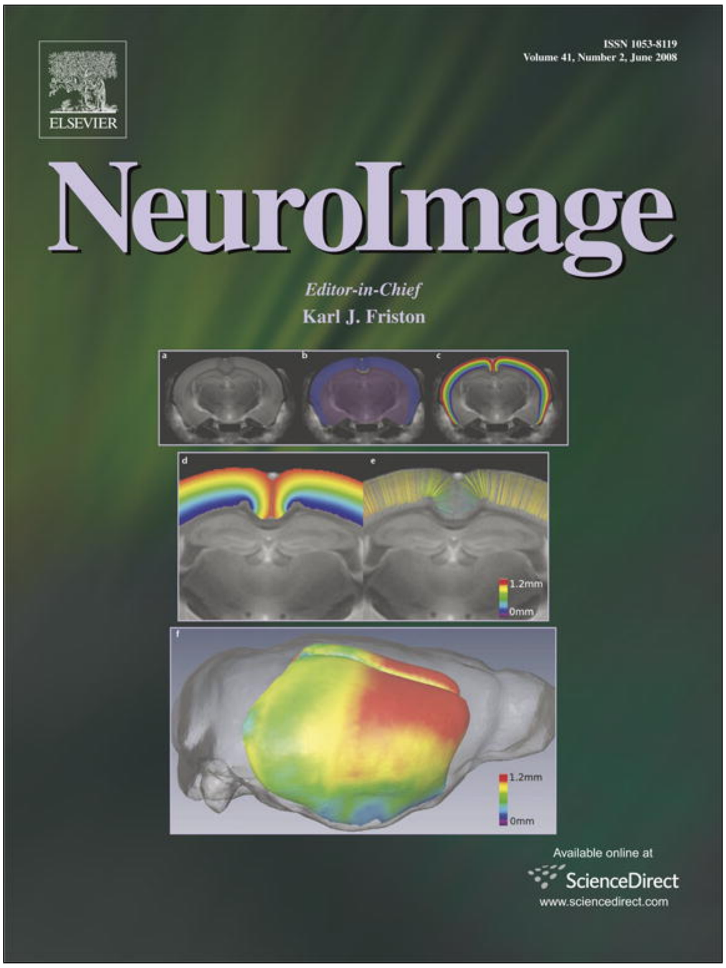
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Brain activation in discourse comprehension: A 3t fMRI study

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To date a very small number of functional neuroimaging studies have specifically examined the effects of story coherence on brain activation using long narratives, a procedure fundamental to the study of global coherence. These studies, however, not only yielded notably divergent results, but also featured a number of caveats. It is the purpose of the present study to try to overcome some of these limitations. A left precuneus/posterior cingulate activation related to global coherence comprehension was in consonance with a part of previous literature. However, our most important results corresponded to left parietal regions (angular gyrus, BA 39), this diverging from the previous studies. Recent developments of the situational models of narrative comprehension could explain all these apparently inconsistent results. According to these, different situation models would be created as a function of the content of the narratives, which would yield in turn different patterns of brain activity. Our data also suggest that the same content might also give place to different situation models as a function of the degree of global coherence achieved by the reader or listener.

Keywords: fMRI; Text comprehension; Global coherence

Introduction

After more than a century of studies in pursuit of the neural basis of human language, the most standard model of language organization in the brain situates language comprehension and production in the perisylvian areas of the left hemisphere (LH). Several lines of evidence, however, suggest that in addition to the well-known LH dominant contribution to language processing, the right hemisphere (RH) may also play an important role in language comprehension. Yet the precise role of the RH in language comprehension is unclear.

A number of neuroimaging studies consistently reveal neural activity in the RH during language tasks, and some patients with RH brain damage have subtle deficits in comprehending natural language (for a good review, see Bookheimer, 2002). A generally accepted assumption has been that the RH appears mainly involved in prosody (Hesling et al., 2005). It has also been widely assumed that the RH supports some semantic operations, particularly those related to global processes, like inference, coherence, conceptual association or text integration during discourse processing. The present paper focuses on this latter assumption, since a review of the literature so far reveals that we cannot be conclusive regarding a genuine central role for the RH in discourse comprehension.

Discourse comprehension arises from both information provided by linguistic cues in texts or in speech, and from background knowledge brought by the reader or listener. However, even more essential to discourse comprehension than these components is the interplay between them, yielding a mental representation of the described situation that has been called a "mental model" or "situation model" (Johnson-Laird, 1983; van Dijk and Kintsch, 1983). At this level, readers or listeners activate knowledge that goes beyond what is explicitly stated in the text, filling in gaps in the text as well as running "mental simulations."

Neuropsychological studies have reported specific deficits following RH damage in the comprehension of narratives and semantic integration, which might support an important role for the RH in discourse processing and, particularly, in constructing situation models. For example, patients with RH damage tend not to elaborate, citing fewer details, producing fewer propositions and fewer complex propositions, although their basic knowledge of scripts or event schema appears to be intact. Right hemisphere damage patients are frequently unable to follow the theme of a conversation, missing the main point altogether (Brownell and Martino, 1998). In laboratory

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experiments, right hemisphere damaged patients have been found to have difficulties drawing certain types of inferences (Beeman, 1993) or revising them when new information comes up in a discourse (Bihrle et al., 1986). Patients with right hemisphere damage often fail to understand jokes (failing to connect the premise to the punch line) (Brownell et al., 1983) and are also reported to experience difficulties in appreciating metaphors, idioms and indirect requests (Weylman et al., 1989). Altogether, the data suggest that RH patients can recognize individual words and comprehend sentences, but have trouble integrating information beyond these levels.

Nevertheless, there does not seem to be a consensus relative to the specific RH regions engaged in these processes. Lesions yielding these symptoms are not necessarily or consistently located within the same RH regions, even if the RH homologues of Broca's and Wernicke's areas might stand out occasionally (Joanette et al., 1990). In addition, neuropsychological evidence based on brain-damaged patients conveys the problem of building conclusions based on altered brains. Reparation and compensatory mechanisms in a damaged brain might notably distort our conclusions on brain lateralization during language comprehension. Hence, neuroimaging studies with intact brains appear desirable to better address this question.

Despite the fact that discourse processes are an integral part of our daily communications, neuroimaging studies on discourse comprehension have been rather scarce (Mason and Just, 2006). It is when reviewing the neuroimaging literature of discourse comprehension that it appears uncertain whether the RH plays a critical role.

On one hand, several studies have found evidence favoring the involvement of the RH, particularly of the right temporal regions, in the construction of situation models. St George et al. (1999) studied the processing of paragraphs which were syntactically well-written but unintelligible when not preceded by a title specifying the subject of the text. The RH became more activated in these situations when compared to the processing of the same texts preceded by a title, which was taken as evidence of a greater effort by the brain areas devoted to mapping information into a text representation. Tomitch et al. (2004) investigated the processing of topic sentences containing a unifying super-ordinate theme in short, three-sentence paragraphs. Although right temporal regions appeared again to be critical, in this case these regions were those most involved when reading the topic sentences, somewhat contradicting the St George et al. (1999) results. Robertson et al. (2000) also found greater right temporal activation when reading texts that used both indefinite and definite articles, but the less coherent, indefinite article texts also resulted in greater right frontal activation than the definite article texts.

On the other hand, several studies have found evidence of a critical role for the LH in discourse processing, sometimes also finding a medial or a bilateral implication in these processes. Ferstl and von Cramon (2001), reported a main left frontomedial cortex activation in relation to discourse coherence, a finding further reinforced by Ferstl et al. (2005) and Siebörger et al. (2007), who also reported a bilateral implication of temporal and parietal regions, even though predominantly left. Bilateral inferior frontal and bilateral middle temporal gyri were activated when a moral judgment was required after reading a set of Aesop's fables (Nichelli et al., 1995). Fletcher et al. (1995) and Mazoyer et al. (1993) also found increased activation of the temporal lobes bilaterally during globally coherent stories compared with control tasks. Partiot et al. (1996) reported bilateral precuneus/posterior cingulated regions, along with bilateral medial parietal cortex, as activated during script processing. These same areas were found to be more active for ambiguous passages preceded by a picture providing global coherence to the text in a Maguire et al. (1999) study. Finally, Eviatar and Just (2006) have recently reported that whereas irony in discourse may be related to right superior and middle temporal regions, metaphor comprehension preferentially taps into left inferior frontal gyrus and infero-temporal areas.

While acknowledging that there is still a significant amount of research to be done to clarify the contributions of the left and right hemispheres in text integration, in a recent review Mason and Just (2006) suggest that the two hemispheres appear to work together to accomplish discourse comprehension. According to these authors, the type of information within the text may play a role in determining which areas are responsible for building and maintaining text representation. An alternative possibility (Mason and Just, 2006 claim), however, is that as text processing becomes more difficult, the specialized text integration network may spill over into the right hemisphere. Definitely, further neuroimaging studies are required.

When reviewing all these previous studies, the large variability in activation patterns regarding the right or left hemisphere becomes apparent, along with the regions involved within each hemisphere, but also apparent is a noteworthy inconsistency relative to the types of discourse and tasks under study. For instance, most of these studies have investigated extremely short paragraphs, consisting of no more than two or three sentences, therefore dismissing the truly global (as opposed to local) coherence processes involved in narratives. Further, several of the previous studies have mainly dealt with the differences between specific aspects of discourse features, such as irony, metaphor, fable interpretation, and other aspects of figurative language, but not with the differences between the absence and the presence of a truly global comprehension. In our view, a sound way to deal with the question of the brain areas critically involved in overall discourse global comprehension would entail using relatively long texts and contrasting manifestly different degrees of global comprehension accomplished by the subjects while reading or hearing them.

Bransford and Johnson (1972) and Dooling and Lachman (1971) found that ambiguous paragraphs, i.e., ones difficult to understand when the theme providing global coherence to the text is not provided to the subjects, are also difficult to remember. It is as if without a title these paragraphs were meaningless as a discourse, just a series of disconnected propositions, which are then difficult to recall. The mere presence of a title renders these paragraphs more comprehensible and effectively doubles the number of words and propositions that readers can recall from them (Bransford and Johnson, 1972). Consequently, by using ambiguous paragraphs, preceded by or devoid of a title, the same text may either possess or lack global coherence, while an objective measurement of the effects of global coherence on performance (based on the number of recalled words or propositions) is achieved. An example of an ambiguous paragraph follows, obtained from Bransford and Johnson (1972):

> "*A newspaper is better than a magazine. The seashore is a better place than the street. At first it is better to run than to walk but walking is fine after a while. You may have to try several times, it takes skill but it's easy to learn. Even young children can enjoy it. Once successful there are very few complications. Birds seldom get too close. Rain, however, soaks in very fast. Too many people doing the same thing can also cause problems. One needs lots of room. If there are no complications it can be very peaceful. A rock will serve as an*

anchor. However, if things break loose from it you will not get a second chance".

This paragraph is noticeably better understood and remembered if preceded by the title: *making and flying a kite*. So far, only two functional neuroimaging studies have specifically examined the effects of story coherence and prior knowledge on brain activation using relatively long texts (typically, more than eight sentences). These are the above-mentioned studies by Maguire et al. (1999) and St George et al. (1999). Strikingly, however, their results were totally divergent. Whereas the former found a larger activation of the anterior medial parietal/posterior cingulated regions related to paragraphs preceded by information making the text globally comprehensible, the latter found a larger right temporal activation for paragraphs not preceded by a title. Neither the direction of the results, nor the hemisphere and brain regions involved were the same, despite the strong overall similarities between studies.

It is true, however, that the studies differed on a series of points that might, at least to some extent, explain these discrepancies. Whereas Maguire et al. (1999) employed PET, St George et al. (1999) used fMRI. This difference should not explain the different results, as both techniques measure hemodynamic processes. However, whereas Maguire et al. (1999) scanned the whole brain St George et al. (1999) scanned only part of the brain and focused on specific regions of interest. Another difference is that the study of Maguire et al. (1999) presented the theme visually with a drawing, paragraphs being presented auditorily; by contrast, St George et al. (1999) presented the titles verbally and both titles and paragraphs appeared visually. This divergence, nevertheless, might not be crucial when studying activity related to global coherence. Importantly, however, the study of Maguire et al. (1999) included trials in which the theme provided could be false, whereas in the study of St George et al. (1999) all the titles were always valid. This difference can be crucial because the subjects were aware of it (they were informed about it) in the study of Maguire et al. (1999) and therefore could have executed discernment processes about the truthfulness of the presented theme, this being a supplementary and interfering task. Finally, whereas the study of Maguire et al. (1999) employed the classic task in which the subjects were asked to rate the comprehensibility of a story and recall as much of the story as possible, in the study of St George et al. (1999) the subjects were not given any specific instruction. Rather, they were only sometimes asked if they had understood the paragraphs. Accordingly, in the St George et al. (1999) study the subjects were not explicitly forced to discern the global coherence of the texts, this yielding a great difference between studies. Indeed, the cognitive processes implied and, consequently, the brain areas involved could be very different for this reason alone (van den Broek, 1994, Siebörger et al., 2007).

It appears therefore that although both studies specifically examined the effects of story coherence and prior knowledge on brain activation using relatively long texts, both studies exhibit a number of pros and cons. It is our aim in the present study to overcome some of the cons identified in these two studies, performing a third study on the effects of coherence in relatively long texts as a function of prior knowledge. First, and exploiting some of the improvements in brain imaging techniques that have occurred of late, we used a high-resolution 3 T fMRI scanner (St George et al., 1999 used a 1.5 T, lower resolution scanner) and explored the whole brain. Second, we did not present false titles, in order to avoid additional and possibly interfering processes, thereby better isolating those processes related to global discourse comprehension. Finally, we included specific instructions about the comprehension of global coherence, also asking the subjects to rate the comprehensibility of the stories and recall as much of each story as possible.

Material and methods

Subjects

The participants were 24 healthy, native Spanish-speaking volunteers (mean age 23 years, range 19–39; half of them were male). During data processing, one of the subjects had to be rejected due to bad signal acquisition. All had normal or corrected-to-normal vision and were right-handed with average handedness scores of +80, ranging from +43 to +100, according to the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants had any history of neurological complaints or other health problems preventing their exposure to the magnetic field. All participants were informed about the harmlessness of the experiment and gave informed consent. Subjects were paid for participating in this experiment.

Materials

The text material consisted of sixteen paragraphs. All the paragraphs were globally coherent when provided with a title describing the theme or topic of the paragraph at the beginning, but difficult to comprehend globally in the absence of that title. To that end, each paragraph was constructed following this procedure: first a topic was chosen, and then the topic was described without using many associated words, trying not to be very specific, and including some informative but unnecessary details. An original set of 22 paragraphs following these requirements was evaluated by a group of 20 subjects different from the participants in the neuroimaging study, in order to rate paragraphs for comprehensibility with and without the title (this balanced). The 16 paragraphs with the greatest differences in comprehensibility as a function of the presence of the title were selected for the neuroimaging study. The selected paragraphs included the adaptations to Spanish of the paragraphs "*making and flying a kite*" from Bransford and Johnson (1972), "*Christopher Columbus discovering America*" and "*the first space trip to the moon*" from Dooling and Lachman (1971), and "*horse-back riding*" from St George et al. (1999).

Paragraphs ranged between 8 and 12 sentences (mean 9.8) in length; sentences varied between 3 and 24 words (mean 8.4) in length. In the control task, words were replaced by strings of Xs of variable length. Paragraphs were presented visuocentrically, one word (duration = 200 ms) every 300 ms. An additional half second delay followed the last word of each sentence.

Procedure

Participants lay flat inside the magnet and viewed the stimuli via special stimulation glasses for MRI environments. Each subject was presented with the whole set of 16 paragraphs (8 titled, 8 untitled) and saw a given paragraph only once. Whether a given paragraph appeared as untitled or titled was counterbalanced across subjects. The materials were presented in four runs lasting 4.5 min each; each paragraph lasted 30 s, each run began and ended with 30 s of flashing

Xs, and there were 30 s periods of Xs between paragraphs. In other words, each run consisted of 4.5 cycles (five half-cycles of Xs; four half-cycles of paragraphs), where a 'cycle' is the total time consumed by one experimental and one control task. Participants saw all four paragraphs of each run as either titled or untitled (i.e. the presentation of conditions was blocked). Half of the participants saw an untitled run first, while the other half saw a titled run first; thereafter the conditions alternated. Special care was taken to keep the total duration of each paragraph to 30 s regardless of the presence of the title. For this purpose, titles were as brief as possible while keeping their informative value (e.g., "Christopher Columbus discovering America" was replaced by "Columbus"). In fact, these short titles were the ones used in the ratings by the group of subjects different from the participants in the neuroimaging study. In addition, the same number of words comprising the title was removed from the paragraph when the paragraph was preceded by the title, reconstructing the sentences from which the words had been extracted to well-formed ones while keeping the relevant information.

At the beginning of the experimental session, subjects were explicitly instructed that they would be reading paragraphs, not a series of unrelated sentences, and were informed about the recall task prior to reading the paragraphs. Immediately after each scan (comprising four paragraphs), subjects were asked to rate the comprehensibility of the stories just read on a seven-point scale (as in Bransford and Johnson, 1972), where a rating of 1 represented a complete lack of understanding and 7 implied the story was fully comprehensible. Subjects were then asked to recall out loud as much of each story as possible, this response being recorded for later scoring. Memory for the stories was scored in terms of the number of 'idea units' recalled, defined by Bransford and Johnson (1972) as corresponding to 'either individual sentences, basic semantic propositions, or phrases' (Bransford and Johnson, 1972). Stories had between 10 and 16 idea units.

Data acquisition

A 3.0-T GE scanner (HD×, 14× with 16 Channels and with gradient specifications as follows: Amplitude = 50 mT/m and slew rate = 150 mT/m × ms), equipped with a standard birdcage head coil, was used for magnetic resonance imaging. In a separate session, high-resolution whole brain images were acquired from each participant using a T1-weighted three-dimensional 3DSPGR sequence (30 axial adjacent slices, 512 × 512 pixel matrix per slice, TR = 11.2 ms, TE = 2.21 ms). These images were rotated and translated into the stereotactic space of Talairach and Tournoux (1988). In the experimental session, anatomical 3DSPGR and EPI-T1 2D images were acquired prior to the functional scans, using the same number and orientation of slices as the functional scans to enable alignment of the functional scans with the high-resolution image. During the functional scans, the BOLD response was measured using a single-shot gradient EPI-sequence (TR = 3 s, TE = 30 ms, flip angle 90°). Horizontal images were acquired for 30 slices (3 mm thickness, 6 mm spacing, matrix 64 × 64, field of view 240 mm, and acquisition in ascending order) parallel to the AC–PC plane and covering the whole brain. In-plane resolution was 3.75 × 3.75 mm, and the total number of volumes was 2400.

Data analysis

Data analysis was conducted using Brain Voyager QX software, which contains tools for preprocessing, co-registration, statistical evaluation, and visualization of fMRI data. As a first step in the analysis, the images were checked and corrected for motion artifacts. Thereafter, time series data for runs of similar conditions (titled/untitled) were averaged together. The averaged titled and untitled runs were analyzed by correlating the time course for each voxel with an ideal 4.5 cycle trapezoidal reference waveform (Bandettini et al., 1993). Voxels meeting or exceeding a correlation coefficient of 0.50 were considered reliably associated with the task. This yielded a first series of maps of functional data related to the language task (processing of the paragraphs) as contrasted with the control, non-linguistic task (seeing strings of Xs).

These first functional maps were then subjected to voxelwise one-sample *t*-tests contrasting the activations related to paragraph processing as a function of the presence or absence of the title. Only those voxels with $t_{7176} > 3.4$ ($p < 0.001$; uncorrected) were considered as significantly differing between conditions. Thereafter, valid clusters were defined as groups of significant voxels at least 50 mm^3 in volume, disregarding the remaining possible differences.

For the display of the results, the normalized anatomical images of one of the participants selected arbitrarily were used to overlay on them the activation patterns obtained in the contrast maps of the group.

Results

Behavioral data

When the paragraphs were untitled, the comprehensibility rate varied from 2.3 to 6.0 (mean = 3.8), whereas in the paragraphs preceded by a title these values ranged from 3.4 to 7 (mean = 5.9), which resulted in a significant difference, $t_{22} = 8.6$, $p < 0.0001$. Clearly, the paragraphs were noticeably more comprehensible when preceded by a title. The number of 'idea units' recalled varied from 0.3 to 5.1 (mean = 2.6) for untitled paragraphs, and from 2.8 to 8 (mean = 5) when they were titled. Accordingly, recall was better for titled paragraphs, this result being significant, $t_{22} = 11.2$, $p < 0.0001$, as predicted for an effect of global coherence (Bransford and Johnson, 1972) (Fig. 1).

fMRI results

The first functional maps obtained for both the titled and the untitled paragraphs separately mainly consisted of extended areas

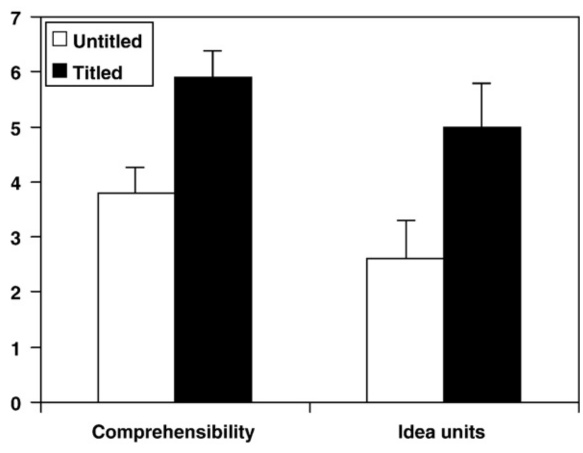

Fig. 1. Mean of comprehensibility judgments and 'number of ideas' units recalled for the paragraphs as a function of the presence of the title providing global coherence.

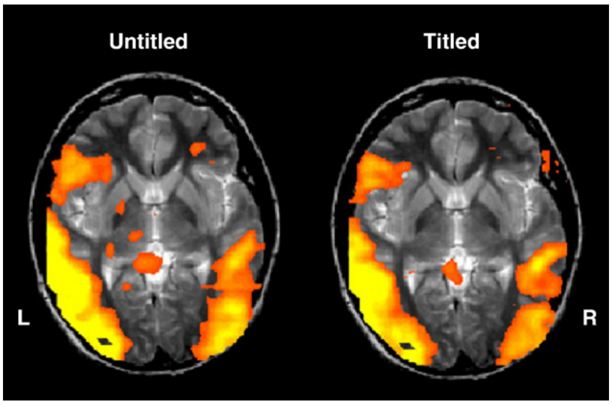

Fig. 2. Functional data averaged across 23 participants, mapped onto the normalized structural images of one of the participants. Functional maps correspond to those obtained for the untitled (left) and the titled (right) paragraphs using as a reference the task of seeing strings of Xs. The results are displayed at slice $Z=0$, as representative of the data obtained at this stage of the analyses. Color shading indicates the percentage of signal change (positive correlation), with thresholds set at $r=0.50$ with the reference waveform.

of activation, primarily over frontal and parieto-temporal regions, bilaterally but with a noticeable left prevalence (Fig. 2). Results pertaining to this first set of functional data are not in the core interest of the present paper, also comprising a large amount of variables resulting from comparing reading texts with seeing strings of Xs. For these reasons, the data obtained at this stage of analyses will not be analyzed in detail. They largely replicate the bulk of earlier fMRI studies on language comprehension, according to which perisylvian regions, mainly left, are most important for these processes (e.g., Bookheimer, 2002), therefore constituting sound validation for the appropriateness of the procedures here employed.

When the activations related to paragraph processing as a function of the presence of the title were compared, the results

Table 1
Brain regions significantly activated ($t_{7176}>3.4$, $p<0.001$, extent>50 mm^3) for the contrast of paragraphs without title vs. paragraphs preceded by title

No title vs. title	BA	Size (mm^3)	*t* max	Side	Talairach coordinates		
					x	y	z
[1] Precentral gyrus	4	139	4.59	L	−39	−22	52
[1a] Sub-peak	4	74	3.84	L	−51	−10	49
[2] Postcentral gyrus	3	113	4.60	L	−45	−19	61
[3] Paracentral lobule	31	96	4.03	L	−6	−13	49
[4] Superior temporal gyrus	42	254	5.49	L	−67	−10	10
[4a] Sub-peak	22	154	3.89	L	−60	−40	15
[5] Inferior parietal lobe	40	70	4.10	R	66	−25	25
[6] Precentral gyrus	6	119	4.61	R	61	−4	43
[7] Cerebellum	–	304	4.98	R	6	−40	−35

displayed the activations specifically related to the title variable. Fig. 3 displays the contrast between untitled and titled paragraphs. Table 1 depicts in detail the brain areas yielding significant results, their size in mm^3, and the Talairach coordinates of the main findings. Brodmann areas and anatomical nomenclature were determined according to the guidelines implemented in the LORETA software package: (http://www.unizh.ch/keyinst/NewLORETA/LORETA01.htm).

Six out of nine activations due to untitled paragraphs were located in the LH. These comprised several pericentral (pre- and postcentral) regions, the paracentral lobule, and the superior temporal gyrus (BA 42, 22), which was the area mainly activated within the LH. In the RH, the main region activated was found in the cerebellum, with further activations in the inferior parietal lobe and the precentral gyrus.

Fig. 4 displays the contrast between paragraphs preceded by the title and paragraphs without the title. Table 2 describes the data corresponding to this contrast.

Except for midline activation in the anterior cingulate gyrus (BA 33), the remaining twelve activations were shared in number (though not in volume) by both LH and RH. The main overall

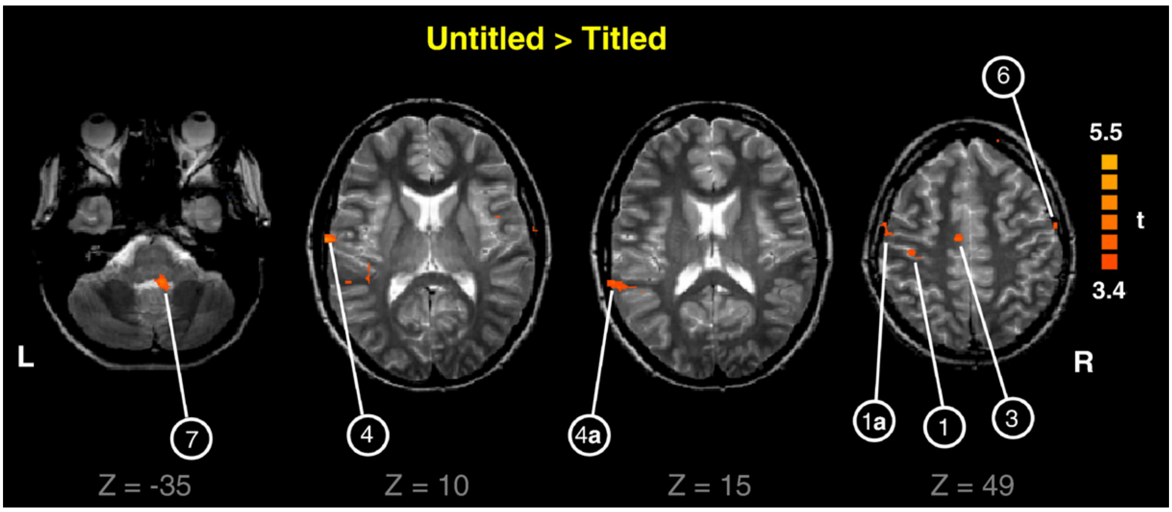

Fig. 3. Averaged activation *t*-maps for the contrast of untitled vs. titled paragraphs. The statistical threshold was set to $t_{7176}>3.4$ ($p<0.001$; uncorrected); minimum size 50 mm^3; $n=23$. The identification numbers refer to the labels in Table 1. A set of main findings corresponded to pericentral activations during the reading of paragraphs in absence of global coherence.

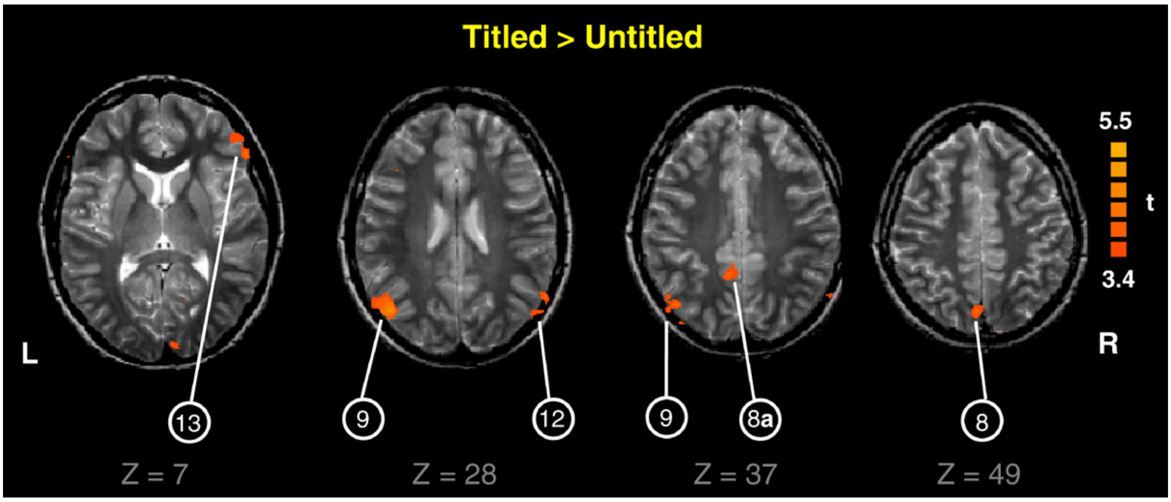

Fig. 4. Averaged activation *t*-maps for the contrast of titled vs. untitled paragraphs. The statistical threshold was set to $t_{7176}>3.4$ ($p<0.001$; uncorrected); minimum size 50 mm^3; $n=23$. The identification numbers refer to the labels in Table 2. The main findings related to left parietal and right frontal activations underlying the reading of paragraphs in the presence of global coherence.

activation clearly belonged to the LH, this corresponding to the middle temporal gyrus (BA 39). Further LH activations for titled paragraphs relative to untitled paragraphs were found at the precuneus, the superior parietal lobule and the middle frontal gyrus. Activations in the RH included the supramarginal and inferior frontal gyri, the insula and the cuneus. Overall, the amount of cortical tissue specifically overactivated by the titled paragraphs was noticeably larger than that by untitled paragraphs. Moreover, the amount of activated tissue was always larger in the left than in the right hemisphere. These data are graphically summarized in Fig. 5.

Discussion

In the present fMRI study we have investigated the processes involved in global coherence during discourse comprehension with the main aim of contributing to the debate on whether global coherence is a main function of the right hemisphere, as some studies suggest, or of the left one, as several others support. In addition to the RH vs. LH debate, the identification of concrete areas within each hemisphere involved in global coherence is also within the scope of the present paper.

For these purposes, we compared the comprehension of relatively long and ambiguous paragraphs as a function of the presence of a title providing global coherence. Without such a title, our paragraphs would be read as a mere sequence of sentences, although the participants could presumably also be attempting to make an effort to elucidate the theme giving meaning to the whole paragraph. Indeed, this was the reasoning applied by St George et al. (1999) to explain larger RH activations for ambiguous untitled paragraphs. With a title, however, and contrasting with untitled paragraphs, our participants could construct a coherent story from the very beginning, the comparison with untitled paragraphs thus yielding activations mainly related to the presence of global coherence. This was the reasoning underlying the study by

Table 2
Brain regions significantly activated ($t_{7176}>3.4$, $p<0.001$, extent>50 mm^3) for the contrast of paragraphs preceded by title vs. paragraphs without title

Title vs. no title	BA	Size (mm^3)	*t* max	Side	Talairach coordinates *x*	*y*	*z*
[8] Precuneus/posterior cingulate	7	302	4.57	L	−3	−70	49
[8a] Sub-peak	31	150	4.23	L	−9	−49	37
[8b] Sub-peak	7	65	3.88	L	−3	−76	40
[9] Angular gyrus	39	1645	5.31	L	−42	−67	28
[10] Superior parietal lobule	7	58	3.89	L	−39	−61	55
[11] Middle frontal gyrus	46	64	3.91	L	−39	29	19
[12] Supramarginal gyrus	40	389	4.29	R	57	−58	34
[13] Inferior frontal gyrus	45	396	4.67	R	54	29	7
[13a] Sub-peak	47	303	4.52	R	51	38	−2
[13b] Sub-peak	10	118	4.47	R	36	53	1
[14] Insula	13	54	3.76	R	27	5	4
[15] Cuneus	17	57	3.74	R	6	−91	4
[16] Anterior cingulate	33	97	4.32	–	0	20	22

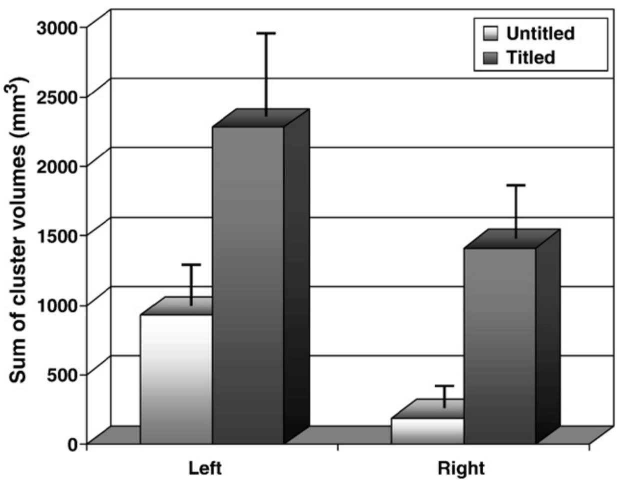

Fig. 5. The overall amount of cortical tissue specifically overactivated by the titled paragraphs was notably greater than that by untitled paragraphs. Furthermore, activations involved a noticeably larger volume in the left hemisphere than in the right.

Maguire et al. (1999) to explain larger activations of the anterior medial parietal/posterior cingulated regions for globally comprehensible paragraphs. To date the studies by St George et al. (1999) and Maguire et al. (1999) have been the only two brain imaging studies using relatively long ambiguous paragraphs contingent upon the presence of a title to attain global coherence, a suitable and valuable procedure to manipulate the latter variable, as established decades ago by Bransford and Johnson (1972) and Dooling and Lachman (1971).

The behavioral data support that our paragraphs were noticeably better understood if preceded by the title. Both comprehensibility rates and 'idea units' recalled were significantly greater for the same paragraphs when titled. Accordingly, the occurrence of high levels of global coherence in the brains of our participants during the reading of the titled paragraphs can be assured, the opposite being true while reading the untitled ones. In the absence of titles, then, the presence of global coherence could be disregarded, though an effort to attain it cannot be totally ruled out. All of our subjects reported such an attempt, as they knew in advance that the paragraphs composed coherent stories. Overall, we could admissibly have both (global coherence and an attempt to attain it) if they were separable, diverging processes. Attempts to achieve global coherence could be seen in the activations that were greater for untitled paragraphs, whereas global coherence as such could be seen in the larger activations for titled paragraphs. This can be better appreciated in the activation maps.

Untitled vs. titled paragraphs

From an overall view of the present fMRI results it appears that the most relevant processes occurring in our experiments, in terms of both the amount of differentially activated regions and brain volume, took place during the reading of narratives understood globally (that is, preceded by a title). Fewer activated brain regions were found to be involved during the reading of untitled as compared to titled paragraphs.

Another assertion that can be drawn from a general review of our results is that the RH does not appear to be more important for the processes occurring during the reading of an untitled paragraph, even if some of these processes could be attributed to efforts to reach global comprehension. Six out of nine activations were found in the left hemisphere. Except for the right cerebellum activation, the brain regions with the largest volume involved were always left. Actually, and again excluding the cerebellum, the most activated region in volumetric terms was the left superior temporal gyrus (BAs 42 and 22, with a total of 408 mm^3), also displaying the largest overall differences in statistical terms. Interestingly, these areas, together with a usually bilateral activation of the cerebellum, have been consistently related to reading words (Cabeza and Nyberg, 2000), which would accord with the fact that untitled paragraphs could have been read as sequences of isolated sentences, even of isolated words. Indeed, a previous study by St George et al. (1994) using ERPs evidenced that the main effects of the titles in reading ambiguous paragraphs were apparent for every word of the paragraph equally, with negligible divergences between different types of words and sentences.

The rest of the most activated regions during the reading of untitled paragraphs roughly corresponded to pericentral regions, bilaterally but clearly more on the left than right, together with a small activation in the right inferior parietal lobe (BA 40). We are tempted to suggest that these activations, overall, could relate to the representation of movements described in the sentences composing the paragraphs, rather than to an effort to find global coherence. Indeed, these activated regions are extending within the motor, premotor, and somatosensory areas, its mainly left lateralization fitting well with the right-handedness of our subjects. The right parietal activation would not be at odds with this reasoning. These features will be taken up again when discussing the data corresponding to the reversed comparison.

Titled paragraphs vs. untitled paragraphs

This comparison yielded a total of 13 activations, comprising both hemispheres, and including the largest area involved in the present study, the left angular gyrus (BA 39). Overall, the total volume of the clusters involved in this comparison was larger in the left than in the right hemisphere. It could therefore be asserted that understanding the global coherence of a narrative appears to involve both hemispheres, though with a patent LH dominance, and that the region mainly involved in this process is the left angular gyrus. Interestingly, this region has recently been termed as the "Geschwind territory" by Catani et al. (2005), suggesting this area's main role (considered by these authors as the "third language area", besides Broca and Wernicke) in language comprehension. The specific function of this area in language comprehension, usually considered as part of the semantic system (Price, 2000), appears elusive. Yet its relevance for language acquisition is obvious: it not only directly connects both Wernicke and Broca's areas, but is also the last cortical region to maturate (Catani et al., 2005). Actually, the development of this area and its perisylvian connections is thought to have coincided with the emergence of language in humans (Aboitiz and García, 1987). As a matter of fact, it can also be mentioned that the posterior part of mirror system neurons, proposed as the origin of human language, largely corresponds to this brain region (Rizzolatti and Buccino, 2005). Catani et al. (2005) proposed that this region may play a crucial role in ideational speech, following a suggestion by N. Geschwind that, through cortico–cortical interactions, the convergence of multimodality sensory inputs in this region allowed the development of semantic content.

Considering these facts, and in light of our present results, it is tempting to assume that this area might be significantly involved in the comprehension of the global coherence of narratives. That the previous fMRI study by St George et al. (1999) using the present paradigm did not find this region as important for this process is easily understood when considering that these authors did not analyze the brain at this level (i.e., their ROIs were below this region). However, it appears more difficult to elucidate why the PET study by Maguire et al. (1999) did not report this region as important for global coherence comprehension. Certainly, the PET technique is probably not as accurate as fMRI in the study of subtle cognitive processes as those studied here, but Maguire et al. (1999) did find activations within the precuneus/posterior cingulate regions that have been seen activated here during the reading of narratives that were coherent to the subjects. Remarkably, precuneus/posterior cingulate regions were again out of the ROIs studied by St George et al. (1999). The implication of these latter regions in global discourse coherence, therefore, appears consistent so far, which would also be in agreement with previous interpretations of the precuneus/posterior cingulate regions as linking incoming information with a repository of activated knowledge to form a coherent representation of discourse (Maguire et al., 1999). The implication of these areas in memory retrieval (Cabeza and Nyberg, 2000) and the processes presumably underlying global discourse comprehension (van Dijk and Kintsch, 1983) strongly support this suggestion.

But we still have to explain why Maguire et al. (1999) did not find an activation of the left angular gyrus for coherent paragraphs, particularly considering that the involvement of this region in our experiment was so pronounced. Other activations found here, as those in the right inferior frontal gyrus, were also not found by Maguire et al. (1999). As a possible explanation for these discrepancies, recent developments (e.g., Zwaan and Rapp, 2006) of the situational model of narrative comprehension originally proposed by van Dijk and Kintsch (1983) could be brought into play. These theoretical advancements suggest the existence of an imagery strategy for representing visuo-spatial aspects of situation models (e.g., Glenberg and Kaschak, 2002; Zwaan, 2004), giving place to the perceptual embodiment of language comprehension, as the reader or listener would directly create an appropriate visual situation model as comprehension unfolds. What is more, it has been proposed to abandon the idea of abstract, amodal, and arbitrary representations during language comprehension, viewing language comprehension instead as language-guided mental simulation of the described situation (Zwaan and Rapp, 2006). As a result, the type of information within a text plays a crucial role in which areas are responsible for building and maintaining representation of that text.

As a consequence, both language and language-related processes should be differentially engaged during the succession of the narrative segments, which should be reflected in fluctuating patterns of activity (Xu et al., 2005). Indeed, text reading or listening to speech is a highly immersive activity, by virtue of which the comprehender immerses himself into the narrative, thereby activating brain regions related to the content of the text. As an instance, motor and somatosensory regions are active during the comprehension of action words (Hauk et al., 2004) and sentences (Tettamanti et al., 2005; see also Willems and Hagoort, 2007 for a good review). Therefore, divergences between studies in the content of the paragraphs might account for different activation patterns related to global coherence. In fact, the authors of the Maguire et al. (1999) study were asked regarding the paragraphs they used, and only one out of their four paragraphs (*Columbus*) matched with one of our sixteen paragraphs.

Along this line, it appears to be the case that the same content can also give place to different situation models as a function of the degree of global coherence achieved by the reader or listener. In our data, on one hand we have found as a main result a left parietal (angular gyrus, but also superior parietal region) activation while reading globally comprehended narratives, together with the contralateral implication of seemingly parallel areas (right supramarginal gyrus). On the other hand, when the paragraphs could not be globally understood but rather read as isolated words and sentences, noticeable activations involved pericentral areas of the motor, premotor, and primary somatosensory regions. These different patterns could be compatible with the following depiction. When global comprehension is possible, the subjects create situation models into which they get immersed as experiencers in comprehensive large-scale actions. For these reasons, higher-order multimodal areas are more prone to being activated, as they probably represent the activities described in the paragraphs and performed in a personally represented space. This would explain the important activation of the right frontal regions under these circumstances, as they have been seen as crucially involved in spatial working memory and orientation (Bor et al., 2006). By contrast, when the situation cannot be globally understood, it is more likely that isolated (that is, not globally coordinated) motor actions are to be represented, and for this reason mainly primary or secondary sensori-motor areas are concerned. The fact that the LH was the most involved in either case may be attributable to the right-handedness of all our subjects. Nevertheless, since the content of our paragraphs was not explicitly manipulated, this description should remain as merely speculative.

It can be suggested, therefore, that activations occurring during discourse processing appear largely dependent on the content of the narratives. Parietal regions, mainly of the LH, seem to play an important role in the global coherence processing of *our* paragraphs, together with right frontal portions of the brain. However, it can be concluded that some regions might appear as involved in global coherence comprehension regardless of the content of the discourse, such as the precuneus/posterior cingulate regions, as these areas have been found consistently activated for these processes. A final but noteworthy conclusion is that the RH does not seem to be more important for discourse comprehension than the LH.

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