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ORIGINAL RESEARCH

Differences in functional brain network connectivity during stories presented in audio, illustrated, and animated format in preschool-age children

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Abstract

The American Academy of Pediatrics (AAP) recommends that parents begin reading to their children soon after birth, and limits on screen-based media. Benefits of traditional book-sharing are well documented in children, while cited deleterious effects of animated content on narrative processing are controversial. The influence of story format on underlying functional brain networks has not previously been studied. Thirty-three healthy children were recruited for this study via advertisement at an academic medical center, which involved functional magnetic resonance imaging (fMRI) at a single visit. Twenty-seven of them completed fMRI (82%; 15 boys, 12 girls; mean 58 ± 8 months old). The fMRI protocol involved the presentation of 3 similar, unrhymed stories by the same author lasting 5 min each in audio, illustrated, and animated format during separate runs, followed by a test of factual recall. Within- and between-network functional connectivity (FC) was compared across formats involving five functional networks, which were defined via literature review and refined via a data-driven parcellation method: visual perception, visual imagery, language, Default Mode (DMN), and cerebellar association. For illustration relative to audio, FC was decreased within the language network and increased between visual, DMN, and cerebellar networks, suggesting decreased strain on the language network afforded by pictures and visual imagery. Between-network connectivity was decreased for all networks for animation relative to the other formats, particularly illustration, suggesting a bias towards visual perception at the expense of network integration. These findings suggest substantial differences in functional brain network connectivity for animated and more traditional story formats in preschool-age children, reinforcing the appeal of illustrated storybooks at this age to provide efficient scaffolding for language, and suggesting novel neurobiological correlates of how functional networks may contribute to this process.

Keywords fMRI · Functional connectivity · Narrative processing · Story listening · Children · Visual imagery · Screen time · Shared reading

Abbreviations

AAP	American Academy of Pediatrics
BOLD	Blood oxygen level–dependent
CB	Cerebellar network
DMN	Default Mode Network
FDR	False discovery rate
FC	Functional connectivity
fMRI	Functional magnetic resonance imaging
L	Language network
MNI	Montreal Neurologic Institute

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SES Socioeconomic status
VI Visual imagery network
VP Visual perception network

Introduction

The American Academy of Pediatrics (AAP) recommends that parents begin reading to their children as soon as possible after birth, citing enduring cognitive, social-emotional, and neurobiological benefits (AAP Council on Early Childhood et al. 2014). By contrast, the AAP recommends limits on screen-based media, citing developmental and health risks with early and excessive use (AAP Council on Communications and Media 2016). Led by television, screen-based media is ubiquitous in children's lives, perceived benefits for learning and creativity major motivators for use (Garrison and Christakis 2005; Zimmerman et al. 2007; Rideout 2017). Portable platforms such tablet-based apps add unprecedented dimensions to story sharing, including animation, responsive touch screens, and the option for a device to serve as the reader (Parish-Morris et al. 2013). However, while controversial, animated content has been associated with deleterious effects on narrative comprehension in children, compared to traditional storybooks (Chiong et al. 2012; Parish-Morris et al. 2013; Bus et al. 2015).

As reading is a relatively new invention, children are not born with a hard-wired brain network supporting this ability (Dehaene et al. 2015; Horowitz-Kraus and Hutton 2015). Instead, language, visual, and other networks are "recycled" and integrated in response to reading exposure and practice (Dehaene et al. 2015, Horowitz-Kraus and Hutton 2015). While primary visual and auditory networks mature relatively early, those for higher-order skills exhibit protracted development (Gogtay et al. 2004; Power et al. 2010), including semantic language (Price 2012) and the default-mode network (DMN), implicated in internally-oriented processes such as episodic memory and visual imagery (Fair et al. 2008; Daselaar et al. 2010; Sestieri et al. 2011). The cerebellum plays an important role in the mastery of cognitive skills (Stoodley 2012; Buckner 2013), and is engaged during narrative processing in preschool-age children (Hutton et al. 2017a, b).

Visual imagery is a higher-order skill that enables listeners and readers to "see a story" in their mind's eye and bring it to life, even in the absence of visual stimulus (Bridge et al. 2012), supporting comprehension on cognitive and emotional levels (Gambrell and Jawitz 1993; Just et al. 2004; Ganis and Schendan 2011; Pearson et al. 2015). The use of imagery is associated with enhanced reading ability and learning (Levin 1972; Gambrell and Jawitz 1993; McDonough et al. 2011), memory consolidation and recall (Oliver et al. 2016), and long-term mental health (Pearson et al. 2015). Successful application of imagery involves the integration of primary and higher-order visual, lexical-semantic, executive, and limbic brain areas (Mechelli et al. 2004; Daselaar et al. 2010; Ganis and Schendan 2011). The influence of story format on the integration of brain networks supporting imagery and narrative processing has not previously been studied.

Functional connectivity (FC) analysis via Blood Oxygen Level Dependent functional Magnetic Resonance Imaging (BOLD fMRI) is a powerful means to explore the engagement and integration of brain networks during a variety of cognitive states or task conditions (Bastos and Schoffelen 2015), and comparison between them (Di et al. 2013; Bray et al. 2015). While many questions remain unanswered regarding optimal FC configurations within- and between-networks in such analyses, general principles include topological efficiency, modularity (specialization of different regions for specific functions), and robust integration supporting adaptive, higher-level function (Sporns 2011; Bullmore and Sporns 2012). The aim of this study was to explore FC within and between functional brain networks supporting imagery, language, and learning during stories presented in audio, illustrated, and animated format in preschool-age children. This age range is particularly important as it represents a dynamic span of brain development and plasticity (Knudsen 2004; Power et al. 2010) highly influenced by cognitive stimulation in the home (Hutton et al. 2015; 2017a, b), notably shared reading and screen-based media use (Rideout 2017). Our hypothesis was that increasing visual stimulus would be associated with progressively higher FC for visual perception, lower FC involving imagery and language, and less cerebellar engagement for more visually stimulating formats, attributable to less need to access and integrate internally derived images.

Methods

Participants

This study involved 33 healthy, preschool-age children recruited recruited via advertisement at our institution. Exclusion criteria included prematurity before 38 weeks, developmental delay, head trauma, bilingual/non-English speaking household, kindergarten attendance, and standard contraindications to MRI. Written informed consent was obtained from a custodial parent for each child, families were compensated for time and travel, and our study was approved by the Cincinnati Children's Hospital Institutional Review Board.

Magnetic resonance imaging and preprocessing

MRI was performed via a 3 T Philips Ingenia scanner with a 32-channel head coil equipped with an Avotec audiovisual system. For fMRI, BOLD-weighted scans covering the entire brain with voxel size $2.5 \times 2.5 \times 3.5$ mm were acquired via multiband acquisition, with multiband factor of 4, SENSE =

1.5, flip angle 57 degrees, and TR/TE = 597/30 ms. Details of play-based acclimatization techniques used with children prior to MRI are described by Vannest, et al. (Vannest et al. 2014). All children were awake and non-sedated during MRI, alertness monitored with a ViewPoint® visual eye-tracking system (Arrington Research, Inc., Scottsdale, AZ). Our protocol involved a T1-weighted anatomical scan lasting approximately 6 min, and four BOLD fMRI sequences lasting approximately 5 min each (resting state and 3 active tasks).

MRI data pre-processing was performed in the CONN toolbox using standard spatial and temporal pipelines (Whitfield-Gabrieli and Nieto-Castanon 2012). As connectivity analyses are highly susceptible to bias from head movement, CONN's Artifact Detection Tool (ART) was used to calculate framewise composite movement, and frames with >1 mm motion or global mean intensity z-score > ± 6 were demarcated as outliers and excluded from first-level analyses. In addition to this scrubbing, temporal preprocessing and denoising included bandpass filtering (0.008–0.09 Hz) and regression of the following: zero- and first-order derivatives of framewise translational and rotational motion parameters, principal components of BOLD signals originating from white matter and cerebrospinal fluid compartment (top 5 of each), and the hemodynamic response convolved effect of task time series.

fMRI story protocol

Our fMRI protocol involved a series of continuous task states increasing in density of visual stimuli. Three different children's storybooks lasting approximately 5 min each (294 ± 6 s) were presented without interruption in three formats (audio, audio + illustration, animation), separated by 2–3-min pauses. We developed this protocol to address concerns regarding excessive motion and confusion/anxiety with traditional fMRI block designs in children, and to present an "ecological" task state comparable to story presentation in the real world (Hasson et al. 2010). A different story was used for each format to address the potential confound of repeated exposure to narrative content (i.e. the same story 3 times) rendering later trials less difficult or interesting. The order of story presentation was the same for each child (audio ➔ audio + illustration ➔ animation), to address potentially confounding visual priming effects and concerns that exposure to animated content can negatively influence cognitive function during subsequent tasks at this age (Lillard and Peterson 2011).

The three stories used were published picture books written by the same author and intended to be read aloud, non-rhymed, and similar in lexical, syntactic, and semantic content, with Lexile® level from 460 to 490 (MetaMetrics, Durham NC). Content for the audio and illustrated stories was downloaded with permission from the author's website (RobertMunsch.com), read aloud by the author without music or other enhancement. During the audio task, children watched a blank screen with cross fixation. During the illustrated task, high-resolution images from the book were paired with audio narrative and presented via a video screen. The animated story was from a series adapted for television (A Bunch of Munsch, YouTube) that closely adheres to the storybook version, presented via a video screen.

Immediately following MRI, children were asked three questions per story regarding basic factual content, whether they could hear the story well (1 = yes, 2 = no), and how interesting it was (1 = very, 2 = kind of, 3 = not very). Of note, these questions were added to our protocol midway along, and administered to 14 of 27 children. Responses were compared between formats via 2-tailed t-tests.

Functional brain network definition and parcellation

Five functional brain networks involved with narrative processing were defined via literature review, emphasizing meta-analyses and connectivity-based research involving children, summarized in Table 1. These were: 1) visual perception (VP; (Calhoun et al. 2001)), 2) higher-order visual/imagery (VI; (Mechelli et al. 2004, Daselaar et al. 2010)), 3) Default Mode (DMN; (Fair et al. 2008, Uddin et al. 2009)), 4) language (L; (Binder et al. 2009, Price 2012)), and 5) cerebellar association (CB; (Stoodley 2012, Buckner 2013)). The DMN was included given its core role in visual imagery, notably via access to episodic memory (Daselaar et al. 2010; Sestieri et al. 2011). The cerebellar network was included given its established role in narrative processing and other cognitive functions (Buckner 2013; Hutton et al. 2017a, b). The language network emphasized semantic processing, given behavioral evidence of lexical-semantic benefits associated with shared reading (High and Klass 2014), cited negative effects of animated content on narrative comprehension (Chiong et al. 2012; Parish-Morris et al. 2013; AAP Council on Communications and Media 2016), and no known association of either with acoustic or phonological abilities.

The spatial extent of the functional networks was generated in terms of neurological Brodmann Areas (BA) and, when appropriate, anatomically delineated structures (e.G. *hippocampus* and cerebellar regions (Diedrichsen et al. 2009)). Although these delineations are useful for framing hypotheses and contextualizing results, in particular with respect to a methodologically varied body of neuroimaging literature, they are ill-suited as region of interest (ROI) definitions in connectivity analyses for two related reasons: 1) The shape and volumes of these delineations are heterogenous and often encompass very large areas of the cerebrum, and 2) Actual patterns of functional connectivity often do not closely follow anatomical or cytoarchitectural boundaries and typically have a much finer resolution. Thus, using such definitions as ROIs can bias results and substantially reduce the sensitivity of connectivity analyses. Accordingly, we applied an

Table 1 A priori defined functional brain networks

Brain Network (reference)	Brodmann Areas (bilateral)	Functional Areas (bilateral)	Number of areas defined by parcellation
Default Mode (DMN) (Fair, 2008; Uddin 2010)	7	Precuneus	117
	8, 9, 10	Dorsomedial Prefrontal (DMPFC)	
	23, 29, 30, 31 39	Posterior cingulate gyrus	
	34, 35, 36	Angular gyrus	
		Parahippocampus	
Visual Imagery (Mechelli, 2004; Daselaar 2010)	7	Precuneus	83
	9	Dorsolateral Prefrontal (DLPFC)	
	19	Visual association cortex	
	37	Fusiform gyrus	
	Hippocampus	Hippocampus	
Visual Perception (Calhoun, 2001)	17, 18	Primary visual cortex	47
	37	Fusiform gyrus	
Semantic Language (Price 2012, Binder 2009)	21	Middle temporal gyrus	79
	22	Superior temporal gyrus (Wernicke's)	
	38	Temporal pole	
	39	Angular gyrus	
	44, 45	Inferior frontal gyrus (Broca's)	
	47	Orbitofrontal gyrus	
Cerebellar Association (Stoodley 2012, Buckner 2013)	N/A	Crus I, II, Lobule VI, VIIb	46

Functional brain networks defined a priori as neurological Brodmann Areas or anatomical names via the Harvard-Oxford Functional Brain or Automated Anatomical Labeling Atlas. Primary references for each network are included in parentheses. The number in the right column is the number of areas (nodes) for the respective network derived via parcellation established, data-driven parcellation approach (Craddock et al. 2012) to generate functionally homogenous ROIs of similar sizes within the spatial extent of our five networks. First, the preprocessed functional data from the resting state were masked to each of our networks of interest. Then, voxelwise temporal correlation matrices were computed for each subject. These matrices were then averaged across subjects and a normalized cut spectral clustering algorithm was applied to generate N preliminary ROIs per network where N was chosen such that resultant ROIs were roughly 2.14 mL in volume (or, spheroids of ~8 mm radius). Lastly, the networks were refined to eliminate functionally incongruous ROIs that resulted from the inclusion of very large Brodmann Areas in the initial network definitions. Connectivity matrices were generated for each network using the resting state data, and ROIs with median connectivity strength (Fisher transformed r) of less than 0.1 across all subjects were discarded. Using this approach, 372 ROIs were defined, comprising our five refined networks (Table 1).

Functional connectivity analysis

The CONN toolbox was used for all FC analyses (Whitfield-Gabrieli and Nieto-Castanon 2012), to extract ROI time series data from spatially preprocessed functional data, apply temporal denoising (aCompCor, bandpass filtering), and compute first-level connectivity measures for each of the story formats. We then used custom MATLAB-based programming to explore second-level FC within and between our refined networks. Because we hypothesized format-dependent differences in connectivity at the network level, we computed aggregate functional connectivity (FC) measures, which were calculated as the mean of the sum of pair-wise, Fisher-transformed, bivariate correlation coefficients for all ROIs within or between networks. FC scores were then compared between story formats (e.g. audio vs. illustration) via 2-tailed, paired t-tests. False discovery rate correction (FDR) was applied, accounting for the number of network comparisons in each contrast (15).

Significant results at the network level were further explored via post hoc analyses. For each of these, ROI-level connections within/between relevant networks were tested between story formats using 2-tailed, paired t-tests. False discovery rate correction was applied, accounting for the number of possible connections in each analysis (on the order of 10^3).

Results

Demographics

Twenty-seven of the thirty-three children arriving for their study visit (82%) completed functional MRI (15 boys, 12 girls; mean 58 ± 8 months, range 44–71; all Caucasian). Fifty-six percent of mothers were college graduates, 26% graduate level, 15% high school, and 4% below high school. Fifteen percent reported household income under \$50,000/year, 33% \$50,000–\$100,000/year, and 52% over \$100,000/year.

Story post-tests

Fourteen children completed story post-tests. All reported being able to hear each story equally well, and there was no significant difference in interest (all "kind of" interesting, on average). Mean correct responses were 81% for audio (± 33%), 70% for illustration (± 22%), and 50% for animation (± 33%), a significant difference for audio>animation ($p < 0.05$), marginal for illustration>animation ($p < 0.1$), and not significant for audio>illustration.

Subject motion during story formats and resting state

For quality assurance, several summary motion statistics were computed for each subject and each task condition: number of demarcated outliers, mean framewise composite motion, and root-mean square of framewise change in global mean intensity. The number of outliers was significantly greater for rest than for each story format ($p < 0.05$), yet not significantly different between story formats. Similarly, composite motion was consistently yet non-significantly greater during rest compared to each story format ($p = 0.11$, 0.15, and 0.08, respectively), yet not significantly different between story tasks. Intensity was not significantly different between rest and each format, or between story formats.

Functional connectivity for individual story formats and resting state

Within-network FC was significantly, though variably, positive for all networks in each story format and during resting state, suggesting network coherence. Between-network FC was significantly, even more variably, positive in all story formats for all network pairs, with the exception of VP-L, which was marginally positive for illustration only. Within- and between-network FC did not significantly correlate with gender, maternal education, or income level in any formats or resting state.

Functional connectivity differences between story formats

Comparisons of within- and between-network FC changes across story formats are summarized in Fig. 1 and Table 2. In addition to examples below, three-view renderings of significant within- and between-network FC differences between story formats elucidated via post hoc tests are provided online (eFigure 1–9).

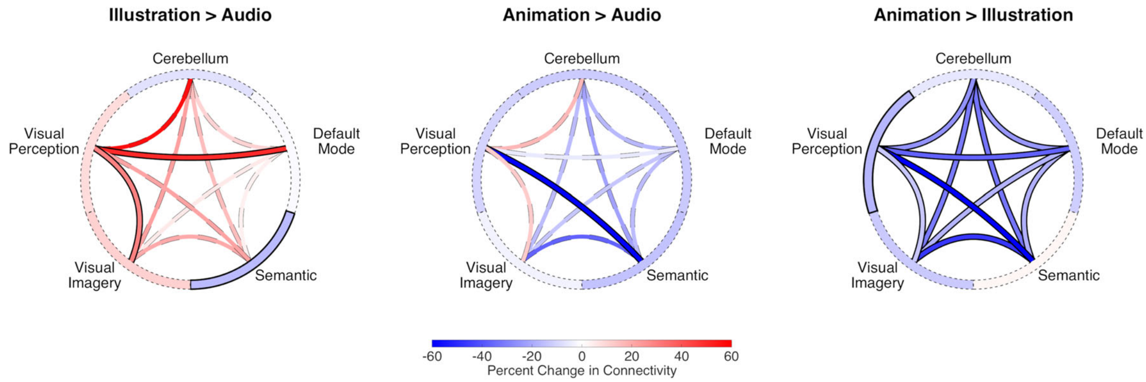

Fig. 1 Comparison of within- and between-network functional connectivity changes between story formats. Connectivity wheels show the percent change in functional connectivity (FC) within and between networks, for audio, illustrated, and animated format. For each wheel, the "tread" represents within-network FC and the "spokes" represent between-network FC, applying false discovery rate correction ($p < 0.05$). Solid lines reflect statistically significant differences, with red reflecting increased FC and blue reflecting decreased FC. There were significant changes in illustration relative to audio (within-L decrease; VP-CB, VP-DMN, and VP-VI increases), animation relative to audio (VP-L decrease), and animation relative to illustration (decreases within-VP and between all networks)

Illustration relative to audio

For illustration relative to audio, within-L FC was decreased 16%, largely driven by fewer inter-hemispheric connections, shown in Fig. 2. Regions of interest (ROI) highly involved in these changes were anterior/superior temporal (BA 22, 38) and inferior frontal (BA 44, 45) areas, classical language areas in the Wernicke-Geshwind model (Holland et al. 2007; Price 2012).

Between-network FC was increased for VP-CB (66%), VP-DMN (55%), and VP-VI (32%), largely driven by increased inter-hemispheric connections, and for VP-CB, increased connections with the left cerebral hemisphere, especially fusiform areas (BA 37). An example (VP-DMN) is shown in Fig. 3.

Animation relative to illustration

For animation relative to illustration, within-VP FC was decreased 19%, largely driven by decreased inter-hemispheric connections and connections between primary visual and fusiform (BA 37) areas. Between-network FC was decreased

Table 2 Summary of significant functional connectivity changes for each story format contrast

Contrast	Network(s)	Avg ΔConnectivity	% Change	Total ROI-ROI	Altered ($p < 0.05$)	% Positive/ Negative	% L/R/Cross-Hemispheric
Illustration-Audio	Language	−0.04.0	−16%	3081	43	0/100	37/16/47
	Perception-DMN	0.039	55%	5499	143	90/10	18/38/44
	Perception-Imagery	0.041	32%	3901	292	87/13	29/26/51
	Perception-Cerebellum	0.037	66%	2162	4	75/25	100/0/0
Animation-Illustration	Perception	−0.048	−19%	1081	27	4/96	11/48/41
	Perception-Cerebellum	−0.025	−26%	2162	0	–	–
	Perception-DMN	−0.040	−37%	5499	41	5/95	7/34/59
	Perception-Language	−0.055	−82%	3713	291	0/100	31/20/49
	Perception-Imagery	−0.022	−13%	3901	11	18/82	36/18/45
	Cerebellum-DMN	−0.027	−24%	5382	0	–	–
	Cerebellum-Language	−0.029	−32%	3634	0	–	–
	Cerebellum-Imagery	−0.038	−32%	3818	0	–	–
	DMN-Language	−0.027	−19%	9243	38	11/89	11/34/55
	DMN-Imagery	−0.029	−17%	9711	16	44/56	6/25/69
	Language-Imagery	−0.050	−49%	6557	352	0/100	24/24/52
Animation-Audio	Perception-Language	−0.044	−78%	3713	289	3/97	30/20/50

Significant changes in functional connectivity (FC) within and between networks for each story format contrast surviving false discovery rate correction ($p < 0.05$), detailed by post hoc tests. Columns show involved networks, average change in FC, the percentage of possible connections significantly altered, percentage of positive and negative changes, and percentage involving left, right, and cross-hemispheric connections. We attribute the absence of significantly altered ROI-level connections involving the cerebellar network for animation>illustration as attributable to similar changes in FC across the entirety of the cerebellar network rather than localized effects

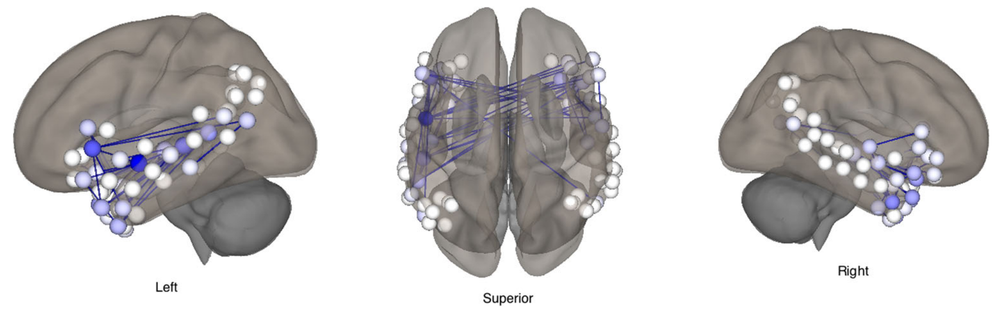

Fig. 2 Changes in functional connectivity within the language network in illustrated format relative to audio. FC was decreased 16%, with 47% of the decrease involving inter-hemispheric connections, 37% involving the left hemisphere, and 16% involving the right hemisphere. Blue lines designate significantly decreased pairwise connections. Nodes represent regions of interest, with red reflecting positive contribution to FC change, blue reflecting negative contribution to FC change, and white reflecting no change, depth of color reflecting magnitude of effect. Post hoc analyses were performed using 2-tailed t-tests, with analysis-level FDR correction, $p < 0.05$

for all network pairs (13% to 82%, mean 33%, summary Table 2), largely involving inter-hemispheric connections. FC decreases involving visual and language ROI were diffuse, particularly precuneus (BA 7), fusiform (BA 37), superior/middle temporal (BA 21, 22), and angular gyri (BA 39). An example is shown in Fig. 4 (VI-L). Despite overall decreases (24%–32%), post-hoc tests did not identify ROI-level changes in FC involving the cerebellar network, attributable to relative functional homogeneity and similar changes across the entirety of the CB network for this contrast.

Animation relative to audio

For animation relative to audio, FC was decreased 78% between VP-L, largely driven by decreased inter-hemispheric connections, highly involving fusiform (BA 37), superior/middle temporal (BA 21, 22), and inferior frontal (BA 44, 45) areas. FC was marginally decreased within-CB, within-DMN, within-L, and within-VP, and between L-VI ($p < 0.15$, FDR corrected).

Discussion

Cognitive, social-emotional, and neurobiological benefits of shared storybook reading are well-documented in children (National Early Literacy Panel 2008, Hutton et al. 2015, U.S. Department of Education 2015, Hutton et al. 2017a, b), and the American Academy of Pediatrics (AAP) recommends parents begin reading to their children as soon as possible after birth (AAP Council on Early Childhood et al. 2014). Despite AAP recommendations and evidence and advocacy behind them, shared reading of traditional storybooks remains relatively low (Scholastic 2015; Rideout 2017; Read Aloud 15 Minutes National Campaign 2018). Fueled by perceived benefits for creativity and learning, screen-based media use is ubiquitous and rising in children, beginning in infancy (Garrison and Christakis 2005; Zimmerman et al. 2007; Rideout 2017). Joining TV, increasingly popular screen-based platforms such as tablets have added unprecedented dimensions to story sharing, including animation and the option of a device to serve as the "reader" (Parish-Morris et al. 2013; Rideout 2017). Portable devices have eliminated barriers to access, providing unprecedented opportunities for

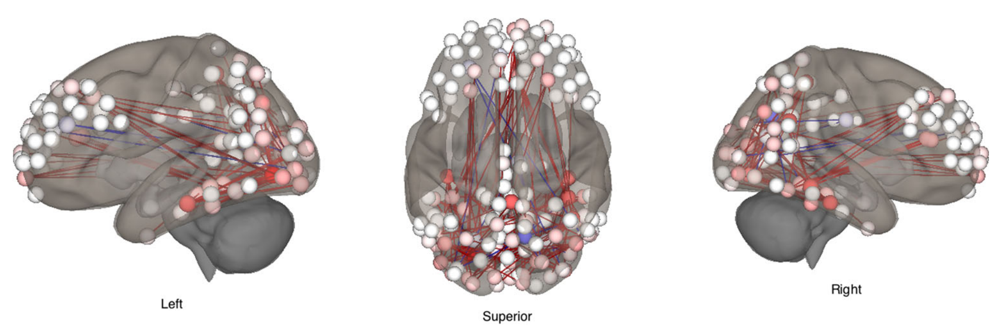

Fig. 3 Changes in functional connectivity between visual perception and Default Mode networks in illustrated format relative to audio. FC was increased 55%, with 44% of the increase involving inter-hemispheric connections, 18% involving the left hemisphere, and 38% involving the right hemisphere. Red lines designate significantly increased pairwise connections (90%) and blue lines designate significantly decreased pairwise connections (10%). Nodes represent regions of interest, with red reflecting positive contribution to FC change, blue reflecting negative contribution to FC change, and white reflecting no change, depth of color reflecting magnitude of effect. Post hoc analyses were performed using 2-tailed t-tests, with analysis-level FDR correction, $p < 0.05$

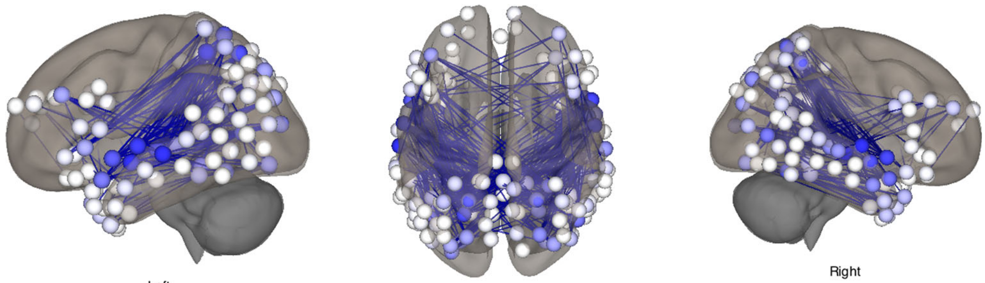

Fig. 4 Changes in functional connectivity between visual imagery and language networks in animated format relative to illustration. FC was decreased 49%, with 52% of the decrease involving inter-hemispheric connections, 24% involving the left hemisphere, and 24% involving the right hemisphere. Blue lines designate significantly decreased pair-wise connections (100%). Nodes represent regions of interest, with blue reflecting negative contribution to FC change, and white reflecting no change, depth of color reflecting magnitude of effect. Post hoc analyses were performed using 2-tailed t-tests, with analysis-level FDR correction, $p < 0.05$

solitary and excessive use (Ma and Birken 2017). While controversial, there is evidence of negative effects of animated content on parent-child engagement, comprehension, and cognitive function relative to traditional storybooks (Chiong et al. 2012; Parish-Morris et al. 2013; Bus et al. 2015; Lillard et al. 2015).

Proposed mechanisms of deleterious effects of inopportune screen-based media use include inadequate practice of self-regulation and creative skills (Christakis et al. 2009; AAP Council on Communications and Media 2016). The aim of this study was to explore the influence of story format on the integration of functional brain networks involved with skill refinement (cerebellar), language, and imagery, the latter a critical skill that helps bring stories "to life" in support of narrative comprehension and learning (Gambrell and Koskinen 2002; Ganis and Schendan 2011; McDonough et al. 2011). This question is particularly relevant for preschool-age children, whose brains are growing rapidly (Knudsen 2004; Power et al. 2010) and responsive to cognitive stimulation at home (Hutton et al. 2015; 2017a, b), of which shared reading and screen-based media are major contributors (Rideout 2017). Our hypothesis was that increasing visual loading, especially animated content, would bias functional networks towards visual perception, with progressively less integration of the other networks, particularly visual imagery and language.

Decreased within-network FC during the illustrated story relative to audio in the language (L) network is consistent with our hypothesis and the adage that "a picture is worth 1000 words." Diffuse, bilateral activation in frontal and temporal language areas during audio story listening is well-described in children, interpreted as reflecting difficulty or strain (Holland et al. 2007; Berl et al. 2010). Thus, diffusely lower inter-hemispheric FC in these areas found for this contrast (Fig. 2), suggests reduced workload in the L network. It is reasonable to infer that the catalyst for this finding was increased FC between VP, VI, and DMN (an "imagery module"), a potential mechanism by which illustrations and internally-generated images could be integrated to illuminate the narrative. Primary visual processing areas are known to participate in imagery, notably via access to fusiform lexical-semantic regions (Schmithorst et al. 2007; Whittingstall et al. 2014), which were major drivers of the increase in FC for this contrast (Fig. 3). This cognitive/developmental process has been described in behavioral-educational literature as "scaffolding," where support necessary for a given child, age, and task is incrementally provided to assist with mastery (Wood et al. 1976; Crain-Thoreson and Dale 1999; McDonough et al. 2011). Our findings provide a novel neurobiological correlate for the appeal of illustrated storybooks for young children. Consistent with evidence that they provide scaffolding for language (Crain-Thoreson and Dale 1999), we observed maximal FC between networks involved with perception (VP; illustrations) and imagery (VP, VI, DMN) with decreased strain on the language network (within-L, cross-hemispheric) during the illustrated story relative to other formats.

Within-network FC in the language network was only marginally decreased during animation relative to audio, suggesting less effective scaffolding provided by animated content. Possibly fueling this blunted effect was a sharp drop in FC between VP-L involving fusiform and superior/middle temporal areas and intraparietal sulcus (IPS), well-described collaborators in visual-language association (Price 2012; Ardila et al. 2015), and marginal decreases between VI-L and DMN-L. Within-network FC in the VP network was attenuated by less inter-hemispheric connectivity and lower FC between primary visual and fusiform areas. FC for visual perception has been shown to be more focal in primary visual areas than during image retrieval (i.e. imagery), consistent with this finding (Seidkhani et al. 2017). Altogether, these findings suggest a bias towards focal visual perception for animation relative to the other formats, which may occupy constrained neural resources at this age such that integration with language, imagery, and other higher-order networks is less favorable.

The possibility that animated story presentation may hyperstimulate visual perception networks at the expense of their integration with higher-order cognitive networks is consistent with our finding of globally decreased FC between all networks for animated format relative to illustration (13% to 82%; Table 2). Interestingly, such a decrease did not occur for illustration relative to audio and was less pronounced for animation relative to audio, suggesting a complex, non-linear effect. For animation relative to illustration, sharply lower FC between VI-L involving the IPS (Fig. 4) and DMN-L involving precuneus (Huijbers et al. 2011), are consistent with decreased recruitment of imagery for this contrast (Just et al. 2004; Price 2012). Similarly, the precipitous drop involving VP-L (82%) concentrated in fusiform and superior/middle temporal/IPS is consistent with decreased imagery, given the overlapping functional role of VP for image retrieval (Ardila et al. 2015). In addition to imagery effects, decreases in FC between VP-DMN suggest diminished self-referential processing during animation relative to the other formats (Molnar-Szakacs and Uddin 2013; Xiao et al. 2015). Antagonism between the DMN and task-positive, especially visual, networks is well-documented (Uddin et al. 2009; Raichle 2015). However, Raichle proposed a model of DMN/task-positive integration where a "sense of self" is applied to the task (Raichle 2015). It is possible that illustration provides a moderate level of visual stimulation to not interfere with this self-referential aspect of story sharing (e.g. Fig. 3), manifest in children as introspection, or sense of wonder. By contrast, diminished DMN engagement during animated content seems consistent with absent screen gazing often noted in children watching cartoons. The DMN is a core network associated with numerous aspects of higher-order cognitive function and long-term mental health, including imagery (Daselaar et al. 2010), memory consolidation (Mohan et al. 2016), and creativity (De Pisapia et al. 2016). Thus, these findings related to potential effects of story format on DMN recruitment and integration, seem important for further study.

While classically associated with motor skills, the cerebellum is increasingly recognized as playing a supporting role in language and other cognitive functions (Stoodley 2012; Buckner 2013), including a proposed "turbocharger" effect during story listening (Hutton et al. 2017a, b). Increased FC between CB-VP for illustration relative to audio and broadly attenuated cerebellar FC during animation align with this role, suggesting cerebellar engagement proportional to the level of cognitive work required. Lower comprehension scores for animation relative to other formats suggest a more passive, perhaps less "turbocharged" experience, though our assessment was rudimentary. As decreased cerebellar engagement has been associated with deficits in skill refinement and learning (Guell et al. 2015), it is possible that lower FC involving CB during animation reflects sub-optimal neural configuration for the application and refinement of imagery and related skills, though our cross-sectional design cannot discern such effects. By contrast, it is intriguing to speculate that higher cerebellar FC during illustrated format may reflect more favorable neural configuration for the practice of such skills at this age.

Altogether, our findings suggest that neurobiological mechanisms underlying animated story processing are substantially different from audio and especially illustrated formats in preschool-age children. The moderate level of visual stimulus contributed by illustrations may provide age-appropriate scaffolding to generate imagery and assist the language network, an integrative skill reinforced by cerebellar association areas. This is consistent with the age-old appeal of illustrated storybooks books for young children, their well-documented potential to fuel imagery and comprehension (Levin 1972; Gambrell and Jawitz 1993; Gambrell and Koskinen 2002), and Bruner/Vygosky theories of learning (Wertsch 1980; Christakis et al. 2007). While a precise definition has not yet been determined, the FC pattern observed during illustrated format may be optimal in terms of general principles of healthy brain networks, notably robust connectivity between functional modules supporting higher-order skills (Bullmore and Sporns 2012). By contrast, FC patterns during audio alone suggest greater strain in the language network and less well-integrated scaffolding, potentially attributable to less efficient access to images referenced in the narrative at this age. At the other extreme, by providing a stream of fast-moving visual content, animated story format may more broadly suppress the integration of language and higher-order brain networks such as imagery and Default Mode, which may be suboptimal for the developing brain.

Our study has limitations. Our results are in terms of mean FC during each format, while dynamic FC analyses may reveal other differences. The stories used were by the same author with a particular style, and our findings may not apply to other styles. We view this as a worthwhile tradeoff, allowing us to control for important narrative variables across formats. The three stories used were different, presented in the same order for each child. However, this design eliminated the confound of repeat exposure to the same story likely to make subsequent trials less interesting, or easier. Gradually increasing visual stimulus also minimized visual priming effects, while addressing concerns about the potential of animated content to negatively affect performance on subsequent tasks at this age (Lillard and Peterson 2011 and Lillard et al. 2015). Given technological constraints, shared reading during MRI is not currently feasible. However, audio and animation were presented in a reasonably ecological way (headphones and screen), and we suspect that greater differences between illustrated and other formats would manifest on a parent's lap. Our sample size was relatively small (27), though respectable especially given the young age of our sample population, and exceeding sample sizes in recently published, connectivity-based analyses involving functional networks and continuous task paradigms (Bray et al. 2015; Horowitz-Kraus et al. 2018; Weber et al. 2018). Our assessment of story recall was rudimentary and administered to only 14 of 27 children, though its finding of equivalent interest and significantly lower scores for the animated story provides useful insights into our MRI results. Our sample involved Caucasian, largely higher-SES children, though general mechanisms of neural processing seem unlikely to be influenced by race, and SES-related covariates did not significantly influence our results. Our analyses were limited to five functional networks, though these were rigorously determined affording a hypothesis-driven approach that increased our statistical power. Our networks were largely defined in terms of Brodmann Areas, with some included in more than one network, yet refined via an established parcellation approach (Craddock et al. 2012).

Our study also has important strengths. Our fMRI paradigm involved continuous story presentation akin to the real world, resulting in a high success rate in very young children. Our analyses involved an innovative, connectivity-based approach affording comparisons of functional networks in aggregate and at the ROI level, which aligns with the current shift away from modular views of brain function towards network-level analyses (Sporns 2013). Our hypothesis was in the context of documented benefits of shared reading (National Early Literacy Panel 2008, Hutton et al. 2015) and concerns about animated content in young children (Chiong et al. 2012; Parish-Morris et al. 2013; Lillard et al. 2015). While highly preliminary, our findings provide novel, neurobiological insights into these cited benefits and risks, and corresponding AAP recommendations (AAP Council on Early Childhood et al. 2014; AAP Council on Communications and Media 2016). Longitudinal studies involving comprehensive behavioral measures are needed to explore whether short-term effects observed in our study result in long-term differences in these networks and the skills they support, notably reading abilities. These are critical questions in the context of a child's early "cognitive ecosystem," where unprecedented technological shifts influence how content is provided in the digital age.

Conclusions

This study revealed substantial differences in the functional connectivity of visual, language, Default Mode, and cerebellar brain networks during stories presented in audio, illustrated, and animated format in preschool-age children. Illustrated format was associated with reduced strain on the language network and maximal integration of visual perception, imagery, Default Mode, and cerebellar networks, suggesting a novel neurobiological correlate of the well-documented appeal of children's picture books to provide scaffolding for language and learning. By contrast, audio alone may provide suboptimal scaffolding at this age to catalyze such integration, and continuous animated content may render it less favorable, with a bias towards focal visual perception. As higher-order skills require practice, particularly in the home environment, our findings raise important questions regarding the influence of story format on the development and integration of functional brain networks, and provide insights for further research.

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Contributors' statement **John S. Hutton** designed all aspects of the study including brain network selection and definition, collaborated in analyses, drafted the initial manuscript and subsequent revisions, and approved the final manuscript as submitted.

Jonathan Dudley conducted brain network parcellation and all fMRI and other statistical analyses used in this study, created all tables and figures, assisted with manuscript preparation and revision, and approved the final manuscript as submitted.

Tzipi Horowitz-Kraus provided guidance on study design and analysis, assisted with MRI acquisition, reviewed and revised the manuscript, and approved the final manuscript as submitted.

Tom DeWitt provided guidance on study design, analysis, and presentation, reviewed and revised the manuscript, and approved the final manuscript as submitted.

Scott K. Holland provided guidance on study design and presentation, developed the concept for the a priori network connectivity approach used in the analysis, helped develop and oversaw the MRI acquisition protocol, and reviewed and approved the final manuscript as submitted.

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Compliance with ethical standards

Conflict of interest Drs. Hutton, Dudley, Horowitz-Kraus, DeWitt, and Holland declare that they have no conflict of interest.

Informed consent All procedures followed were in accordance with the ethical standards of the responsible committee on human experimentation (institutional and national) and with the Helsinki Declaration of 1975, and the applicable revisions at the time of the investigation. Informed consent was obtained from all patients for being included in the study.

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