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Fairy Tales versus Facts: Genre Matters to the Developing Brain

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Abstract

Neurobiological studies of discourse comprehension have almost exclusively focused on narrative comprehension. However, successful engagement in modern society, particularly in educational settings, also requires comprehension with an aim to learn new information (i.e., “expository comprehension”). Despite its prevalence, no studies to date have neurobiologically characterized expository comprehension as compared with narrative. In the current study, we used functional magnetic resonance imaging in typically developing children to test whether different genres require specialized brain networks. In addition to expected activations in language and comprehension areas in the default mode network (DMN), expository comprehension required significantly greater activation in the frontoparietal control network (FPN) than narrative comprehension, and relied significantly less on posterior regions in the DMN. Functional connectivity analysis revealed that, compared with narrative, the FPN robustly correlated with the DMN, and this inter-network communication was higher with increased reading expertise. These findings suggest that, relative to narrative comprehension, expository comprehension shows (1) a unique configuration of the DMN, potentially to support non-social comprehension processes, and (2) increased utilization of top-down regions to help support goal-directed comprehension processes in the DMN. More generally, our findings reveal that different types of discourse-level comprehension place diverse neural demands on the developing brain.

Key words: comprehension, language, neuroimaging

Introduction

In the last several decades, studies have made significant headway in revealing the cognitive and neural complexities of discourse-level processes (Mar 2004; Ferstl et al. 2008; Swett et al. 2013; Silbert et al. 2014; Aboud et al. 2016), primarily through the study of stories (i.e., “narrative comprehension”). However, successful engagement in modern society involves the ability to comprehend multiple forms of discourse. In particular, long-term educational gains depend on a person’s ability to comprehend

narratives and informational media (i.e., “expository comprehension”) (National Governors Association Center for Best Practices Council of Chief State School Officers 2015). The demand for skilled expository comprehension is particularly salient during development, when children are expected to learn new factual information in school primarily through written expository passages (e.g., science textbooks). Despite the prevalence of expository comprehension, there is a pervasive, negative performance gap in expository comprehension as compared with narratives in

schools (Haberlandt and Graesser 1985; Olson 1985; Best et al. 2008; McNamara et al. 2011), which in the US educational system has been found to become particularly apparent in fourth grade. This has led some to suggest that expository texts are one key contributor to the “fourth grade slump” in reading performance (Best et al. 2008; McNamara et al. 2011). While behavioral research suggests that performance differences may be based on unique cognitive demands required for adequate expository comprehension (Eason et al. 2012), no studies to date have examined whether expository comprehension requires overlapping or unique neural circuits compared with narrative comprehension. The present study examined visual expository and narrative passages in young readers in order to determine whether expository comprehension requires unique neural resources compared with narrative comprehension, and whether neural differences interact with reading expertise.

Requirements of Adequate Comprehension Across Genres

In order to adequately comprehend a text, a reader needs to map the word-form onto the appropriate speech-sounds, connect the word to its meaning, integrate meaning across words and across sentences, and integrate relevant background knowledge to build a coherent internal representation of the text (i.e., a “situation model”). Consequently, comprehension requires complex coordination across a number of cognitive and neural systems (Kendeou et al. 2014). A number of discourse theories have aimed to characterize the nature and interaction of these systems. For example, the Landscape Model of reading proposes that building an adequate situation model of a passage requires both (1) “bottom-up” spreading activations related to passive memory processes that link locally- and distally-related concepts within the passage, as well as (2) “top-down” strategic processes that explicitly connect passage concepts with relevant text- and background-based information to assist with a reader’s coherence goals (processes which may be linked to different brain networks; see below) (van den Broek et al. 1999). While all passages require basic language processing, evidence suggests that higher-level processes like perspective-taking, social cognition, and strategic processes significantly differ depending on the interaction between the demands of the specific passage and an individual’s goals/characteristics (van den Broek et al. 2001; Sesma et al. 2009; Mar 2011; Eason et al. 2012). For instance, brain activations during passage comprehension have been shown to vary depending on a subject’s preferred pronoun perspective and interpretation (van den Broek et al. 2001, 2005; Hartung et al. 2017). These findings provide a strong precedence for investigating variability in the neural requirements for different types of comprehension, including one of the most prominent text characteristics—genre.

Genre is a multidimensional construct that reflects both local (i.e., word-level) and global textual differences that act to support different reading goals (Graesser et al. 2011). While narrative passages are defined as conveying a series of causal events that include characters, goal, setting, and a consistent rhetorical structure (Stein and Glenn 1975; Trabasso and van den Broek 1985), expository passages convey factual information about specific subject domains and can take a number of rhetorical forms (Hiebert et al. 1983). The primary goal of narrative comprehension may be to simulate and learn social behavior (Mar 2004), while the primary goal of expository comprehension is to learn new factual information (Mayer 1996). This framework

suggests that genre may reflect different types of learning, with related differences in real-time processing requirements. Expository passages are generally considered to be “harder” to read than narratives, resulting in a negative performance gap for expository passages in schools (Haberlandt and Graesser 1985; Olson 1985; Best et al. 2008). In particular, expository passages place significantly higher demand on the integration of the passage content with the preceding text and the reader’s background knowledge than narrative passages because they include both novel information (for which students may not have appropriate background knowledge), as well as variable/unknown discourse structures (e.g., compare/contrast versus chronological organization) (Langer and Nicolich 1981; Hiebert et al. 1983; McNamara et al. 2011). Indeed, while students in second grade already know narrative structures (e.g., story grammar) (Best et al. 2008), students in third through fifth grades still struggle with identifying the variable structures of expository texts (Langer and Nicolich 1981; Kamberelis and Bovino 1999). Because of these discourse differences, expository texts are less likely to meet a reader’s standards of coherence (i.e., a reader’s real-time perception of whether the text “makes sense”), and consequently are more likely to require strategic processes to overcome coherence difficulties (van den Broek et al. 2005). This is supported by behavioral findings that expository comprehension requires greater use of executive functions. Samuelstuen and Braten (2005) found that compared with narrative, expository comprehension is particularly influenced by rhetorical strategies such as elaboration, organization, and monitoring. Additionally, Eason et al. (2012) found that while vocabulary and word reading ability broadly contributed to comprehension in texts, expository comprehension ability was significantly more related to individuals’ planning/organizational ability than narrative comprehension. The behavioral and theoretical literature consequently both suggest that expository texts require unique strategic cognition in order to support increased demand for the integration of new information.

Neurobiological Processes Involved in Comprehension

In the realm of neurobiological research, different brain networks are thought to contribute to the relational and strategic processes that support the construction of a reader’s situation model. In addition to canonical language areas that support word recognition, vocabulary, and syntax, narrative comprehension has consistently been found to engage a coordinated set of higher-order regions referred to as the default mode network (DMN; Maguire et al. 1999; Mar 2004; Ferstl et al. 2008; Yarkoni et al. 2008). The DMN canonically includes the dorsomedial prefrontal cortex, bilateral angular gyri (AG), the precuneus/posterior cingulate cortex, bilateral anterior temporal lobes (ATL), and the hippocampus (Buckner et al. 2008). The handful of studies that have examined brain networks involved in expository comprehension (without comparing to narrative) show that language areas and restricted activation of the DMN (left-lateralized) are recruited in adolescent and adult comprehenders (Swett et al. 2013; Aboud et al. 2016). While originally studied in the brain at rest, the DMN (also referred to as the highly overlapping “theory of mind network”) has since been found to support social, inferential, and autobiographical processes that are necessary for an individual to build an appropriate internal representation of a passage (Buckner et al. 2008; Ferstl et al. 2008; Mar 2011). Studies have also found that DMN activation and connectivity are temporally dynamic over the course of passage comprehension and driven by global features

of the text (Swett et al. 2013; Simony et al. 2016). These findings support a role of the DMN in situation model building, and also reveal the dynamic neural requirements of passage comprehension. Interestingly, the semantic processing literature also suggests that the DMN acts as a “representational system” in which automatic spreading of meaning at multiple levels occurs between highly related concepts (Davey et al. 2016), linking the DMN to the passive, bottom-up memory processes proposed in the Landscape Model.

Less discussed in the realm of discourse comprehension is the frontoparietal control network (FPN), which includes bilateral dorsolateral prefrontal cortex (dlPFC), bilateral intraparietal sulcus (IPS), cingulate cortex, and lateral medial temporal lobes. The FPN is a set of executive regions associated with adaptive cognitive regulation, including goal-directed cognition during tasks (Ptak 2012; Cole et al. 2014). Mason and Just (2004) proposed that frontal portions of the FPN play a key role in coherence detection in discourse processing, and others suggest the FPN is involved in aligning retrieved meaning with the discourse goals (Davey et al. 2016). Both theories connect the FPN to the strategic integration processes referenced in the Landscape Model that are necessary for the integration of background information. Additional work suggests that the FPN is a top-down neural scaffold that supports the functions of other brain systems across a range of cognitive skills and clinical populations (Cole et al. 2014), including reading specifically (Aboud et al. 2016, 2018). Consequently, a number of studies suggest that the FPN is a top-down network that, in the context of reading, may assist in strategic processing.

Hypotheses

In the context of discourse theory and behavioral findings, as well as known properties of brain networks, we hypothesized that both narrative and expository passages would require activation in language areas and regions in the DMN to support basic language processes and spreading memory activations, respectively, though from prior studies, we expected DMN activation in expository comprehension to be limited to left-lateralized nodes (Swett et al. 2013). In addition to expected language and more restricted DMN activations, we hypothesized that, compared with narrative, expository comprehension would require greater use of the FPN to support strategic integration of incoming information with a reader’s background knowledge. This would be evidenced by both greater activation of the FPN and greater communication of the FPN with comprehension areas (namely, language regions, and the DMN). We anticipated that stronger readers would implement more strategy, and consequently would show more utilization of the FPN in support of comprehension networks (e.g., the DMN).

Materials and Methods

Participants

Sixty-two subjects were scanned in the summer and fall following completion of third grade (i.e., 8–10 year olds), which was one cross-sectional time point in an ongoing longitudinal study. From the original cohort, subjects were excluded based on the following exclusion parameters: in-scanner motion ($n = 9$ excluded for outlying volumes $> 20\%$), in-scanner task performance ($n = 5$; see below), and inadequate head coverage ($n = 3$). The final analysis included 45 adolescents, aged 8–10 years old (mean age = 9.45 \pm 0.31 years; 20 female). Pre-screening eligibility ensured that all participants were native speakers of American English with

normal hearing and normal or corrected-to-normal vision, with no history of major psychiatric illness or traumatic brain injury/epilepsy, and no contraindication to magnetic resonance imaging (MRI). Participants and their parents gave written assent/consent at the beginning of the study, with procedures carried out in accordance with Vanderbilt University’s Institutional Review Board (IRB; Protocol # 101072). Participants received \$75 compensation for behavioral testing and \$75 for neuroimaging testing as per the study’s IRB.

Behavioral Testing

Participants were confirmed to have typical IQ (standard score >75 on Full Scale IQ of the Wechsler Abbreviated Scale of Intelligence; mean IQ = 114.53 \pm 15.40) (Wechsler 2011). Additionally, to ensure that participants had at least the entry level word recognition/decoding ability to complete the paradigm, participants were required to have a minimum standard score of 75 on the basic reading composite score of the Woodcock Johnson III (Woodcock et al. 2001). Reading comprehension ability was assessed using the Gates MacGinitie et al. (2000), which tests both narrative and expository reading ability (MacGinitie et al. 2000). During this test, participants are asked to silently read narrative and expository passages, and answer 3–6 multiple choice questions of increasing difficulty per passage with a 35-min total time limit. One participant did not complete the Gates MacGinitie and was excluded from reading ability analyses.

Passage Stimuli

General

As part of an ongoing longitudinal study (see below), ten passages (five narrative and five expository; average word count = 146.40 \pm 6.48) were constructed in-lab and equated across the following metrics using CohMetrix (Graesser et al. 2011): syllables/word (1.31 \pm 0.02), word frequency (CELEX frequency mean for content words = 2.17 \pm 0.10), word concreteness (432.71 \pm 20.70), sentence length (11.65 \pm 0.65), and Flesch-Kincaid grade level (4.46 \pm 0.33; range = 4–4.9). Passages were considered equivalent when measures were within a 90% confidence interval of the mean of the remaining passages. The narrativity metric from CohMetrix was used to ensure that individual passages represented the appropriate genre. Narrativity is a component of 17 word- and sentence-level text metrics, and has been shown to be a robust and ecologically-valid reflection of genre (Graesser et al. 2011). Individual metrics that contribute to the narrativity component include pronouns (or “characters”) and intentional action words, among others. The narrativity percentile reflects the narrativity score of an input passage relative to a large ($n = 37\,520$) corpus of real-world texts analyzed by CohMetrix, with higher narrativity reflecting a text that has greater narrative components. The mean narrativity of the five narrative passages was the 74th percentile (range = 68th–83rd percentile), and the mean narrativity of the five expository passages was the 20th percentile (range = 12th–28th percentile), with all passages falling within the 90% confidence interval of the mean of the remaining genre-matched passages.

Current Study

Two visual passages were administered during the third longitudinal study visit (referred to here as “the current study”): “Hydroponics” (expository; Flesch-Kincaid grade level = 4.88; Narrativity = 18th percentile) and “A Game of Kickball” (narrative; Flesch-Kincaid grade level = 4.65; Narrativity = 78th

percentile; see Passage generalizability below). Each passage consisted of two paragraphs (blocks), the first of which served to introduce the topic or narrative scenario while the second elaborated on a particular detail of the subject matter or story outcome. Notably, while not within the scope of the present paper, supplemental analysis of the currently available data from our ongoing longitudinal study confirmed that the main findings for the present paper are generalizable beyond the visit three passages, demonstrating that current findings are not driven by specific, topic-based differences in the passages examined in the present paper (see Supplementary Fig. S1).

Experimental Design

During a single fMRI session, subjects performed two fMRI runs, each consisting of three conditions: Passage reading, Non-alphanumeric symbols, and Fixation. The order for each run was: Passage Paragraph 1, Symbolic Baseline 1, Passage Paragraph 2, Symbolic Baseline 2, and Fixation. To account for order effects, the presentation of narrative versus expository was counterbalanced across subjects ($n = 26$ subjects read expository first). To create a more naturalistic reading experience than single word presentation (Rayner 1986), passages were presented in idea units, ranging from 1 to 7 words in length. In order to determine the potential impact of a controlled versus natural reading presentation, we re-ran all of the analyses and included out-of-scanner subject measures of reading speed (Qualitative Reading Inventory-5; average words per minute reading rate) as a covariate of no interest. Including this measure did not change the results of the study, and so was excluded from the final model.

Stimuli Presentation

For passage stimuli, we allowed 550 ms for each content word and 275 ms for each function word (as in Aboud et al. 2016). The symbolic baseline condition included three non-alphanumeric symbols (two-symbol types) displayed horizontally on a slide, and was matched in presentation time to the passage phrases. Spacing between symbols randomly alternated to replicate the variable phrase lengths in the Passage condition. Average total passage duration (without jitter) was 61.32 s, and average symbolic baseline duration was 62.44 s. The interval between phrase stimuli (Passages and Symbols) was randomly jittered to allow for phrase-level comparisons not included in this study (jitter ranging from 500 ms to 4000 ms). To monitor whether participants attended to all stimuli, 7%–9% of the stimuli were randomly repeated on two consecutive screens (all repetitions modeled out as regressors of no interest; see below).

In-scanner Behavior

Participants pressed a button with their right thumb when they detected repetition of a phrase or symbol configuration. Repetitions were included in the first-level analysis as a regressor of no interest so that activations related only to the performance task were controlled for in the analyses. There were no significant differences in performance on the performance-monitoring task for expository versus narrative passages ($t(44) = 0.47$; $P = 0.64$). All subjects were trained on the task in a mock scanner prior to the actual scan; separate stimuli was used in training in order to avoid learning effects. Additionally, to assess background knowledge on expository and narrative passage topics, subjects were asked prior to the scan whether they

had any knowledge of the general topic. To minimize priming effects, the following script was used: “Can you please tell me anything you know about Hydroponics.” Only two subjects had non-specific background knowledge of the expository topic; two additional subjects were missing pre-scan background knowledge questionnaires (Exclusion of these four subjects did not alter the findings of the present study.). Immediately following the scan, subjects were additionally asked to freely recall information from the passages, with the prompts “Tell me everything you read about (Hydroponics/A Game of Kickball)”. Inclusion in the present analysis required that participants exhibit one of two performance behaviors for both passages: (1) a d' prime value >2 during the repetition task (d' prime = $z(\text{Hit Rate}) - z(\text{False Alarm Rate})$), or (2) correct recall of passage information beyond background information reported prior to the scan session. D' Prime is a sensitivity measurement (Macmillan and Creelman 2008) that reflects subject accuracy, while accounting for false alarm rates; any subjects excluded based on the d' prime value either had excessive button responses non-specific to the repetition task, or inaccurate responses to the repetition task. Subjects were considered to have correctly recalled information if their free recall represented a distinct idea from the passage; passage recall was not significantly different for expository and narrative passages ($\chi^2 = 2.38$; $P = 0.12$).

fMRI Data Acquisition

All fMRI scans were acquired at Vanderbilt University Institute of Imaging Sciences on one of two Philips Achieva 3 T MR scanners with a 32-channel head coil. Scanner was regressed out from all analysis unless otherwise noted. Functional images were acquired using a gradient echo planar imaging sequence with 40 (3 mm thick) slices with no gap and consisted of two runs (single run duration (TA) = 9 min 25.4 s; 250 dynamics per run). Slices were parallel to the anterior–posterior commissure plane. Additional imaging parameters for functional images included echo time (TE) = 30 ms, FOV 240 × 240 × 120 mm, 75 degree flip angle, and repetition time (TR) = 2200 ms, and 3 mm³ voxels. Because the phrase presentation duration (average = 1.1 s) and jitter duration (average = 1.5 s) exceed the TR of 1 volume per 2.2 s, events were able to be adequately modeled with the current acquisition parameters.

fMRI Data Analysis

Preprocessing and single subject first-level analyses were performed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>) (Friston et al. 1997) and MATLAB (R2013a; Mathworks, Natick MA). The functional data for each participant was slice-timing corrected, aligned to the mean functional image, normalized to the Haskins Pediatric affine template (MNI space) (Molfese et al. 2015), and spatially smoothed with an 8 mm FWHM Gaussian filter. Individual registrations of the functional image to the T1 template were manually inspected for fit along all three dimensions to ensure quality. At the individual subject level, a high-pass temporal filter (128 s) was applied to remove slow-signal drifts. Phrases were modeled as events, and convolved with a canonical HRF for each condition. Conditions included Expository text, Narrative text, and the Symbolic baseline. The Expository condition was comprised of 57 events and Narrative condition was comprised of 48 events. Size motion parameters and outlying volumes as determined using Artifact Detection Tools (ART; http://www.nitrc.org/projects/artifact_detect/) were included in the design matrix as regressors of no

interest. Subjects with greater than 20% outlying volumes on any single run were excluded from the final analysis ($n = 9$). For the standard GLM analyses, three contrasts for each participant were created: Expository vs. Symbols, Narrative vs. Symbols, and Symbols vs. Fixation. Due to variability in head size (and resulting variability in field of view), the cerebellum was not included in our analysis. As recommended by Durnez et al. (2016), power analysis of passage reading activation from a separate developmental study within our lab (with similar stimuli presentation; whole-brain, one-sample t -test, uncorrected; $\alpha = 0.05$, and screening threshold of $t = 2.7$) yielded predicted statistical power of 0.84 for the current study's sample size.

Group-level analysis. For group statistics, SPM8 and MATLAB were used to generate whole-brain activation maps. AFNI's 3dClustSim algorithm (compilation date 2016) (Cox et al. 2017) was used to correct for multiple comparisons through iterative Monte Carlo simulations ($n = 10,000$). All group-level analyses were subjected to a statistical threshold of P -corrected <0.05 (P -uncorrected <0.005 ; $k = 152$). Individual contrast maps of Expository vs. Symbols and Narrative vs. Symbols were brought up to a paired t -test to analyze Expository vs. Symbols, Narrative vs. Symbols, and Expository vs. Narrative group maps. To identify shared activation regions for expository and narrative passages, minimum t -value conjunction was performed between Expository $>$ Symbols and Narrative $>$ Symbols. To examine neural correlates of reading comprehension ability, regression was performed between the subject's contrast of interest beta values (output from the aforementioned paired t -test) and the subject's reading comprehension ability (Gates MacGinitie). This covariate analysis was performed within the mask of significant FPN activations in the Expository $>$ Narrative contrast in order to test whether observed differences for Expository $>$ Narrative were positively related to our covariates of interest.

Connectivity Analysis

Connectivity analysis was performed using the Conn toolbox (Conn 17b) (Whitfield-Gabrieli and Nieto-Castanon 2012). The seed region was derived from the GLM maps generated in the general group analysis. Specifically, the seed region included significant areas found in Expository $>$ Narrative that fell within the FPN (i.e., GLM findings were masked with a canonical FPN pediatric masks; <https://www.nitrc.org/projects/r-spit/>). For each subject, voxel time-series within the seed region of interest (ROI) were extracted and averaged across voxels. Confounding signals were estimated from white matter and CSF (derived from T1 images) through the CompCor method (Behzadi et al. 2007). The CompCor output, motion outliers and six movement parameters (as determined by ART) were regressed out from all voxel time-series, and a high-pass filter of 0.008 Hz was applied; linear detrending and despiking algorithms were additionally applied. To remove correlations driven by general, task-related co-activations (e.g., onset/offset effects), task effects and their first temporal derivative were also removed from the signal (Whitfield-Gabrieli and Nieto-Castanon 2012). For every subject, bivariate correlation maps were generated between the seed of interest (i.e., the FPN) time-series and whole-brain voxel-by-voxel time-series; to normalize the distribution of the correlation maps, r -values were converted to Fisher's z -scores. To determine group-level differences, first-level z -scores were brought up to group ANCOVA analysis, which modeled subject, task, and scanner. The primary group-level contrast of interest was (Expository $>$ Symbols) vs.

(Narrative $>$ Symbols). Supplemental examinations of Expository $>$ Symbols and Narrative $>$ Symbols were confirmatory in nature, and consequently performed as ROI-to-ROI analyses of the main Expository $>$ Narrative findings (i.e., FPN seed and DMN whole-brain results). For covariate analysis, the specific goal of examination was to test whether observed differences for Expository $>$ Narrative connectivity were related to our covariates of interest (Gates MacGinitie percentile). As such, regression analysis was performed between the covariate of interest and the average connectivity values of the FPN seed and whole-brain findings (i.e., DMN) seen in the Expository $>$ Narrative connectivity results, and positive results were examined.

Dynamic Connectivity

Previous work in narrative processing has found that dynamic changes in functional connectivity are an important marker of discourse processing over the course of the story (Simony et al. 2016). As such, in the present study, dynamic connectivity analysis was run in order to examine the way in which functional correlations between the FPN and DMN changed over time. As in the regular connectivity analysis, denoised time-series (as described above) for FPN and DMN ROIs were extracted for Narrative and Expository conditions for each subject. In order to get the most detailed understanding of connectivity changes, we divided each condition into six sliding windows of 30 s each (the minimum duration to reach appropriate power) (Prete et al. 2017). Due to differences in passage duration, the overlap for Expository was 2.7 s, while the overlap for narrative was 5 s. Follow-up analysis in which the overlap period was held equal showed that this difference did not affect the significance of the final results. For each subject, z -transformed correlation values were generated between the FPN and DMN time-series in Narrative and Expository conditions. One-sample and two-sample t -tests were then used to determine the significance of FPN-to-DMN correlations within each moving window in Expository $>$ Narrative. The effect of scanner did not significantly contribute to the model across any of the time points, and so was removed from the analysis. In order to determine whether network-level findings were consistent when looking at individual regions, z -transformed correlation matrices were then run between FPN and DMN regions for each condition and time window (see Fig. 3), and a two-sample t -test was used to compare Expository $>$ Narrative.

Results

Mean GLM

Conjunction of Expository $>$ Symbols and Narrative $>$ Symbols. We first examined areas that were active in both expository and narrative comprehension as compared with the symbolic baseline. This initial examination revealed that both expository and narrative comprehension showed expected, overlapping recruitment of regions within bilateral language processing areas, as well as regions within the DMN (see Table 1). Expository passages did not recruit a key right-hemisphere DMN area—the right angular gyrus (AG). These findings are consistent with previous work in discourse processing (Swett et al. 2013; Silbert et al. 2014; Aboud et al. 2016).

Expository versus Narrative. A direct contrast of expository versus narrative passages revealed significant differences between passages. First, despite the conjunction findings above that both passage genres rely on DMN areas, this DMN activation was significantly lower in expository passages relative to the robust

Table 1 Significant activations in expository and narrative comprehension as compared with symbolic baseline

Contrast	MNI Coordinates			k	Max T	BA
	x	y	z			
Expository > Symbols						
L Lingual Gyrus	10	-82	4	20 448	15.77	18
L Middle/Superior temporal g.	-54	-42	4	[]	11.08	22, 21
L Inferior frontal gyrus/dIPFC	-52	18	20	[]	9.83	45, 44, 46
L Caudate	-10	12	12	[]	6.53	[]
L Precentral	-42	-2	42	[]	6.38	6
L Occipitotemporal area	-38	-52	-12	[]	6.07	37
L Temporal pole	-46	6	-16	[]	5.98	38, 20
L Hippocampus	-22	-28	-6	[]	5.68	27
L Inferior frontal gyrus	-32	30	-6	[]	5.29	47
L Parahippocampal Gyrus	-32	-34	-14	[]	5.20	36
R Hippocampus	24	-30	-2	[]	4.79	27
L AG/IPS	-40	-66	26	[]	4.45	39, 40
R Superior/Middle temporal g.	46	-34	4	11 79	7.68	22, 21
R Temporal pole	46	6	-14	[]	5.38	38
R Inferior frontal gyrus	52	22	10	256	5.25	45, 44, 47
L dorsomedial prefrontal cortex	-12	44	36	491	4.79	9, 10
Narrative > Symbols						
L Lingual Gyrus	-20	-92	-4	18 686	13.11	18
L Middle/Superior temporal g.	-50	-10	-10	[]	12.03	21, 22
R Lingual Gyrus	8	-82	2	[]	11.45	18
L Middle temporal g./AG	-46	-58	14	[]	9.24	39
L Inferior frontal gyrus	-50	20	8	[]	8.71	45
L Occipitotemporal area	-36	-40	-12	[]	8.36	37
L Posterior cingulate cortex	-12	-56	8	[]	7.82	30
L Temporal pole	-42	6	-22	[]	7.81	38
R Posterior cingulate cortex	12	-52	10	[]	6.73	30
Left Hippocampus	-20	-26	-12	[]	6.23	35, 36
L Thalamus	-22	-26	0	[]	5.65	[]
R Parahippocampal	20	-36	-12	[]	5.37	36
Bi. Precuneus	0	-56	30	[]	5.01	7
R Superior/Middle temporal g.	48	-10	-12	2 780	10.30	22, 21
R Temporal pole	38	10	-26	[]	7.14	38
R AG	44	-52	20	[]	6.75	39
Bi. dorsomedial prefrontal cortex	-8	52	28	827	7.43	9, 10
R Inferior frontal gyrus	48	26	0	282	5.60	45, 47, 44
L Precentral	-42	-4	44	212	4.78	6

All results significant at P -corrected < 0.05 . For large clusters, brackets indicate sub-cluster peaks in anatomical regions distinct from the primary peak, extracted using a decreased peak search space of 4 mm within the main cluster.

activations seen in narrative passages (bilateral AG and anterior superior temporal sulcus; aSTS; see Fig. 1 and Table 2), including in areas of shared activation with narrative comprehension. Significant regions with lower, positive activation in expository comprehension (as compared with narrative comprehension) are more specifically associated with theory of mind than other areas of the DMN (Saxe and Kanwisher 2003; Saxe et al. 2006; Deen et al. 2015). Critically, results additionally revealed that, as hypothesized, expository comprehension activated unique areas in the FPN compared with narrative comprehension, including positive activation in dIPFC and intraparietal sulci (IPS; see Fig. 1 and Table 2). Given the unique role of the FPN in expository passages, we were next interested in how the FPN coupled with other brain areas during expository versus narrative comprehension.

Functional Connectivity

Expository versus Narrative. Examination of correlations between the FPN and the rest of the brain revealed that the FPN was

significantly more correlated with the major hubs of the DMN in expository compared with narrative comprehension (see Fig. 2a and Table 3), even though overall expository comprehension relied less on the DMN. Further analyses revealed that this pattern was unique for expository comprehension (Expository > Symbols: $t(43) = 6.44$, $P < 0.0001$; Narrative > Symbols: $t(43) = -6.50$, n.s.; see Fig. 2a; Table 3). In conjunction with our GLM findings, these results demonstrate that expository comprehension requires the unique recruitment and utilization of the FPN to support the comprehension-related processes of the DMN, a pattern that is notably absent in narrative comprehension.

Reading Expertise

Given the finding that expository comprehension requires additional neural resources as compared with narrative comprehension, we were next interested in identifying whether observed patterns of difference between expository versus narrative increased or decreased with reader expertise. Consequently, we next tested whether reading ability corresponded with (1) degree

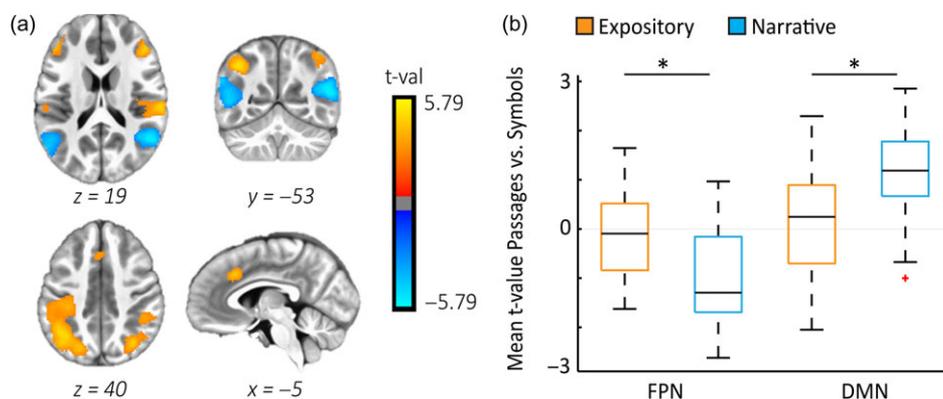


Figure 1. Expository comprehension relies on different networks than Narrative comprehension. (a) GLM contrasts of Expository (orange) > Narrative (blue) activations reveal that expository comprehension recruits significantly more FPN and less DMN than narrative comprehension. (b) Boxplots of GLM contrasts for Expository > Baseline (orange) and Narrative > Baseline (blue) activations across subjects, masked by significant areas in the FPN and DMN. Left hubs of the FPN showed positive activations in Expository > Symbols (left dlPFC and left IPS; not shown, see Table 1). All figure results significant at P -corrected < 0.05 .

of FPN recruitment (i.e., activation), and/or (2) FPN utilization (i.e., connectivity) in expository comprehension. First, we examined correspondence between task activation and an out-of-scanner standardized assessment of reading ability (Gates MacGinitie Reading Test) (MacGinitie et al. 2000). Interestingly, reading ability did not correspond with positive changes in the FPN, suggesting that the *degree* of expository FPN recruitment does not correspond with out-of-scanner comprehension ability. Secondly, we investigated whether reading ability corresponded with FPN utilization, specifically whether reading ability corresponded with FPN-to-DMN connectivity. As hypothesized, ROI-to-ROI connectivity analysis (see Methods) revealed that better readers showed significantly higher correlations between the FPN seed and the DMN in Expository > Narrative ($t(41) = 3.09$, $P = 0.002$; see Fig. 2b). Further analyses confirmed that this finding was unique to expository comprehension (Expository > Symbols: $t(41) = 1.84$, $P = 0.04$; Narrative > Symbols: $t(41) = -1.96$, n.s.). Therefore, our results suggest that not only does expository comprehension uniquely utilize the FPN to support the comprehension-related processes of the DMN, but also that stronger readers make greater use of this facilitative relationship.

Dynamic Functional Connectivity

In a final analysis, we were interested in determining whether FPN coupling with the DMN during expository comprehension was a pattern driven by features across the entire passage, or if instead, certain portions of the expository passage, for instance the first introduction of the topic, were driving FPN facilitation. To examine this, we ran a dynamic functional connectivity analysis in which we looked at six sliding windows of connectivity patterns across expository and narrative passages. We found that when compared with narrative, FPN-DMN connectivity during expository comprehension was significantly greater in expository as compared with narrative comprehension during the first three time points (i.e., the first half) of the passage (see Fig. 3a), with the statistics as follows: Time 1: $t(88) = 5.17$; $P < 0.0001$; Time 2: $t(88) = 5.04$, $P < 0.0001$; Time 3: $t(88) = 3.82$, $P < 0.0001$; Time 4: $t(88) = 0.53$, $P = 0.60$; Time 5: $t(88) = 1.05$, $P = 0.30$; Time 6: $t(88) = 1.82$, $P = 0.07$ (see Fig. 3a). Expository alone showed significant FPN-to-DMN correlations across all time windows (see Fig. 3b). Subsequent examination of individual nodes within the FPN and DMN revealed that this pattern was stable across network nodes, rather than driven by an

Table 2 Significant activations in expository versus narrative comprehension

Contrast	MNI Coordinates			k	Max T	BA
	x	y	z			
Expository > Narrative						
L dlPFC	-36	40	10	803	5.43	46, 10
R dlPFC	40	32	16	738	5.38	46, 10
L IPS	-36	-56	42	2002	5.01	40
R Postcentral gyrus	56	-22	20	422	4.77	13, 40
R IPS	30	-62	40	870	4.44	7, 40
L Cingulate	-6	22	34	325	4.35	32
R Caudate	12	16	10	163	4.11	NA
R Insula	38	0	10	178	3.51	13
Narrative > Expository						
L AG	-48	-56	12	819	5.79	39
R aSTS	46	-6	-16	432	5.73	21
R AG	48	-54	18	681	5.54	39
L aSTS	-44	-8	-14	159	3.95	20, 21

All results significant at P -corrected < 0.05 .

individual region within the network (see Supplementary Table S1 and Fig. 3a). Examination of individual time points also revealed that in certain time windows, expository comprehension showed significantly less within-network connectivity for the DMN and FPN compared with narrative. Specifically, expository had significantly lower correlations between left and right AG (time window 1) and left and right dlPFC (time window 3; see Table S1).

Discussion

We found that expository comprehension requires unique neural resources as compared with narrative comprehension in typically developing children. These results emphasize that not all types of discourse-level comprehension processes are the same. Instead, different genres require important trade-offs between different high-level neural systems. Specifically, expository comprehension necessitates (1) recruitment of language and left-lateralized DMN regions that are also seen in narrative comprehension, and also (2) unique facilitation of DMN activity via a top-down, goal-directed network (the FPN). Based on discourse theory and behavioral studies of genre, we

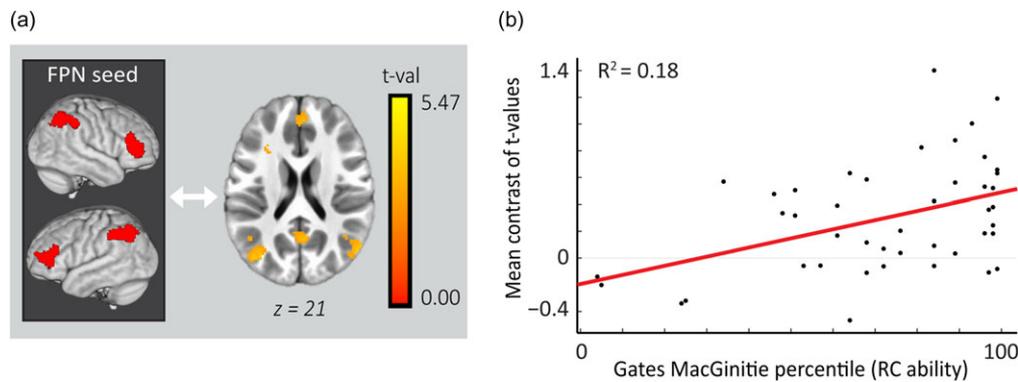


Figure 2. General and skilled expository comprehension is marked by greater communication between the FPN and DMN. (a) Functional connectivity analysis from the FPN seed (extracted from the Expository > Narrative GLM activations) reveals that in Expository > Narrative, the FPN has significantly greater correlations with all major hubs of the DMN (findings also significant for Expository > Symbols, see Results). (b) FPN-to-DMN correlations are stronger in stronger readers, as shown by a scatterplot of reading ability \times (Expository – Narrative t-values for FPN-to-DMN connectivity) across subjects, within significant DMN regions. All figure results significant at P -corrected <0.05 .

Table 3 Significant connectivity differences for Expository > Narrative comprehension from the FPN seed to the rest of the brain

Result	MNI Coordinates			k	Max T	BA
	x	y	z			
Expository > Narrative						
L Precuneus/Poster Cingulate g.	-6	-46	56	21 883	5.48	7, 30, 29
L Temporal pole	-27	9	-21	1208	4.49	38
L Superior frontal gyrus	-10	32	46	3496	4.43	8
R Middle temporal gyrus/AG	50	-66	18	2008	4.37	21, 39
R Superior frontal gyrus	22	24	48	1272	4.31	8
L Middle temporal gyrus/AG	-29	-65	17	2216	4.29	21, 39
R Inferior frontal gyrus	40	22	-14	3488	4.25	47
L Inferior temporal gyrus	-57	-13	-15	384	4.06	21, 20
L Inferior frontal/precentral g.	-53	15	7	536	4.04	44
R Middle temporal gyrus/AG	54	-10	-16	736	3.99	21
R Middle temporal gyrus	44	-34	-6	328	3.89	21, 22
L Precentral gyrus	-31	1	39	523	3.73	6
L Middle frontal gyrus	-27	19	29	1365	3.71	9
L Anterior cingulate cortex	0	42	18	512	3.62	10, 32
R Middle frontal gyrus	4	62	4	1285	3.56	10
R Superior frontal gyrus	14	46	42	216	3.56	8
L Inferior frontal gyrus	-45	19	-9	560	3.51	47
R Caudate	6	4	-4	192	3.42	NA
R Middle frontal gyrus	4	56	-12	184	3.16	11
L Parahippocampus	-23	-39	-5	208	3.34	36
L AG	-45	-55	27	416	3.21	39
Bi. Cingulate	0	-18	38	152	3.05	24

All results significant at P -corrected <0.05 .

propose that expository comprehension requires increased use of the FPN to facilitate a reader's comprehension goals through interactions with the DMN (Samuelstuen and Braten 2005; Best et al. 2008; van den Broek 2010; Eason et al. 2012).

Expository Comprehension Relies on a Different DMN Configuration

Our findings reveal that narrative and expository comprehension both recruit areas within the DMN. The fact that both types of comprehension elicit activation in the majority of DMN nodes, including in the non-social expository passage, suggests that the DMN does not just support social cognition during reading comprehension. Instead the DMN may play a more

general role of building an internal situation model of the text—a process which involves memory/background knowledge and semantic retrieval processes (Van Dijk and Kintsch 1983). The role of the DMN during passage comprehension is consistent with passive memory processes described in the Landscape Model of reading: as a reader proceeds through a text, the current concept is co-activated with all previous concepts, and this co-activation creates an updated “cohort” of related ideas that are associated in memory (van den Broek et al. 2005). This co-activation is bottom-up and automated, and is similar to the proposed passive memory properties of the DMN during semantic cognition (Davey et al. 2016). In addition to the shared activations in the DMN, expository comprehension also showed robust activation differences in this network from narrative

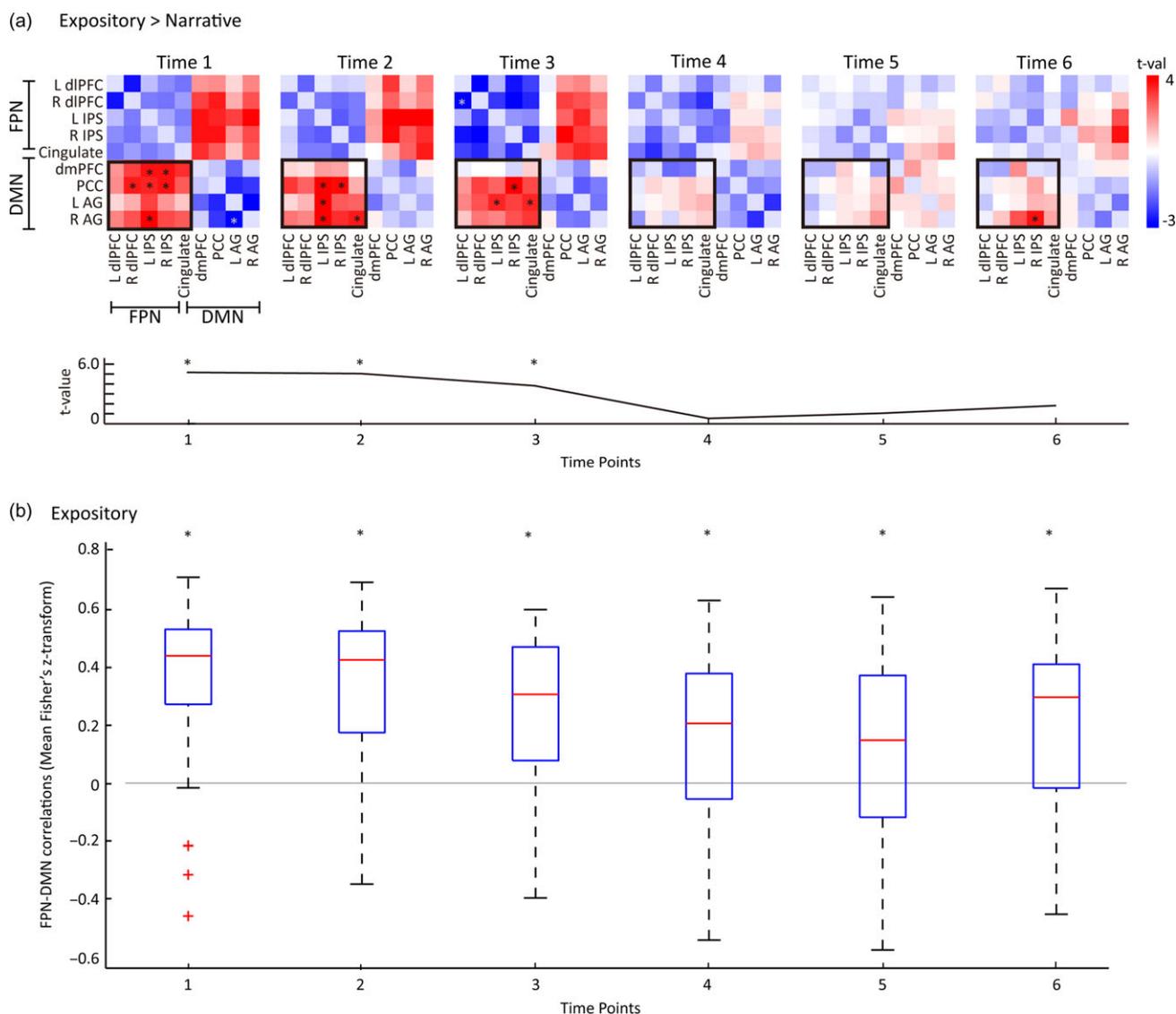


Figure 3. Dynamic connectivity across FPN and DMN nodes. Examination of connectivity changes across six time windows revealed that (a) patterns of greater FPN-to-DMN correlations in Expository > Narrative were significant across the first three time points (line graph: time \times Expository > Narrative t-value for FPN-to-DMN network correlation), and significant across individual regions within those time points (pairwise correlation map; red = greater in Expository, blue = greater in Narrative), and (b) FPN-to-DMN correlations (Fisher's z-transformed r-values) were significant for Expository alone across all time points. * indicates significance at P -corrected < 0.05 (for pairwise graph, only lower diagonal used to mark significant pairs; see Supplementary Table S1).

comprehension. In particular, expository comprehension exhibited different activation and connectivity patterns in bilateral AG compared with narrative. Expository texts (1) did not recruit the right AG, (2) showed decreased activation in the left AG, and (3) showed significantly less communication between left and right AG. This pattern of lateralization is consistent with previous studies of expository comprehension (although, not compared with narrative), which have found that left-lateralized portions of the DMN, and the left AG in particular, are key to skilled expository comprehension in both adults (Swett et al. 2013) and adolescents (Aboud et al. 2016). Interestingly, the right AG has been found to be more specifically related to mental states (Saxe and Wexler 2005), a mode of cognition that is particularly necessary in assessing character intentions in narratives. In contrast to the right AG, the left AG not only participates in social cognitive processes of the DMN, but also is a key

node in the semantic processing network. Specifically, the left AG is strongly linked to global coherence building in discourse, combinatorial semantic processing, event semantics, and thematic associations (Seghier 2013; Price et al. 2015). Of particular interest to the present study are recent findings indicating that the left posterior MTG (coordinates of which overlap with our left AG activation/connectivity findings) is a key communication point between the DMN and the FPN. Davey et al. (2016) propose that this portion of the left temporoparietal junction integrates automatic and strategic information from the DMN and FPN, respectively, in order to support more targeted semantic retrieval in the temporal lobes. Thus, while the increased activation and correlations between left and right AG in narrative are likely driven by increased social cognition demands, activations in the left AG during expository comprehension may be related to more specialized semantic processes. The

current findings consequently support a growing body of literature suggesting that expository comprehension requires a different configuration of the DMN to potentially support the unique requirements of comprehending expository passages (Jacoby and Fedorenko 2018).

Expository Comprehension Requires Greater Use of the FPN

The primary finding that expository comprehension has greater recruitment and utilization of the FPN is consistent with (1) proposed roles for the FPN in regulating distal networks, as well as (2) cognitive theories of discourse comprehension. The FPN is a set of executive regions associated with adaptive cognitive regulation, including goal-directed cognition during tasks (Ptak 2012; Cole et al. 2014). Recent work has found that the FPN facilitates more effective processing within other networks regardless of task, potentially through feedback loops with distal brain systems to achieve a specific goal (Cole et al. 2013). Recent work has also specifically pointed to FPN-DMN connectivity as a marker of goal-oriented internal thought, including fictional simulations of future goals (Gerlach et al. 2014) and goal-directed autobiographical recall (Spreng et al. 2010). In this context, the increased use of the FPN in expository comprehension could reflect increased demand for goal-directed cognition to facilitate the internalized comprehension goals of the reader (Best et al. 2008; Ferstl et al. 2008; van den Broek 2010; Egidi and Caramazza 2013). At a neural level, “facilitation” could mean that the FPN supports the most efficient DMN configuration for specific types of comprehension processes, in some cases by facilitating the inhibition of less useful activations (Cole et al. 2014). And indeed our regional connectivity analysis revealed that individual FPN nodes were most consistently interconnected with the right AG. Given that the right AG is notably not activated in expository comprehension relative to the baseline task, the FPN could be acting, in part, to suppress unnecessary comprehension activations (in this case, social cognition; see above), which are necessary in other types of comprehension tasks (i.e., narratives).

The interpretation of the FPN as a strategic facilitator of comprehension goals is also consistent with the coherence-based retrieval processes described in the Landscape Model of reading. In this account of reading comprehension, top-down mechanisms must be used to meet a reader’s coherence goals: strategic retrieval of text- or background-based information assists a reader when his/her standards of coherence are not being met in real-time. Importantly, this type of strategic thinking is in greater demand during expository comprehension (Samuelstuen and Braten 2005; Eason et al. 2012), as well as in the beginning rather than the end of texts (Haberlandt 1980; Giora 1996). Since expository comprehension requires greater reliance on background knowledge (of both content and rhetorical structures), the current cohort of text is more likely to require additional resources to obtain adequate coherence. Additionally, greater strategic cognition is needed during the initial construction of the situation model compared with later maintenance processes (Haberlandt 1980; Yarkoni et al. 2008). And indeed, our dynamic connectivity analysis reveals that the FPN-to-DMN connectivity is particularly prominent in the beginning of expository versus narrative comprehension. Consequently, our findings strongly suggest that expository comprehension requires utilization of the FPN to facilitate a reader’s comprehension goals through interactions with the DMN. In this context, it is not surprising that the present

results show a strong correspondence between increased reading comprehension expertise and greater FPN-DMN activity. Stronger readers have greater comprehension monitoring, i.e., they are better able to identify in real-time when they do not understand text content (Paris and Myers 1981; Zinar 2000; Helder et al. 2016). Thus, stronger readers are more likely to have stricter standards of text coherence, and recruit the FPN more often to resolve perceived lapses in their understanding. Future studies should examine how this reader-text interaction changes over the course of development and with different types of texts.

Conclusions

The present study is the first to identify different neural requirements for different types of discourse, and in so doing, helps illuminate the roles of the FPN and DMN in comprehension. Based on behavioral studies of genre, we propose that the FPN may specifically be involved in facilitating goal-directed comprehension processes in the DMN during reading, and this facilitation is in greater demand during expository comprehension. These results both enhance and are consistent with previous work that indicates the FPN may act to assist task-specific networks through goal-directed, top-down mediation processes, resulting in better clinical and learning outcomes (Cole et al. 2013, 2014; Aboud et al. 2018).

Limitations and Future Directions

The current study has several limitations. First, due to the age of the subjects, passage number was limited to one passage per genre. The narrativity score, however, suggests that the passages used in the present study are highly representative of their respective genres, and additional supplemental analysis demonstrates that the observed network differences are indeed generalizable (see Supplementary Fig. S1). However, replication of the present findings using a larger number of passages would be valuable. Additionally, the current study presented passages at a controlled reading speed. While examination of out-of-scanner measures of subjects’ reading speed were not found to significantly contribute to the current findings, controlled reading speed interferes with natural reading behaviors, including the ability to scan previous sentences to assist comprehension. Future studies may wish to examine the impact of reading presentation type and rate within or between genres. Lastly, the present study treats genre as a binary construct, instead of as a continuum. Future studies on the full range of narrativity would be intriguing, including analysis of scientific, historical, and narrative texts that vary along the narrativity dimension, as well as examine the many text properties that contribute to narrativity.

Summary

The present findings highlight the diverse demands involved in successfully comprehending multiple types of discourse. In so doing, these results lay the groundwork for future examinations into how the neural demands of different types of discourse interact with individual differences across developing and adult populations. Placed within a developmental context, our findings also have significant implications for educational research, policy, and practice given the heavy emphasis on early classroom exposure to different genres.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

Authors' Contributions

L.E. Cutting developed the study concept. K.S. Aboud and L.E. Cutting contributed to the study design. Data collection was performed by K.S. Aboud, S.K. Bailey, S.N. Del Tufo, and L.A. Barquero. Data analysis was performed by K.S. Aboud and S.K. Bailey under the supervision of L.E. Cutting. Data interpretation was performed by K.S. Aboud and L.E. Cutting, with input from all other authors. K.S. Aboud drafted the manuscript under the supervision of L.E. Cutting, and all other authors provided critical revisions. All authors approved the final version of the manuscript for submission.

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Note

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