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Monitoring the coherence of texts : coherence-break detection across development

Helder, A.

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Neural correlates of coherence-break detection during reading of narratives

This chapter is based on

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Abstract

Successful comprehension of texts requires readers to construct a coherent mental representation of a text. This involves that a reader continuously monitors whether the emerging mental representation is coherent, for example by engaging in cognitive processes related to coherence-break detection. This study examined the neural correlates of coherence-break detection during reading while simultaneously obtaining a behavioral measure of coherence-break detection. We collected fMRI data from young adults ($N = 31$, ages 19-27) reading 32 six-sentence narratives that were presented sentence-by-sentence in a self-paced, slow event-related design. Half of the narratives contained a break in coherence. Behavioral results showed increased reading times for incoherent compared to coherent target sentences, indicating that participants engaged in additional cognitive processes when detecting breaks in coherence. The contrast of incoherent > coherent target sentences resulted in a large network of active clusters including the dorsomedial prefrontal cortex, precuneus, bilateral temporal lobes, and inferior frontal gyrus. Whereas most regions were active in response to both coherent and incoherent information, the dorsomedial prefrontal cortex, precuneus, hippocampus and amygdala were uniquely responsive to incoherent information. Whole-brain regression analyses on the incoherent > coherent contrast revealed that activation in the precuneus was negatively correlated with working-memory capacity, measured outside the scanner. 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.

4.1 Introduction

We read every day, to be informed, to communicate with others, or simply to entertain ourselves. Text comprehension is a complex, fundamentally human ability to which many cognitive processes contribute. Although there is 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 the 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, 1990; 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 also 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 the 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 the reader does not notice this break in coherence, comprehension of the text is likely to be insufficient. If, however, the 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 of an unfolding text, by detecting breaks in coherence during reading is important because it enables a reader to engage in repair processes that may restore coherence (Baker, 1984; Graesser, Singer, & Trabasso, 1994; Long & Chong, 2001; Zabrocky & Ratner, 1989).

The cognitive processes involved in coherence monitoring, 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; Long & Chong, 2001; Kendeou, Smith, & O'Brien, 2013; 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) and this is taken to reflect 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, 2014a; 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 contribute to the construction of coherent mental representations of texts (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). In a comprehensive meta-analysis of neuroimaging studies on text comprehension processes, Ferstl, Neumann, Bogler & von Cramon (2008) show that this type of higher-level language

comprehension involves activation in many brain regions that are not considered typical language regions. More specifically, in addition to analyses of the contrast of language processing versus a resting baseline, and language processing versus a non-language 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), reading of coherent sentence pairs with reading of incoherent sentence pairs (Ferstl and von Cramon, 2001), and processing of more coherent sentences (with definite articles) with processing of less coherent sentences (without definite articles) (Robertson et al., 2000). This makes it difficult to determine to what extent the regions in this network contribute to the specific cognitive processes that contribute 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 research 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, and von 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. The authors interpreted activation in the ventral inferior frontal gyrus regions as reflecting violations of participants' expectations and subsequent decision-making processes related to their coherence judgments, and activation in the dorsomedial prefrontal cortex 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. (2007) used a passive task that did not involve an explicit coherence judgment but instead measured participants' recognition of the sentences after the scan. The purpose for using a passive task was 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. (2007) observed greater activation for unexpected than for expected sentences in bilateral temporal and inferior parietal regions, bilateral middle and superior frontal gyri, as well as 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. Interestingly, 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. The 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, the BOLD response 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, 2014a; Singer 2013).

The findings reviewed above provide insight into which regions are associated with the cognitive processes involved in the detection of coherence breaks. 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 importantly, 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 had two goals. The main goal was 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 compared 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 enabled us to obtain a behavioral measure of coherence-break detection during reading. Because we are interested in coherence-break detection during reading, we presented the experimental narratives visually instead of aurally. In addition, the use of a whole-brain, slow event-related design allowed us to accurately estimate the shape of the BOLD response to target sentences. This approach enabled a relatively fine-grained analysis of the time course of the hemodynamic response to incoherent and coherent narratives which allowed 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).

4.2 Material and Methods

4.2.1 Participants

Thirty-one, right-handed, native speakers of Dutch participated in the study (19 female; ages 19-27; $M_{\text{age}} = 22.1$, $SD_{\text{age}} = 1.9$). 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 SD 's below the group mean). Data from one additional participant was removed from the individual differences analyses because this participant had a working-memory span score more than 3 SD 's 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 WAIS-III-NL (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 University Medical Center approved the study and all participants provided written informed consent. Anatomical scans were reviewed and cleared by a radiologist.

4.2.2 Coherence-break detection task

Participants read 32 six-sentence narratives that were written for this study 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 that was 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, in the other half of the narratives it did not. Incoherent

and coherent trials were presented in pseudorandomized order in which consistent or inconsistent narratives could not occur more than three times consecutively. Before reading the narratives in the scanner, participants performed four practice trials (two coherent, two contradictory) on a laptop computer outside the scanner to ensure that they understood task instructions.

On each trial a screen was presented with instructions to the participant to press a button to start the trial. Upon a button press, this was followed by the sentence-by-sentence presentation of a narrative, in black letters on a grey background. Sentences remained on the screen for a minimum of 500 ms and a maximum of 10 seconds. 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 7000 ms to allow the BOLD response to return to baseline. Following this fixation participants were presented with two yes/no questions that remained on the screen until a response was given; the first question required participants to judge the coherence of the narrative they had just read, the second question required participants to answer a comprehension question on the content of the narrative. Participants responded with a button press using their left middle finger (yes) or left index finger (no). Presentation of these questions was self-paced as well. Trials were separated by a 2000 ms fixation. Narratives were presented in three runs with two short breaks after 12 and 22 trials. Reading times on target sentences in coherent narratives and incoherent narratives were compared as a behavioral measure of online coherence-break detection.

An important advantage of presenting written materials in a self-paced design is that it more closely mirrors performance demands of standard behavioral tests (Birn et al., 2010). Also, performance demands are similar across participants by taking into account differences in processing speed. 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).

4.2.3 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). The Sentence Span Task requires both maintenance and manipulation of information in working memory. Participants are asked to listen to sets of sentences that the experimenter reads to them and to remember the last word from each sentence (maintenance). Following each set of sentences, participants answer a question on the content of one of the sentences to ensure that they comprehended the sentences (manipulation) and are then asked to recall the words. 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).

4.2.4 fMRI data acquisition, preprocessing and analysis

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. T2*-weighed whole-brain Echo-Planar Images (EPI) were acquired in three runs (TR = 2.2 s; TE = 30 ms, flip angle = 80 degrees, 38 transverse slices, 2.75 x 2.75 x 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 (version 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-weighted anatomical scan was obtained for registration purposes (TR = 9.76; TE = 4.59, flip angle = 8°, 140 slices, voxel size = 0.875 x 0.875 x 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) 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 re-sampling of the data to 3 mm cubic voxels using a 12-parameter affine transformation and a nonlinear transformation involving cosine basis functions.

4.2.5 Whole-brain analysis

Statistical analyses were performed on individual participants' data using the General Linear Model (GLM) in SPM8. Data for all valid trials were modeled at the onset of each

target sentence and convolved with SPM8's canonical hemodynamic response function (HRF). All valid trials were modeled as events with individual participants' target-sentence reading times as duration. 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 seconds. Invalid trials were modeled separately as regressors of no interest. 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 HRF for each condition separately were used in pair-wise contrasts at the subject level. The resulting contrast images were submitted to group analyses where participants were treated as a random effect. At the group level contrasts between conditions were computed by performing whole-brain one-tailed *t*-tests. Working-memory span scores were used in 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 (FDR; 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).

4.2.6 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, and used the MarsBaR toolbox (<http://marsbar.sourceforge.net/>) for use with SPM8 (Brett, Anton, Valabregue, & Poline, 2002) to extract blood oxygenation level-dependent (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.

4.3 Results

4.3.1 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 ms per syllable were submitted to a repeated measures analysis of variance (ANOVA) with story coherence (coherent vs. incoherent) as within-subjects factor. This resulted in a significant effect of coherence; reading times for incoherent target sentences ($M = 162.18$, $SE = 6.23$) were longer than reading times for coherent target sentences ($M = 149.57$, $SE = 5.40$), $F(1, 30) = 16.44$, $p < .001$, $\eta_p^2 = .354$ replicating findings in the behavioral literature (e.g., Albrecht & O'Brien, 1993). Participants' working-memory span scores ranged between 4.00 and 19.00 ($M = 10.90$, $SD = 4.24$).

4.3.2 Whole-brain analysis neural correlates of coherence-break detection.

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 4.1; Figure 4.1). As can be seen in Figure 4.1, most regions in this coherence-break detection network (4.1c) showed considerable overlap with the network recruited by processing of coherent target sentences (Figure 4.1a), but activation in response to incoherent target sentences (Figure 4.1b) 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.

4.3.3 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 4.2 activation in these regions showed an increase in activation compared to a fixation baseline in incoherent narratives but not in coherent narratives.

Table 4.1. Whole-Brain Group Activations in Response to (In)Coherent Target Sentences.

Anatomical Region	L/R	MNI coordinates			k	I	p
a. Results for the contrast Incoherent > Coherent		x	y	z			(cluster)
Dorsomedial Prefrontal Cortex (82 %)	L	-9	48	21	1983	7.78	.000
<i>Anterior Cingulate Gyrus (76 %)</i>	R	6	48	12			
<i>Anterior Cingulate Gyrus (67 %)</i>	L	-9	42	9			
Precuneus (42 %)	L	-12	-45	42	598	7.03	.000
<i>Middle Cingulate (94 %)</i>	R	6	-21	42			
<i>Middle Cingulate (97 %)</i>	L	-3	-18	39			
Temporal Pole (79 %)	R	36	15	-36	559	6.40	.000
<i>Middle Temporal Gyrus (52 %)</i>	R	51	6	-30			
<i>Parahippocampal Gyrus(55 %)</i>	R	21	-6	-21			
Inferior Frontal Gyrus (94 %)	L	-42	24	-12	567	6.32	.000
<i>Triangular part (97 %)</i>	L	-42	24	6			
<i>Opercular part (70 %)</i>	L	-45	12	21			
Supramarginal Gyrus (70 %)	R	63	-42	24	525	6.12	.000
<i>Middle Temporal Gyrus (100 %)</i>	R	60	-42	3			
<i>Angular Gyrus (88 %)</i>	R	60	-54	30			
Inferior Temporal Gyrus (73 %)	L	-48	-3	-33	197	5.77	.000
<i>Middle Temporal Gyrus (97 %)</i>	L	-54	3	-24			
<i>Middle Temporal Gyrus (97 %)</i>	L	-51	-12	-21			
Middle Temporal Gyrus (94 %)	L	-57	-60	12	541	5.70	.000
<i>Supramarginal gyrus (42%)</i>	L	-57	-57	27			
<i>Middle Temporal Gyrus (100 %)</i>	L	-51	-54	3			
Amygdala (40 %)	L	-18	-6	-12	112	5.4	.000
<i>Hippocampus (94 %)</i>	L	-24	-12	-21			
<i>Parahippocampal Gyrus (61 %)</i>	L	-27	-27	-18			
Caudate (79 %)	L	-9	6	9	177	4.76	.000
<i>Thalamus (97 %)</i>	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

The probability of each cluster’s location in % based on the AAL toolbox in SPM8; L/R = left/right hemisphere; MNI coordinates = cluster peak voxel coordinates in mm; k = cluster size in voxels. p –values correspond to the cluster-level statistic tests with FDR correction at $p < .01$, and $p < .05$ cluster corrected for the regression analysis.

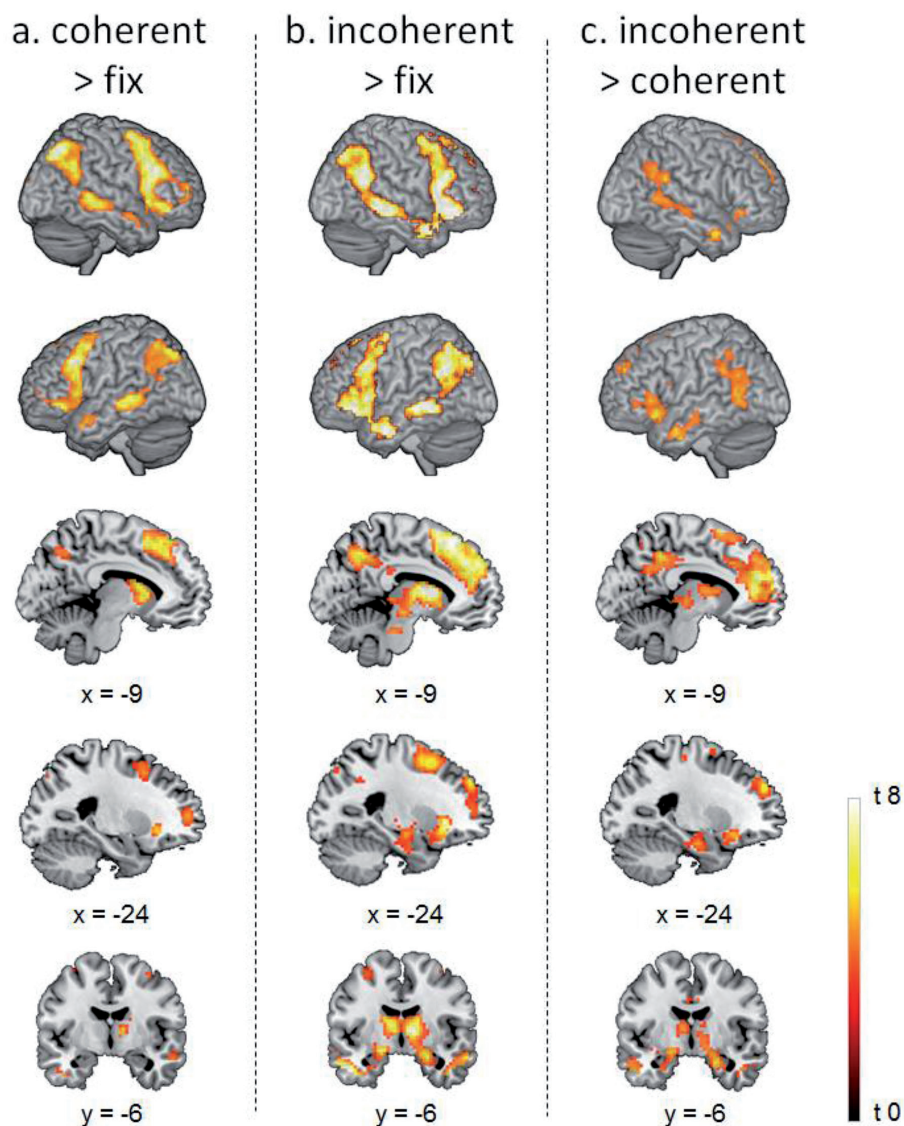


Figure 4.1. Whole-brain statistics maps for the contrast of incoherent > coherent (c) across all participants (thresholded at $p < .01$ FDR corrected, at least 10 contiguous voxels). Whole-brain statistics maps for the contrast of coherent target sentences > fixation (a), incoherent target sentences > fixation (b) are plotted for comparison.

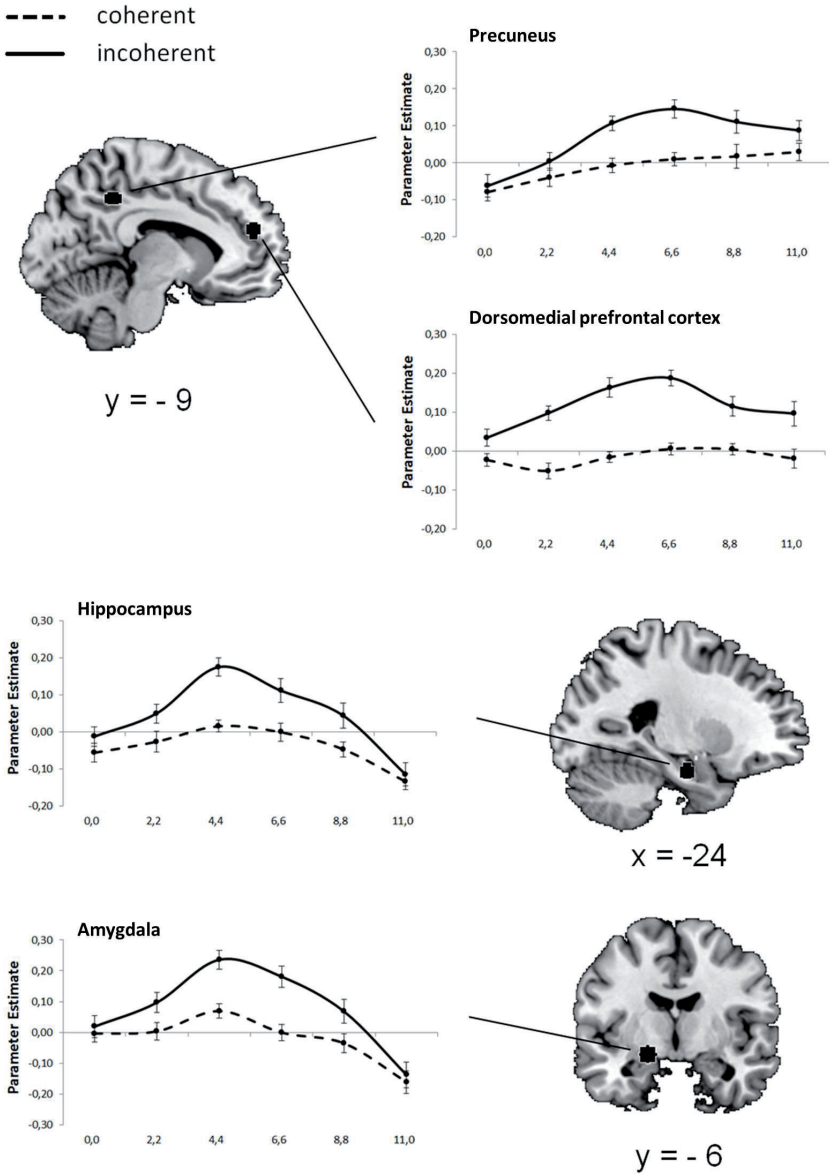


Figure 4.2. ROI time series for regions that were exclusively active in response to incoherent target sentences for four 6-mm spherical ROIs (depicted in black) centered at MNI coordinates [-12, -45, 42] (precuneus), [-9, 48, 21] (dorsomedial prefrontal cortex), [-24, -12, -21] (left hippocampus), and [-18, -6, -12] (left amygdala). The time-series plots show estimated BOLD signal change in these ROIs from the moment the target sentences are presented in coherent (dashed lines) and incoherent (solid lines) narratives, respectively.

4.3.4 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 $p < .01$ (FDR), but at a more lenient threshold of $p < .05$ (cluster corrected). This 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 4.3a). To better understand this relation we created a functional ROI and extracted the mean contrast value for each participant. The scatterplot in Figure 4.3b 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.

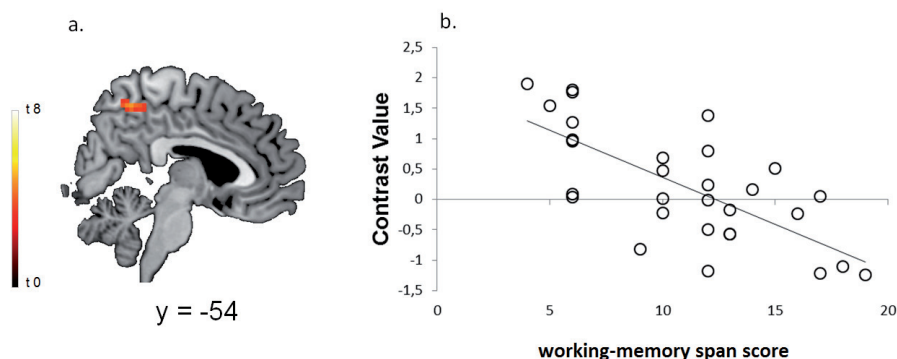


Figure 4.3. Cluster of activation in the precuneus (a) (peak voxel MNI coordinate [0, -54, 54]) which shows a significant correlation between working-memory capacity and brain activation in the incoherent > coherent contrast (thresholded at $p < .05$ cluster corrected). The scatter plot (b) shows individual participants' contrast values from this cluster as a function of their working-memory span scores.

4.4 Discussion

In this fMRI study we examined the neural responses to the detection of coherence breaks during reading of narratives while obtaining reading times as a behavioral measure of coherence-break detection. In addition we explored the relation between working-memory capacity and the pattern of activation in this coherence-break detection network. Behavioral results showed that participants were slower to read incoherent compared to coherent target sentences, indicating that they detected coherence breaks during reading. Imaging results showed that 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 – was involved in coherence-break detection. 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. Below we discuss the behavioral and fMRI results in relation to those of previous studies that have used variations of the contradiction paradigm to investigate the neural correlates of coherence-break detection. We then discuss the possible roles of brain regions involved in the processing of incoherent target sentences and, finally, reflect on our findings related to individual differences in working-memory capacity.

4.4.1 Neural correlates of coherence-break detection

The behavioral findings are consistent with those of prior studies: Participants were slower to read incoherent target sentences compared to coherent target sentences (Albrecht & O'Brien 1993; O'Brien & Albrecht, 1992; O'Brien, Rizella, Albrecht, & Halleran, 1998). This slow down suggests that participants engaged in additional cognitive processes when they detected coherence breaks during reading (Cook & O'Brien, 2014; Isberner & Richter, 2014a; Singer 2013; van den Broek & Kendeou, 2008). This allows 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, both in terms of the regions involved and in terms of the pattern of activation in these regions. With regard to the brain regions involved, our network includes the regions reported by Ferstl et al. (2005), i.e., 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. (2007), 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 the dorsolateral prefrontal cortex 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 proposal is the finding from a recent study on discourse production by patients with lesions in the dorsolateral prefrontal cortex. In these patients discourse coherence was impaired 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 clearly coherent or incoherent texts, such as the narratives in Ferstl et al. (2005) and in our study, it is the participants' task to detect breaks in coherence, and resolving inconsistencies is not required to perform the experimental task. 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 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.

4.4.2 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. The slow event-related design of our study allows us to speculate on the possible roles

of different brain regions, based on the results from our ROI analyses. 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 re-activation of episodic memory traces of the text or re-activation 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 reader's memory (Okon-Singer, Lichtenstein-Vidne, & Cohen, 2012; 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. 2005; Ferstl et al., 2008; 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.

4.4.3 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 and Just, 2007). For example, Newman, Malaia, Seo, & Cheng (2008) 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. (2008) 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, the precuneus is not included in a model of the neural correlates of discourse comprehension processes (Mason & Just, 2006), but 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). 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), as well as episodic memory retrieval (Cavanna & Trimble, 2006; Newman et al. 2008). 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.

To conclude, this study on the neural correlates of coherence-break detection 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 are 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. 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.

