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ABSTRACT

This functional magnetic resonance imaging study examined the neural correlates of coherence-break detection during reading in the context of a contradiction paradigm. Young adults (N = 31, ages 19–27) read short narratives (half contained a break in coherence) that were presented sentence by sentence in a self-paced, slow event-related design. Reading times were longer for incoherent compared to coherent target sentences, and coherence-break detection was associated with activation in a large network of brain regions that were more active in response to incoherent than to coherent information. Some regions seemed exclusively associated with processing of incoherent information. In addition, activation in the precuneus was negatively correlated with working-memory capacity. Together, these findings shed light on the functional contributions of these brain regions to coherence-monitoring processes during reading and help bridge cognitive and neurobiological accounts of the cognitive processes involved in the construction of coherent mental representations of narrative texts.

Text comprehension is a complex, fundamentally human ability to which many cognitive processes contribute. Despite a rich behavioral literature on the cognitive processes that allow readers to comprehend a text, the neural correlates of these processes are poorly understood. On one hand, insight in the brain basis of text comprehension can test the biological plausibility of existing cognitive theories. On the other hand, it can inform models of brain functioning during comprehension of texts. The present study aims to contribute to bridging the gap between the cognitive-behavioral and neuroimaging fields by examining the process of coherence-break detection during reading. Coherence-break detection is an important component of text comprehension and, as a consequence, has been a testing ground for theories of discourse processing.

Cognitive theories of text comprehension share the notion that, to comprehend written information as an organized whole, readers use various cognitive processes to construct a meaningful, coherent mental representation of a text in which idea units from the text are connected to each other and to background knowledge (Gernsbacher, 1991; Kintsch, 1998; Kintsch & Van Dijk, 1978; McKoon & Ratcliff, 1992; Trabasso & van den Broek, 1985; Zwaan, Langston, & Graesser, 1995). For example, during comprehension, readers access the meaning of words and sentences, and they generate inferences by identifying semantic connections between pieces of information (e.g., Cook & O'Brien, 2015; Perfetti & Stafura, 2015; van den Broek, Beker, & Oudega, 2015). As they proceed through a text, readers have to incorporate incoming information into the context in which it is presented and monitor the coherence of their emerging mental representation of the text (e.g., Baker, 1984; Gerrig & O'Brien, 2005; van den Broek, Young, Tzeng, & Linderholm, 1999). All these

processes are executed within a reader's limited working-memory capacity (Daneman & Carpenter, 1980; Engle, 2002; Just & Carpenter, 1992).

Working memory, which generally is described as the ability to maintain and manipulate a relatively small amount of information in mind (Cowan, 2010), enables a reader to detect a break in coherence provided that the contradictory pieces of information are simultaneously available in working memory (e.g., Gerrig & O'Brien, 2005; McKoon & Ratcliff, 1992; van den Broek & Kendeou, 2008; van den Broek, Rapp, & Kendeou, 2005). Insight into how and what incoming information is incorporated in the reader's mental representation during reading is highly relevant to our understanding of how readers comprehend texts. If coherence is maintained, the meaning of incoming information is readily incorporated in the emerging mental representation of the text (e.g., Cook & O'Brien, 2014; Kintsch, 1988; McKoon & Ratcliff, 1992; Singer, 2013). In contrast, if coherence is disrupted and a reader does not notice this break in coherence, comprehension of the text is likely to be insufficient. If, however, a reader does notice the coherence break, this offers an opportunity to maintain a sufficient level of comprehension by adapting his or her reading behavior, for example, by rereading parts of the text, searching memory of the prior text and/or background knowledge, or otherwise trying to resolve the inconsistency (Duke & Pearson, 2002). Thus, the ability to monitor coherence by detecting coherence breaks during reading is important because it enables a reader to engage in repair processes to restore coherence (Baker, 1984; Graesser, Singer, & Trabasso, 1994; Long & Chong, 2001; Zabrucky & Ratner, 1989).

The cognitive processes involved in coherence monitoring,[1] particularly those involved in coherence-break detection, have been investigated behaviorally using a contradiction paradigm that reveals the ease of integration of incoming information into the reader's mental representation (e.g., Albrecht & O'Brien 1993; Cook, Halleran, O'Brien, 1998; Kendeou, Smith, & O'Brien, 2013; Long & Chong, 2001; O'Brien & Albrecht, 1992; O'Brien, Rizella, Albrecht, & Halleran, 1998). In the contradiction paradigm participants are presented with short narratives, some of which contain a target sentence that semantically contradicts information presented earlier in the text. For example, if the protagonist in a narrative is introduced as a vegetarian, a later target sentence in which she orders a cheeseburger contradicts the previously read information (that she is a vegetarian) and information in the reader's background knowledge (that vegetarians do not eat meat). This contradiction causes a break in coherence. Reading times are typically longer on target sentences in incoherent narratives compared to the same target sentences in coherent narratives (e.g., in which the protagonist is introduced as a fan of fast food), reflecting a reader's engagement in additional cognitive processes when a break in coherence during reading is detected. For a coherence break to be detected, both pieces of information (in this case, the concepts "vegetarian" and "cheeseburger") need to be active in working memory, integrated into the mental representation, and validated against background knowledge (Cook & O'Brien, 2014; Isberner & Richter, 2014; Singer, 2013; van den Broek & Kendeou, 2008).

In recent years functional magnetic resonance imaging (fMRI) studies have begun to reveal a network of regions that contributes to the construction of coherent mental representations of narratives (e.g., Egidi & Caramazza, 2013; Ferstl & Von Cramon, 2001; Mason & Just, 2006; Virtue, Haberman, Clacny, Parrish, & Beeman, 2006; Xu, Kemeny, Park, Frattali, & Braun, 2005; Yarkoni, Speer, & Zacks, 2008), as well as expository texts (e.g., Aboud, Bailey, Petrill, & Cutting, 2016; Moss & Schunn, 2015; Swett et al., 2013). In a comprehensive meta-analysis of neuroimaging studies on text comprehension processes, Ferstl, Neumann, Bogler, and von Cramon (2008) showed that this type of higher level language comprehension involves activation in many brain regions. For example, this network includes regions associated with language processing, such as regions in the

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[1]In this article we refer to coherence monitoring instead of comprehension monitoring. We prefer to use the term coherence monitoring because comprehension monitoring traditionally (e.g., Baker, 1984) includes more metacognitive processing than we examined in our study. The current study focuses specifically on the detection of coherence breaks and, thus, reflects evaluation rather than regulation of reading behavior in response to encountering a break in coherence.

left temporal and left inferior frontal gyrus, as well as regions that are not considered typical language regions that have been associated with executive functioning and social cognition, such as the dorsomedial prefrontal cortex and the precuneus. More specifically, in addition to analyses of the contrast of language processing versus a resting baseline, and language processing versus a nonlanguage perceptual baseline, this meta-analysis included an analysis of brain regions associated with cognitive processes in response to coherent language compared to those in response to incoherent language. These analyses revealed a network of regions that was more active for coherent compared to incoherent (or less coherent) language. This network comprises bilateral anterior temporal lobes, bilateral posterior superior temporal sulci, left middle temporal gyrus, left inferior frontal gyrus, medial prefrontal cortex, posterior cingulate cortex, and inferior precuneus. However, task demands differed widely between the studies included in the meta-analysis. For example, the coherence contrast included studies that compared processing of coherent stories with processing of unrelated sentences (Fletcher et al., 1995; Xu et al., 2005) and reading of coherent sentence pairs with reading of incoherent sentence pairs (Ferstl & von Cramon, 2001). This makes it difficult to determine to what extent the regions in this network contribute to the specific cognitive processes related to coherence monitoring, such as those involved in coherence-break detection.

Despite the importance of detecting coherence breaks for successful comprehension and the extensive behavioral literature on this topic, only a few studies have focused on the brain regions that are involved in coherence-break detection. Two fMRI studies are particularly relevant in this respect because they employed variations of the contradiction paradigm (Ferstl, Rinck, & Cramon, 2005; Hasson, Nusbaum, & Small, 2007). First, Ferstl et al. (2005) examined coherence-break detection and subsequent integration processes aimed at restoring coherence by contrasting participants' brain activation in response to incoherent narratives with their brain activation in response to coherent narratives. After each narrative participants were explicitly asked to judge its coherence. Coherence-break detection was associated with a region in the right anterior temporal lobe that was more active in response to incoherent compared to coherent target sentences. Integration processes following the detection of coherence breaks were associated with activation of the bilateral ventral inferior frontal gyri and the dorsomedial prefrontal cortex. Activation in the ventral inferior frontal gyri was interpreted as reflecting violations of participants' expectations and subsequent decision-making processes related to their coherence judgments, and activation in the dorsomedial prefrontal cortex was interpreted as reflecting increased evaluative processing or inferencing in response to a coherence break.

Second, Hasson et al. (2007) examined brain activation in response to narratives that, on half of the experimental trials, contained a target sentence that was unexpected in the context of the prior text and, thus, caused a break in coherence. In contrast to the Ferstl et al. (2005) experiment, Hasson et al. used a passive task that did not involve an explicit coherence judgment but instead measured participants' recognition of the sentences after the scan to capture more natural language processing. Greater activation in response to unexpected target sentences than to expected target sentences was observed in a network comprising regions in the dorsomedial prefrontal cortex, bilateral anterior temporal lobes, and bilateral inferior frontal gyri. These findings are consistent with those of Ferstl et al. (2005), which also showed that these regions are more active in response to incoherent compared to coherent target sentences. In addition, Hasson et al. observed greater activation for unexpected than for expected sentences in bilateral temporal and inferior parietal regions, bilateral middle and superior frontal gyri, and regions in the posterior cingulate cortex. Further support for the role of these latter regions in coherence-break detection comes from an analysis of their contribution to the subsequent memory for the narratives: Regions in the left inferior frontal gyrus, bilateral inferior parietal lobes, bilateral temporal lobes, and right dorsomedial prefrontal cortex were more active for narratives that were later remembered. Of interest, this subsequent memory effect was larger for unexpected compared to expected narratives in the precuneus, right superior temporal gyrus, and dorsomedial prefrontal cortex, indicating that these regions were involved in encoding the narratives into memory and were sensitive to coherence breaks as well.

To summarize, previous studies have identified a network of brain regions associated with the ease of integration of new information into the reader's mental representation of a text. This network consists of the bilateral temporal and inferior frontal regions as well as inferior parietal, lateral prefrontal, dorsomedial prefrontal, and posterior midline regions (posterior cingulate and precuneus). In this network, neural activity is generally found to increase in response to breaks in coherence, and no regions are more active for coherent than incoherent information. In addition, both studies suggest that some of these regions are involved in additional processing following the initial detection of a coherence break: The anterior temporal lobe seems involved in detection, whereas the bilateral ventral inferior frontal gyri and dorsomedial prefrontal cortex seem involved in subsequent integration processes (Ferstl et al., 2005). Similarly, increased activation in response to coherence breaks is thought to reflect enhanced encoding into memory (Hasson et al., 2007). This would be consistent with the idea that participants engage in additional cognitive processing when encountering a break in coherence (Cook & O'Brien, 2014; Isberner & Richter, 2014; Singer, 2013).

The findings just reviewed provide insight into which regions are associated with the cognitive processes involved in coherence-break detection. However, for a number of reasons it is difficult to determine whether participants' neural responses reflected cognitive processes elicited at the moment a break in coherence was detected. First, in the two previous studies, trials on which a reader did or did not detect a coherence break were not analyzed separately. Second, and more important, these studies did not include a behavioral measure of coherence-break detection *during* language processing. The fact that recognition of narratives containing unexpected sentences was better than that of narratives containing expected sentences (Hasson et al., 2007) suggests a difference between conditions in processing during listening, but this measure is collected *after* participants listened to the narratives. In the Ferstl et al. (2005) study, participants were explicitly prompted to judge the coherence of each narrative after they were presented. This leaves open the possibility that participants did not notice a break in coherence during the presentation of the target information, but rather *after* each trial. Third, the auditory presentation of narratives in both these studies allowed good control over stimulus presentation rates but did not allow the collection of a behavioral measure of target-information processing upon encountering a coherence break. For this reason, in the current study we employ a self-paced reading design that allows the collection of a behavioral measure of coherence-break detection during reading.

The present study has two goals. The main goal is to examine the neural responses to the detection of coherence breaks, and to do so while obtaining a behavioral measure of coherence-break detection during reading. Similar to Ferstl et al. (2005) and Hasson et al. (2007), we compare brain activation to incoherent target sentences with brain activation to coherent target sentences. The present study adds to the existing knowledge by examining coherence-break detection using a self-paced reading paradigm, which enables us to obtain a behavioral measure of coherence-break detection during reading. In addition, the use of a whole-brain, slow event-related design allows us to accurately estimate the shape of the blood-oxygenation-level dependent (BOLD; which reflects the amount of oxygenated blood in the brain and provides the basis for measuring neural activity with fMRI) response to target sentences. This approach enables a relatively fine-grained analysis of the time course of the hemodynamic response to incoherent and coherent narratives, which allows further exploration of the cognitive processes involved in coherence-break detection. If the regions reported by Ferstl et al. (2005) and Hasson et al. (2007) indeed reflect coherence-break detection and related cognitive processes, then detection of coherence breaks during reading would be associated with enhanced activation in response to incoherent target sentences relative to coherent target sentences in a network of brain regions that includes bilateral temporal and inferior frontal regions, as well as in inferior parietal, lateral prefrontal, dorsomedial prefrontal, and posterior midline regions (posterior cingulate and precuneus).

An additional goal is to examine individual differences in brain activation related to coherence-break detection. Specifically, we examined whether activation in the coherence-break detection network differs as a function of participants' working-memory capacity. Working-memory capacity

is a prime candidate as a source of individual differences because influential theoretical models of text comprehension emphasize the importance of working memory in the construction of a coherent mental representation of texts (e.g., Hannon, 2012; Kintsch, 1988; Linderholm, Virtue, van den Broek, & Tzeng, 2004).

Material and methods

Participants

Thirty-one right-handed, native speakers of Dutch participated in the study (19 female; ages 19–27; M_{age} = 22.1, SD_{age} = 1.9). All participants were undergraduate students who were paid for participating. Data from two additional participants had to be excluded because of poor performance on the coherence-break detection task (more than 3 SDs below the group mean). Data from one additional participant were removed from the individual differences analyses because this participant had a working-memory span score more than 3 SDs above the group mean. All participants had normal or corrected-to-normal vision, and none of the participants reported a history of neurological or psychiatric disorders, including reading disorders or use of psychotropic medication. Participants completed two subtests of the Wechsler Adult Intelligence Scale (3rd ed., Dutch version; Wechsler, 1981): Similarities and Block Design. Estimated IQ scores for all participants were average to above average (M = 107.75, SD = 10.11). The internal review board at the Leiden University Medical Center approved the study, and all participants provided written informed consent. Anatomical scans were reviewed and cleared by a radiologist.

Coherence-break detection task

Participants read 32 six-sentence narratives that were previously used in a behavioral study (Helder, van Leijenhorst, & van den Broek, 2016) based on the contradiction paradigm developed by O'Brien and colleagues (e.g., Albrecht & O'Brien, 1993; O'Brien & Albrecht, 1992; O'Brien et al., 1998) while in the scanner. Each narrative consisted of an introductory first sentence followed by a second sentence that described a situation or a characteristic of the protagonist. These sentences were followed by three filler sentences and the sixth, target sentence. Crucially, in half of the narratives the target sentence presented information that contradicted the information presented in the second sentence, and in the other half of the narratives it did not. Sixteen coherent and 16 incoherent trials were presented in pseudorandomized order in which coherent or incoherent narratives could not occur more than three times consecutively. Before reading the narratives in the scanner, participants performed four practice trials (two coherent, two incoherent) on a laptop outside the scanner to ensure that they understood task instructions.

On each trial, participants saw a screen with instructions to press a button to start the trial, which was followed by the sentence-by-sentence presentation of a narrative in black letters on a gray background. Sentences remained on the screen for a minimum of 500 ms and a maximum of 10 s. Within this time window, the presentation rate was self-paced. Participants were instructed to read for comprehension at their normal pace and to advance to the next sentence by pressing a button with their left index finger. A fixation cross was presented for 500 ms between sentences. Reading times (in ms) for each sentence were recorded and divided by the number of syllables of that sentence to adjust for differences in sentence length across stories. The length of target sentences varied between 10 and 20 syllables (M = 14.72, SD = 2.80). Each narrative was followed by a fixation cross that was presented for 7,000 ms to allow the BOLD response to return to baseline. Following this fixation, participants were presented with two questions that remained on the screen until a yes (left middle finger) or no (left index finger) response was given; the first question was "Does this story make sense?" and required participants to judge the coherence of the narrative they had just read, and the second question required participants to answer a comprehension question on the content of the narrative. Trials were separated

by a 2,000 ms fixation. Narratives were presented in three runs with two short breaks after 12 and 22 trials. Reading times on target sentences in coherent and incoherent narratives were compared as a behavioral measure of online coherence-break detection.

An important advantage of presenting written materials in it is that it more closely mirror performance demands of standard behavioral tests (Birn et al., 2010). Another advantage is that readers are not forced to read at a pace that is not their own. A potential disadvantage is that possible observed reading time differences could be driven by effort-related processing differences. In a recent study, Krinzinger et al. (2011) directly compared fMRI results of fixed and self-paced designs. The results showed that for examining the neural networks underlying complex cognitive processes, the sensitivity of a self-paced study design is at least comparable to that of a fixed design (Krinzinger et al., 2011).

Working-memory capacity

To obtain a measure of participants' working-memory capacity, a Dutch version of the Sentence Span Task was administered outside the scanner (based on Swanson, Cochran, & Ewers, 1989). Participants are asked to listen to sets of sentences that the experimenter reads to them and to remember the last word from each sentence. Following each set of sentences, participants answer a question on the content of one of the sentences to ensure that they comprehended the sentences and are then asked to recall the words they had to remember. Demands on working memory vary because sets consist of two, three, four, five, or six sentences with two sets at each working-memory load. If participants successfully complete both tasks (recall of final words and correctly answer the content question) for at least one of the two sets at a particular load, they advance to the next, higher load. The total number of words recalled correctly on sets for which the question was answered correctly is used as a measure of participants' working-memory capacity (Conway et al., 2005; Friedman & Miyake, 2005).

fMRI data acquisition and preprocessing

The fMRI data were acquired using a standard whole head coil on a 3-Tesla Philips Achieva MRI scanner. Foam inserts that surrounded the head were used to minimize head movement. Motion never exceeded one voxel in any direction for any of the participants during the experiment. T2*-weighed whole-brain Echo-Planar Images were acquired in three runs (repetition time (TR) = 2.2 s; echo time (TE) = 30 ms, flip angle = 80°, 38 transverse slices, voxel size = 2.75 × 2.75 × 2.75 mm), including two dummy scans preceding each run to allow for equilibration of T1 saturation effects. Stimuli were projected using E-prime software (v. 2.0.10.242) onto a screen at the head of the scanner bore, which participants viewed through a mirror attached to the head-coil. Following the functional runs, a high-resolution 3D T1-weighed anatomical scan was obtained for registration purposes (TR = 9.76s; TE = 4.59s, flip angle = 8°, 140 transverse slices, voxel size = 0.875 × 0.875 × 1.2 mm).

Imaging data were preprocessed and analyzed using SPM8 statistical parametric mapping image analysis software (Wellcome Trust Centre for Neuroimaging, University College London, UK) implemented in Matlab (MathWorks, Natick, MA). Preprocessing included slice-timing correction to the first slice using SPM8's Fourier phase shift interpolation, and realignment using rigid body transformation. Functional images were then registered to individual structural T1 images, normalized to the MNI305 stereotaxic space template, and spatially smoothed using a 6 mm, full-width at half-maximum isotropic Gaussian kernel. Normalization involved resampling of the data to 3 mm cubic voxels using a 12-parameter affine transformation and a nonlinear transformation involving cosine basis functions.

Whole-brain analysis

Statistical analyses were performed on individual participants' data using the general linear model in SPM8. Data for all valid trials were modeled as events with individual participants' target-sentence reading times as duration at the onset of each target sentence and convolved with SPM8's canonical hemodynamic response function (Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008). Regressors were defined separately for coherent and incoherent target sentences. Trials were considered valid if both the coherence judgment and the comprehension question were answered correctly and if reading times for all sentences were shorter than 10 s. Invalid trials (7.01% of all coherent trials; 17.54% of all incoherent trials), sentences 1 through 5, and the coherence judgment and the comprehension question were modeled separately as regressors of no interest. Everything that was not modeled (the intra- and intertrial fixations) was used in the main effect contrasts. The model contained a basic set of cosine functions that high-pass-filtered the data. The least-squares parameter estimates of the height of the best-fitting canonical hemodynamic response function for each condition separately were used in pairwise contrasts at the subject level, resulting in four contrast images for each subject (coherent > fixation, incoherent > fixation, coherent > incoherent, and incoherent > coherent). These contrast images were submitted to group analyses where participants were treated as a random effect, using whole-brain one-tailed t-tests. Working-memory span scores were used in the whole-brain regression analyses to examine brain–behavior relations. Resulting whole-brain statistics images were considered significant if they consisted of at least 10 contiguous voxels that exceeded a voxel-wise threshold of $p < .01$ corrected for multiple comparisons using the false discovery rate (Genovese, Lazar, & Nichols, 2002) unless otherwise specified in the text. All local maxima are reported as MNI coordinates. Anatomical location was determined using the AAL toolbox for SPM8 (Tzourio-Mazoyer et al., 2002).

Region-of-interest analysis

In addition to whole-brain analyses, region-of-interest (ROI) analyses were performed to further illustrate the patterns of activation in the clusters that we identified in the whole-brain analysis. We created 6 mm spherical ROIs centered at the peak active voxel for these clusters, as well as a ROI comprising the cluster of activation that resulted from the whole-brain regression analysis with working-memory span scores. We used the MarsBaR toolbox (http://marsbar.sourceforge.net/) for use with SPM8 (Brett, Anton, Valabregue, & Poline, 2002) to extract BOLD activity time series, averaged across all voxels in each ROI for each run. Mean time courses for each condition were then constructed by averaging together appropriate trial time courses, which were defined as 11-s windows of activation after each target sentence onset. These condition-averaged time courses were then averaged across runs and across participants.

Results

Behavioral results

Accuracy was high for both the coherence judgments ($M = 92.54\%$ correct, $SD = 5.63$) and the comprehension questions ($M = 94.66 \%$ correct, $SD = 2.01$), indicating that participants comprehended the narratives and detected the coherence breaks. For valid trials, participants' target sentence reading times in milliseconds per syllable were submitted to a repeated measures analysis of variance with story coherence (coherent vs. incoherent) as within-subjects factor. This resulted in a significant effect of coherence; reading times for incoherent target sentences ($M = 162.18$ ms/syllable, $SE = 6.23$) were longer than reading times for coherent target sentences ($M = 149.57$ ms/syllable, $SE = 5.40$), $F(1, 30) = 16.44$, $p < .001$, $\eta_p^2 = .354$. Participants' working-memory span scores ranged between 4.00 and 19.00 ($M = 10.90$, $SD = 4.24$).

Whole-brain analysis

To examine the neural correlates of coherence-break detection, we compared activation on trials in which participants read target sentences that were incoherent in the context of the narrative to activation on trials in which participants read target sentences that were coherent in the context of the narrative. This whole-brain contrast resulted in activation in a large network of brain regions, including the dorsomedial prefrontal cortex, precuneus, right temporal pole, left inferior frontal gyrus, right supramarginal gyrus, and left inferior and middle temporal gyri. In addition, activation was observed in subcortical clusters in the left amygdala, left hippocampus, and bilateral caudate (see Table 1; Figure 1). As can be seen in Figure 1, most regions in this coherence-break detection network (1c) showed considerable overlap with the network recruited by processing of coherent target sentences (1a) and incoherent target sentences (1b), but activation in response to incoherent target sentences was stronger than that in response to coherent target sentences. However, clusters within the dorsomedial prefrontal cortex, precuneus, left amygdala, and left hippocampus were uniquely involved in processing of incoherent sentences. The reverse whole-brain contrast yielded no clusters that showed more activation to coherent target sentences than to incoherent target sentences.

Table 1. Whole-brain group activations in response to (in)coherent target sentences.

Anatomical Region	L/R	MNI Coordinates x	y	z	k	t	p (Cluster)
a. Results for the contrast incoherent > coherent							
Dorsomedial prefrontal cortex (82%)	L	−9	48	21	1983	7.78	.000
Anterior cingulate gyrus (76%)	R	6	48	12			
Anterior cingulate gyrus (67%)	L	−9	42	9			
Precuneus (42%)	L	−12	−45	42	598	7.03	.000
Middle cingulate (94%)	R	6	−21	42			
Middle cingulate (97%)	L	−3	−18	39			
Temporal pole (79%)	R	36	15	−36	559	6.40	.000
Middle temporal gyrus (52%)	R	51	6	−30			
Parahippocampal gyrus (55%)	R	21	−6	−21			
Inferior frontal gyrus (94%)	L	−42	24	−12	567	6.32	.000
Triangular part (97%)	L	−42	24	6			
Opercular part (70%)	L	−45	12	21			
Supramarginal gyrus (70%)	R	63	−42	24	525	6.12	.000
Middle temporal gyrus (100%)	R	60	−42	3			
Angular gyrus (88%)	R	60	−54	30			
Inferior temporal gyrus (73%)	L	−48	−3	−33	197	5.77	.000
Middle temporal gyrus (97%)	L	−54	3	−24			
Middle temporal gyrus (97%)	L	−51	−12	−21			
Middle temporal gyrus (94%)	L	−57	−60	12	541	5.70	.000
Supramarginal gyrus (42%)	L	−57	−57	27			
Middle temporal gyrus (100%)	L	−51	−54	3			
Amygdala (40%)	L	−18	−6	−12	112	5.4	.000
Hippocampus (94%)	L	−24	−12	−21			
Parahippocampal gyrus (61%)	L	−27	−27	−18			
Caudate (79%)	L	−9	6	9	177	4.76	.000
Thalamus (97%)	L	−9	−21	0			
Caudate (94%)	R	18	18	9	15	4.45	.079
Precentral gyrus (55%)	L	−21	−27	57	11	4.08	.127
b. Results for the contrast coherent > incoherent							
No significant clusters							
c. Regression incoherent > coherent; negative correlation with working-memory span scores							
Precuneus (70%)	L/R	0	−54	54	54	4.89	.002

Note. The probability of each cluster's location in percentage based on the AAL toolbox in SPM8. *p* values correspond to the cluster-level statistic tests with false discovery rate correction at *p* < .01, and *p* < .05 cluster corrected for the regression analysis. L/R = left/right hemisphere; MNI coordinates = cluster peak voxel coordinates in mm; *k* = cluster size in voxels.
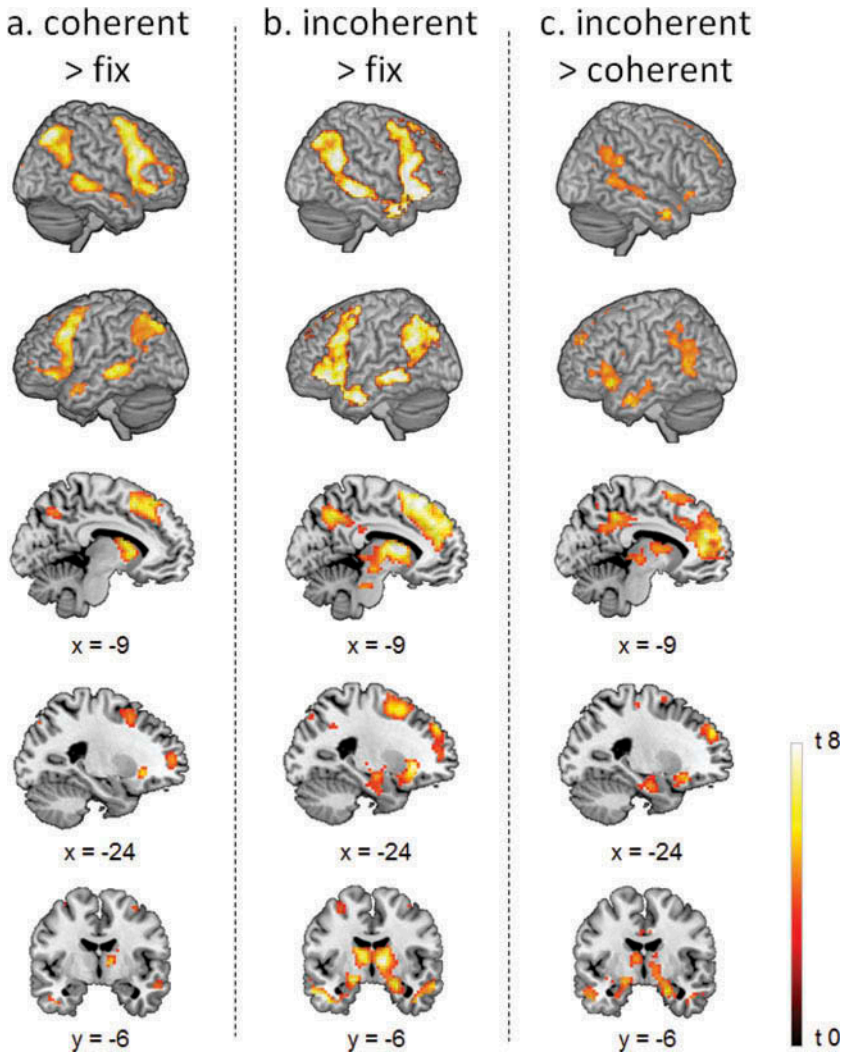
Figure 1. Whole-brain statistics maps for the contrast of (a) coherent target sentences > fixation, (b) incoherent target sentences > fixation, and (c) incoherent target sentences > coherent target sentences across all participants (thresholded at $p < .01$ false discovery rate corrected, at least 10 contiguous voxels). The contrast of coherent > incoherent target sentences showed no significant clusters.

ROI analysis

To better understand the pattern of activation of the four clusters that were exclusively active during reading of incoherent narratives, we created 6-mm spherical ROIs centered at the peak active voxel for these four clusters in the dorsomedial prefrontal cortex (−9, 48, 21), precuneus (−12, −45, 42), left hippocampus (−24, −12, −21) and left amygdala (−18, −6, −12). From these ROIs we extracted average time-series, time locked at the onset of the target sentence, for incoherent and coherent narratives separately. As can be seen in Figure 2, activation in these regions showed an increase in activation compared to a fixation baseline in incoherent narratives but not in coherent narratives.
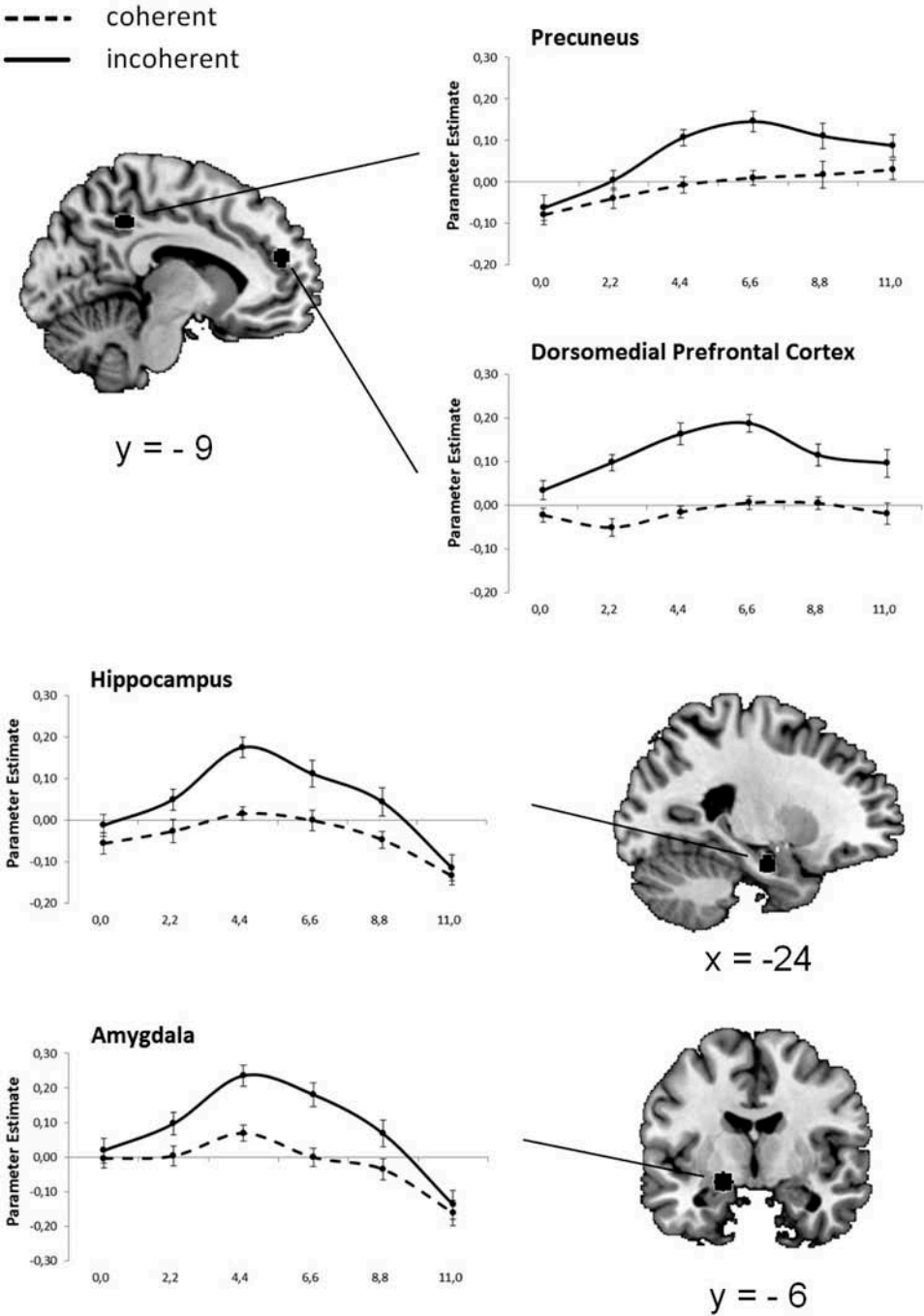
Figure 2. Region-of-interest (ROI) time series for regions that were exclusively active in response to incoherent target sentences for four 6-mm spherical ROIs (depicted in black) centered at MNI coordinates (−12, −45, 42) (precuneus), (−9, 48, 21) (dorsomedial prefrontal cortex), (−24, −12, −21) (left hippocampus), and (−18, −6, −12) (left amygdala). The time-series plots show estimated blood-oxygenation-level dependent signal change in these ROIs from the moment the target sentences are presented in coherent (dashed lines) and incoherent (solid lines) narratives, respectively.
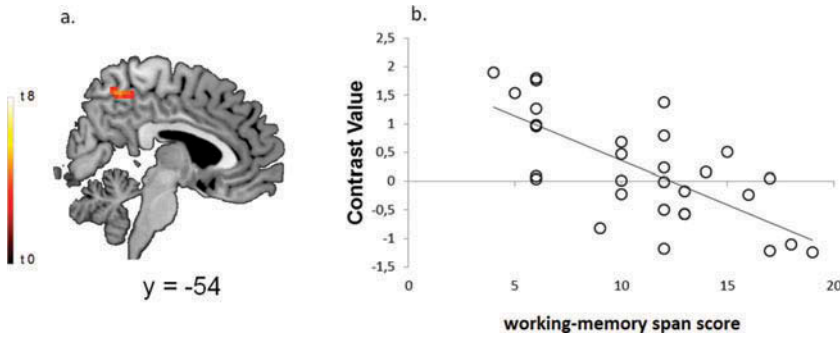
Figure 3. Cluster of activation in the precuneus (a) (peak voxel MNI coordinate [0, −54, 54]) which shows a significant correlation between working-memory capacity and brain activation in the incoherent > coherent contrast (thresholded at $p < .05$ cluster corrected). The scatter plot (b) shows individual participants' contrast values from this cluster as a function of their working-memory span scores. (To view this figure in color, please see the online version of this Journal.)

Individual differences in working-memory capacity

We performed a between-participants whole-brain regression analysis to identify regions in which neural activity during coherence-break detection correlated with participants' working-memory capacity. Participants' working-memory span scores were entered as a covariate in a whole-brain regression analysis on the contrast of incoherent > coherent target sentences. No significant clusters were found at a threshold of $p < .01$ (false discovery rate), but at a more lenient threshold of $p < .05$ (cluster corrected) the analysis resulted in a significant cluster in the precuneus ($k = 54$, peak voxel coordinates [0, −54, 54]), showing a negative correlation between brain activation in response to coherence-break detection and working-memory span scores (see Figure 3a). To better understand this relation we created a functional ROI and extracted the mean contrast value for each participant. The scatterplot in Figure 3b shows that activation in the precuneus when detecting coherence breaks was negatively correlated with working-memory span scores. No regions showed a positive correlation with working-memory span scores.

Discussion

This fMRI study examined the neural responses to coherence-break detection during reading of narratives and explored the relation between brain activation patterns and working-memory capacity. Consistent with previous behavioral studies, participants were slower to read incoherent target sentences compared to coherent target sentences (Albrecht & O'Brien 1993; O'Brien & Albrecht, 1992; O'Brien et al., 1998), indicating that they engaged in additional cognitive processes when they detected coherence breaks during reading (Cook & O'Brien, 2014; Isberner & Richter, 2014; Singer, 2013; van den Broek & Kendeou, 2008). This detection of coherence breaks was associated with activation in a large network of cortical regions including the dorsomedial prefrontal cortex, precuneus, right temporal pole, left inferior frontal gyrus, right supramarginal gyrus, and left inferior and bilateral middle temporal gyri, as well as subcortical regions including the left amygdala, left hippocampus, and bilateral caudate. In this network, brain activation in response to incoherent target sentences was increased relative to coherent target sentences. In addition, brain activation related to coherence-break detection in the precuneus was negatively correlated with working-memory capacity.

Neural correlates of coherence-break detection

Our behavioral findings allow us to extend previous fMRI studies that did not include a behavioral measure of coherence-break detection *during* reading (Ferstl et al., 2005; Hasson et al., 2007). The large network of brain regions that we found corresponds with the results previously reported. With regard to the brain regions involved, our network includes the regions reported by Ferstl et al. (2005), that is, anterior temporal lobe, inferior frontal gyrus, and dorsomedial prefrontal cortex, and has considerable overlap with the network of brain regions reported by Hasson et al. (2007). With regard to the pattern of activation in these regions, similar to Ferstl et al. (2005) and Hasson et al., regions in our network showed greater activation in response to incoherent compared to coherent information.

The current findings differ from previous findings in several ways that help shed light on the function of the different brain regions in this network in the context of coherence-monitoring processes, such as coherence-break detection. For example, previous studies suggest a role for the dorsolateral prefrontal cortex in coherence-break detection (Hasson et al., 2007; Mason & Just, 2006), but we did not find this region to be more active for incoherent compared to coherent sentences. In the context of discourse comprehension, the bilateral dorsolateral prefrontal cortices have been proposed to form a coherence-monitoring network (Mason & Just, 2006) that increases its activation in response to diminished coherence in the text. Consistent with this, a recent study found that patients with lesions in the dorsolateral prefrontal cortex produced less coherent discourse compared to control participants (Coelho, Lê, Mozeiko, Krueger, & Grafman, 2012). These seemingly inconsistent findings related to the involvement of the dorsolateral prefrontal cortex in coherence-break detection may depend on task demands: In an explicit task with texts that were either clearly coherent or incoherent, such as the narratives in Ferstl et al. (2005) and in our study, participants should detect breaks in coherence, which does not require inconsistencies to be resolved. In contrast, in an implicit task with materials containing more subtle breaks in coherence, such as the narratives in the Hasson et al. (2007) study, participants may be more likely to engage in cognitive processes related to resolving a perceived break in coherence. The combination of these findings would suggest a role for the dorsolateral prefrontal cortex in resolving rather than detecting coherence breaks. This fits well with the literature on cognitive performance monitoring in which the dorsolateral prefrontal cortex is part of a frontoparietal control network (Carter & Van Veen, 2007; Fox et al., 2005; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). This network appears involved in top-down cognitive control processes, possibly including those that are recruited when a break in coherence needs to be resolved.

Brain regions uniquely involved in processing of incoherent target sentences

A second difference with previously reported findings is that some regions in our study seem to be uniquely involved in processing of sentences that are incoherent in the context of the narrative. These regions—the anterior part of the dorsomedial prefrontal cortex, precuneus, left amygdala, and left hippocampus—showed significant activation only when processing incoherent information, not when processing coherent information. Our slow event-related design enabled ROI analyses that allow us to speculate on the possible roles of these brain regions. The time course of neural activation in response to a coherence break suggests a relatively early peak of the BOLD response in two subcortical regions in the temporal lobe: the hippocampus and amygdala. Hippocampal activation may reflect early reactivation of episodic memory traces of the text or reactivation of background knowledge (Frankland & Bontempi, 2005), for example, by recalling that the protagonist is a vegetarian and that vegetarians do not eat meat. Activation of the amygdala may reflect an affective alerting response (Phelps & LeDoux, 2005), for example, in response to noticing that something does not make sense when a coherence break is detected. Together, activation in hippocampal areas and the amygdala may reflect relatively fast-

acting processes that modulate the reader's attention and influence how information from the text is encoded into a readers memory (Okon-Singer, Lichtenstein-Vidne, & Cohen, 2013; Richardson, Strange, & Dolan, 2004). In contrast, the peak of the BOLD response occurs later in cortical regions such as the dorsomedial prefrontal cortex and precuneus. This is in line with the proposed roles of these last two regions in coherence building and updating of a mental representation, respectively (Ferstl et al., 2008; Ferstl et al., 2005; Whitney et al., 2009). It should be noted that these interpretations of the ROI time-courses are speculative given the relatively poor temporal resolution of fMRI. Future work using techniques with greater temporal resolution such as EEG or MEG could further explore the timing of different coherence-monitoring processes.

Individual differences in working-memory capacity

Individual differences in working-memory capacity were related to differences in activation associated with coherence-break detection in a region in the precuneus. In this region, participants' working-memory capacity was negatively correlated with activation in response to coherence breaks. In the context of sentence comprehension, a few studies have reported increased brain activation for participants with lower relative to higher working-memory capacity (e.g., Buchweitz, Mason, Tomitch, & Just, 2009; Prat, Keller, & Just, 2007). For example, Newman, Malaia, Seo, and Cheng (2013) found that increased brain activation in the precuneus and inferior frontal gyrus during sentence processing was negatively correlated with working-memory capacity. They interpreted this to mean that participants with lower working-memory capacity recruit episodic-memory systems more when constructing a mental representation of sentences than do participants with higher working-memory capacity. Our results on narrative comprehension are consistent with those on sentence comprehension by Newman et al. (2013) and, thus, also may reflect episodic-memory retrieval during the construction of a mental representation of the text.

To date the exact role of the precuneus in text comprehension (i.e., texts with more than one or two sentences) is unclear. For example, precuneus activation is often reported in conjunction with activation in the posterior cingulate cortex (e.g., Ferstl et al., 2008; for a review, see Ferstl, 2015). Even though the precuneus is not included in a model of the neural correlates of discourse comprehension processes (Mason & Just, 2006), it has been related to differential effects of working-memory capacity as a function of contextual difficulty in three-sentence passages (Prat, Mason, & Just, 2012). Moreover, it has been suggested that the precuneus is involved in updating of the mental representation (Ferstl, 2010), encoding of information into long-term memory (Hasson et al., 2007), integrating new information with existing information to create a coherent mental representation (Bird, Keidel, Ing, Horner, & Burgess, 2015), and episodic memory retrieval (Cavanna & Trimble, 2006; Newman et al., 2013). Our data could be interpreted to indicate that participants with a lower working-memory capacity were retrieving information from their episodic memory of prior text when detecting a coherence break, whereas participants with a higher working-memory capacity may not need this episodic memory search because they still have the relevant prior text information available in working memory at the moment the break in coherence is encountered. This possible interpretation of the role of the precuneus in episodic-memory retrieval in the context of discourse comprehension suggests an important line of future research.

Although it was our intention to examine the neural correlates of an essential but very specific component of reading comprehension, as well as how this relates to individual differences in working-memory capacity, other factors and processes are likely to be involved in successful text comprehension as well. Individual differences in reading-specific skills, such as decoding ability, reading fluency, and vocabulary, background knowledge, (2x) and the reader's standard of coherence may play a role in whether readers are able to detect coherence breaks during reading. In addition, as the imaging results suggest, more domain general processes, such as attention, and other cognitive-control processes are also likely to be involved in coherence monitoring. To fully understand how

readers construct coherent mental representation of texts and how this relates to individual differences in reading-related abilities, future studies could take these factors and processes into account.

To conclude, this study extends previous findings by showing that the additional cognitive processes in which participants engage upon encountering a break in coherence elicit increased activation of regions involved in the processing of coherent text, as well as activation of regions that seem exclusively related to processing of incoherent information. Moreover, the data suggest that regions associated with coherence-break detection and subsequent coherence-building processes can be dissociated in the brain and that individual differences in working-memory capacity are related to activation of a region in the precuneus. It is important to note that the findings in this study do not directly lead to the identification, prevention, and/or treatment of reading comprehension difficulties. However, our imaging results give insight in commonalities and differences in how reader process coherent and incoherent narratives, something that we could not tell from behavioral measures alone. These findings shed light on the functional contributions of these regions to coherence-monitoring processes during reading and help bridge cognitive and neurobiological accounts of the cognitive processes involved in the construction of coherent mental representations from narrative texts.

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