Mindfulness (2022) 13:198–210
https://doi.org/10.1007/s12671-021-01785-4

ORIGINAL PAPER

Adolescents with High Dispositional Mindfulness Show Altered Right Ventrolateral Prefrontal Cortex Activity During a Working Memory Task

Jade A. Stein[1] · Signe Bray[2,3] · Frank P. MacMaster[1,4] · Lianne Tomfohr-Madsen[4,5] · Daniel C. Kopala-Sibley[1,6]

Accepted: 29 October 2021 / Published online: 13 November 2021

Abstract

Objectives The use of mindfulness interventions have increased in schools with little knowledge of how dispositional mindfulness affects cognitive processes in the developing brain. The primary objective of this research was to investigate the association between dispositional mindfulness and the neural correlates of working memory in adolescents. A secondary objective was to examine the link between adolescent dispositional mindfulness and working memory performance.
Methods Adolescents aged 11–18 ($M = 13.75$, $SD = 1.56$, $n = 83$) completed the Adult and Adolescent Mindfulness Scale and a functional magnetic resonance imaging N-back task. The blood oxygen level–dependent signal as well as functional connectivity of the right dorsolateral and ventrolateral prefrontal cortex was contrasted between 2-back versus 0-back conditions.
Results Lower blood oxygen level–dependent signal in the right ventrolateral prefrontal cortex was correlated to higher Attention and Awareness scores, controlling for participants' experience with a mindfulness practice ($k = 112$, FWE$p = .011$). Reduced functional connectivity between right ventrolateral prefrontal cortex and right dorsomedial prefrontal cortex/supplementary motor area during the 2-back compared to 0-back task was associated with higher Nonreactivity, although this did not survive correction for multiple comparisons. Dispositional mindfulness did not correlate to working memory performance.
Conclusions Adolescents with higher levels of Attention and Awareness and Nonreactivity may require less cognitive effort to inhibit distractors for the same level of working memory performance.

Keywords Dispositional mindfulness · Working memory · Adolescence · fMRI · Prefrontal cortex

Mindfulness is broadly defined as present-centered attention of one's internal and external environment, whereby perceptual behavior is monitored and regulated to be accepting, curious, and open in nature (Bishop et al., 2004; Lindsay & Creswell, 2017). It is important to distinguish *dispositional mindfulness* from mindfulness practices, as overgeneralization of the term "mindfulness" has been reported in the literature (Tomlinson et al., 2018). According to Wheeler et al. (2017), the study of mindfulness can be conceptualized and organized in the literature by (i) the degree of intentionality of one's engagement in mindfulness (i.e., dispositional mindfulness vs. deliberate mindfulness), and (ii) the extent of deliberate mindfulness training one has (i.e., no training, novice, experienced, or expert). Dispositional mindfulness is one's ability to be mindful on a moment-to-moment basis and can involve both intrinsic and learned factors. Deliberate mindfulness is a practice whereby a mindful state is intentionally cultivated and in which dispositional mindfulness is increased (Baer et al., 2019; Quaglia et al., 2016). An individual with no deliberate mindfulness training has only intrinsic or unlearned levels of dispositional mindfulness, referred to here as "intrinsic dispositional mindfulness."

✉ Jade A. Stein
jade.stein@ucalgary.ca

1 Department of Psychiatry, University of Calgary, Calgary, AB, Canada

2 Department of Radiology, University of Calgary, Calgary, AB, Canada

3 Child and Adolescent Imaging Research Program, Calgary, AB, Canada

4 Department of Pediatrics, University of Calgary, Calgary, AB, Canada

5 Department of Psychology, University of Calgary, Calgary, AB, Canada

6 Mathison Centre for Mental Health Research & Education, Calgary, AB, Canada

Recently, mindfulness-based interventions have garnered interest in schools to improve child and adolescent social, emotional, and cognitive function (Zenner et al., 2014). The beneficial effects of mindfulness-based interventions appear to occur, at least in part, through increases in dispositional mindfulness (e.g., Quaglia, et al., 2016). As dispositional mindfulness is linked to child and adolescent cognitive performance (Zenner et al., 2014), characterizing the neural associations of this attribute in youth may provide insight into the mechanism and advantage of instituting these interventions in schools and youth-based programs.

Dispositional mindfulness is thought to involve working memory to facilitate present-centered nonjudgmental awareness (Maltais et al., 2020). Working memory is the cognitive process by which individuals simultaneously maintain and manipulate goal-relevant information in the mind over short periods of time while avoiding distraction (Baddeley & Hitch, 1974). Working memory emerges in childhood and develops protractedly into late adolescence in parallel with maturation of the frontoparietal neural network, including the dorsolateral and ventrolateral prefrontal cortex (dlPFC, vlPFC; Best & Miller, 2010). The dlPFC is associated with manipulation (i.e., continuous updating and temporal ordering) of stimuli and the vlPFC is implicated in the temporary maintenance (i.e., top-down control of the neural networks that represent information) and inhibition of irrelevant or distracting information (for review, see Nyberg & Eriksson, 2015).

Deliberate mindfulness training, at least temporarily, improves performance on a variety of working memory tasks in adults (Jha et al., 2019) and overall cognitive functioning (Zenner et al., 2014), including working memory performance, in nonclinical and clinical adolescent samples (Dunning et al., 2018). Most dispositional mindfulness studies examining executive function have used the Mindfulness Attention Awareness Scale (MAAS), which measures one's ability to pay attention to the present moment (Brown & Ryan, 2003). For example, intrinsic levels of MAAS were associated with enhanced working memory performance in adults (Jaiswal et al., 2018) and greater self- and parent-reported executive function, including working memory, in adolescents (Geronimi et al., 2019; Riggs et al., 2015). However, it is generally recognized that narrowing dispositional mindfulness into a single construct does not capture its complexity (Baer et al., 2006; Grossman, 2011). Indeed, while higher levels of the *Awareness* facet on the Philadelphia Mindfulness Scale (Cardaciotto et al., 2008) was associated with sustained attention, higher levels of the *Acceptance* facet was associated with better working memory efficiency (i.e., fast but accurate responses) in adults (Ruocco & Direkoglu, 2013). Using the Five Facet Mindfulness Questionnaire (FFMQ; Baer et al., 2006), intrinsic levels of the *Nonreactivity* facet were positively associated with better attention in undergraduate students (Maltais et al., 2020). The development of multifaceted dispositional mindfulness questionnaires for youth is still in the early stages; thus, research is just beginning to uncover the link between adolescent dispositional mindfulness and working memory.

Insights from current literature on the neuroscience of dispositional mindfulness have revealed functional and structural changes in working memory network brain regions. Zhuang et al. (2017) found that FFMQ Nonreactivity was associated with reduced cortical thickness in the right superior PFC and the *Describing* and *Nonjudgment* FFMQ facets were linked to increased surface area and gray matter volume within the superior and dlPFC. In adolescents, MAAS dispositional mindfulness predicted less cortical thinning in the insula (Friedel et al., 2015). Research investigating intrinsic dispositional mindfulness and neural functional connectivity during rest has found increased functional connectivity in the right insula, left orbitofrontal cortex (OFC), and left parahippocampal gyrus, and decreased functional connectivity in right the inferior frontal gyrus (IFG) in adults with high MAAS scores (Kong et al., 2015). During rest, the FFMQ facets in meditation naïve adults have also been associated with increased functional connectivity between the insula and ACC and decreased functional connectivity in the default mode network (DMN; Parkinson et al., 2019). These findings may support the theory that mindfulness enhances the ability to turn off the DMN, thereby dampening narrative self-referential processing, or mind wandering, and strengthening the ability to attend to the present moment (Farb et al., 2007).

The recruitment of frontal cortices during meditation and executive functioning tasks is theorized to be greater in beginners and intermediate meditators compared to naïve controls and long-term mindfulness practitioners (Wheeler et al., 2017). In a study comparing meditation by highly trained monks with varying levels of experience and novice controls, Brefczynski-Lewis et al. (2007) reported that frontal brain activity associated with attention, including the dlPFC and anterior cingulate cortex (ACC), showed significantly higher blood oxygen level–dependent (BOLD) activation during meditation by monks with an average of 19,000 h of meditation training compared to controls. Conversely, the monks with an average of 44,000 h of meditation training demonstrated reduced BOLD activation in the dlPFC. In a study looking at economic decision-making, Buddhist meditators showed less bilateral dlPFC BOLD activity during rational decisions compared to naïve controls (Kirk et al., 2011). Another study found that experienced meditators, compared to non-meditators, had less BOLD activation in the right medial frontal gyrus during a Stroop Task (Kozasa et al., 2012). On the other hand, beginner meditators trained in a 6-week mindfulness course showed more dlPFC BOLD activity during a Stroop Task compared to active controls (Allen et al., 2012). Similar patterns have been found using electroencephalography (EEG). For example, intermediate mindfulness meditators with at least 6 months of regular deliberate mindfulness practice had greater neural activity in right frontal cortices during working memory and better performance (Bailey et al., 2020).

Researchers are beginning to explore the link between frontal cortical activity and dispositional mindfulness. Some research has demonstrated that high dispositional mindfulness relates to less mPFC BOLD activity during emotional regulation compared to controls (Lutz et al., 2014), while other research indicates that individuals high in dispositional mindfulness have an increase of mPFC BOLD recruitment during affect labeling and reappraisal (Creswell et al., 2007). EEG research has found an increase in alpha activity in prefrontal regions and higher working memory capacity in participants with high MAAS scores (Jaiswal et al., 2019).

The primary aim of this study was to examine the association between dispositional mindfulness and PFC neural activity during working memory through functional magnetic resonance imaging (fMRI) in a community-based sample of adolescents. We hypothesized that during a working memory task, adolescents higher in dispositional mindfulness would show less activation of the right dlPFC and right vlPFC and decreased functional connectivity of these seed regions with brain regions involved in the DMN, including the medial PFC (mPFC), inferior parietal, and posterior cingulate. Our secondary aim was to investigate the relationship between working memory performance and dispositional mindfulness in adolescents. We hypothesized that the dispositional mindfulness construct *Attention and Awareness* from the Adult and Adolescent Mindfulness Scale (AAMS) would be associated with greater working memory performance, as measured by accuracy, reaction time (RT), and the inverse efficiency score (IES, i.e., speed-accuracy trade off). Additional AAMS facets were also explored. To determine whether the extent of deliberate mindfulness training within our sample influenced results, we designed questions to assess levels of deliberate mindfulness experience and performed analyses both with and without this control variable.

Methods

Participants

Participants were a convenience sample of 83 youth aged 11–18 years ($M = 13.75$, $SD = 1.56$) recruited using Internet advertisements targeted at parents. Participants were part of a broader study assessing adolescent premorbid risk and resiliency factors for the development of clinical depression and anxiety. To be eligible, participants had a parental history of mood or anxiety disorders but did not meet current or lifetime clinical criteria for these disorders themselves as assessed by the Mini International Neuropsychiatric Interview (MINI; Sheehan et al., 1998) and the MINI-KID for adolescents (Sheehan et al., 2010).

Approximately 57.0% of participants were female ($n = 43$). The sample was 72.3% White/Caucasian ($n = 60$), 9.6% multiracial ($n = 8$), 4.8% Asian/Pacific Islander ($n = 4$), 4.8% Aboriginal (First Nations, Metis, Inuit; $n = 4$), 2.4% Arabic ($n = 2$), 1.2% Filipino ($n = 1$), 1.2% Hispanic/Latino ($n = 1$), and 3.6% ($n = 3$) other or preferred not to disclose. This is comparable to the population of the local catchment area (Statistics Canada, 2017). The average household income was approximately $100,000 and the median household income was $100,000–$124,999, which is comparable to median household incomes in the local catchment area (Statistics Canada, 2017). Approximately 64% ($n = 53$) of parent participants reported some level of post-secondary education: trade/technical/vocational degree (16.9%, $n = 14$), undergraduate degree (28.9%, $n = 24$), partial postgraduate work (2.4%, $n = 2$), or postgraduate degree (15.7%, $n = 13$). The remaining parents either completed partial college/university (26.5%, $n = 22$), partial high school (3.6% $n = 3$), or a high school diploma (6.0% $n = 5$). These levels of education are comparable to typical levels in the local catchment area (Statistics Canada, 2017).

Procedure

Prior to inclusion in the study, participants gave informed consent. Adolescent participants attended two visits to the lab between 1 week and 7 months apart, although 90.4% ($n = 75$) completed their second visit within 2 months ($M_{months} = 1.20$, SD = 1.23). During the first lab visit, participants completed demographic information and dispositional mindfulness measures. Information related to deliberate mindfulness experience was completed at home. In the second lab visit, participants viewed a demonstration of the N-back task on a laptop to ensure they understood the instructions. They then completed the N-back task while undergoing an fMRI scan.

Neuroimaging data were acquired on a GE 3 T 750 MRI. A 12-channel radiofrequency head coil was used with foam padding to restrain head movement. High-resolution T1-weighted 3D BRAVO anatomical volumes were acquired for co-registration with functional images (repetition time (TR) = 7.90 ms, echo time (TE) = 3.06 ms, field of view (FOV) = 24 cm, flip angle = 15°, 180 sagittal slices, 1-mm thickness, 1-mm isotropic voxels). Blood oxygen level–dependent (BOLD) signal during functional runs was acquired using echo-planar T2*-weighted gradient-echo volumes (TR = 2000 ms, TE = 30 ms, FOV = 25.6 cm, flip angle = 75°, 154 axial slices, 4-mm slice thickness, 4 mm isotropic voxels).

Measures

Dispositional Mindfulness The Adult and Adolescent Mindfulness Scale (AAMS; Droutman et al., 2018) is a self-report multifactorial dispositional mindfulness questionnaire validated in adolescents as young as age 11 and consists of 19 items on a 5-point Likert scale. Factor analysis revealed a four-factor model with equal loadings between items for the subscales: (1) *Attention and Awareness*, observing the present moment, which includes all thoughts, feelings, and sensations (e.g., "when I take a shower or a bath, I notice how water feels on my body"); (2) *Nonreactivity*, being accepting of the present moment and inhibiting secondary elaborative processing (e.g., "when you realize that you missed something important in a class … how often do you get angry with self?"); (3) *Nonjudgment*, being non-evaluative the present moment (e.g., "I like to judge whether my ideas and opinions are right or wrong"); and (4) *Self-Acceptance*, being accepting of the self without criticism (e.g., "I tell myself that I shouldn't be feeling the way I am feeling"). Nonreactivity, Nonjudgment, and Self-Acceptance are reverse scored. The AAMS is a relatively new questionnaire, having only received validation from the original publication (Droutman et al., 2018). The internal consistency in our sample was good among facets (Attention and Awareness, $\alpha = 0.85$; Nonreactivity $\alpha = 0.82$; Nonjudgment $\alpha = 0.77$; Self-Acceptance $\alpha = 0.88$).

Deliberate Mindfulness Experience As this was a community-based sample, it was expected that participants would have varying levels of deliberate mindfulness practice (i.e., deliberate mindfulness experience). To assess this, participants reported their frequency of mindfulness meditation experience on a 6-point Likert scale from "0-never" to "6-nearly every day to every day for more than 2 years." For those that practiced mindfulness meditation, they indicated the typical session length from "1–1–3 min" to "6-over 25 min." Additionally, participants reported on yoga experience on a 6-point Likert scale from "0-never" to "6-at least once per week for over 4 years." For those that practiced yoga, the amount of time typically spent actively attending to the sensations of their body and breath during the practice was reported from "0-not at all" to "6-throughout the entire practice." Scores on meditation experience and yoga experience questions were summed to compute total scores on deliberate mindfulness experience. The internal consistency for deliberate mindfulness experience was good ($\alpha = 0.76$).

Mind Wandering To determine if dispositional mindfulness was consistent with state measures of present-focused awareness during the fMRI working memory task, mind wandering was assessed at a single time point post-scan. Participants reported where their attention was during the scan via Likert scale from "0-on task" to "6-completely off task." Higher scores therefore indicate greater mind wandering.

Working Memory Participants completed an fMRI working memory N-back task (Kirchner, 1958) derived from the Human Connectome Project (HCP; Barch et al., 2013). The N-back task is well-validated and reliably elicits activation in the dlPFC and vlPFC in adolescents (Andre et al., 2016). Participants are presented with a series of stimuli (i.e., places, tools, or body parts) and decide whether the current stimulus matches a stimulus from N steps earlier (e.g., two steps earlier), thus evoking maintenance and manipulation of stimuli in the brain. The task involves several components of executive function and working memory, including updating, decision-making, inhibition of previous targets, and interference resolution of familiarity versus recollection at 2-back level and above (Andre et al., 2016; Barch et al., 2013).

Based on Barch et al.'s (2013) paradigm, task parameters involved an 8-block design (4 blocks in each condition), with alternating blocks between the 0-back and 2-back condition. Each block consisted of 10 trials. As shown in Fig. 1, task blocks began with a 3-s instruction cue indicating the task type (0-back or 2-back), then 10 randomized trails where each stimulus was presented for 2 s, followed by a 500-ms interstimulus interval (ISI). Blocks and trails were separated by a fixation crosshair. In each block of 10 trials, 2 stimuli were targets and 2–3 were non-target lures. Participants responded via button presses indicating match or non-match. Participant scores on the N-back task reflect the total number of correct button-presses for each condition. Percent accuracy, mean RT (measured in ms), and IES ($\frac{RT_{correct}}{\text{proportion of correct}}$), to measure speed-accuracy trade-off, were computed for each participant. For IES to be valid, accuracy should be 90% or above and there should be a high correlation between the portion of correct responses and RT (Bruyer & Brysbaert, 2011; Vandierendonck, 2017).

Data Analyses

Two participants were deemed outliers as they were three standard deviations above or below the mean on at least one working memory variable, and thus were excluded from all

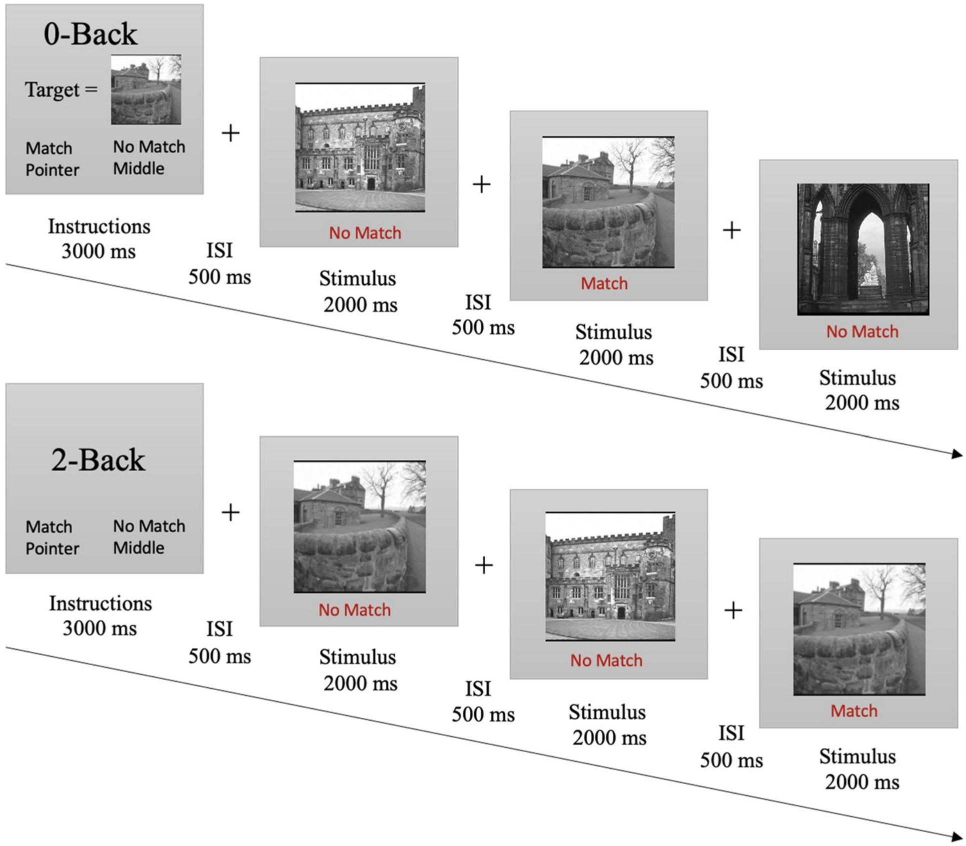

Fig. 1 fMRI N-back task. *Note*: Adapted from Barch et al. (2013). ISI = interstimulus interval

data analyses, leaving $n = 83$. Two participants were missing data on working memory performance measures and were excluded from behavioral analyses ($n = 81$), although they were included in neuroimaging analyses. Using IBM SPSS Statistics 26, bivariate correlations were computed to examine the association between working memory performance, dispositional mindfulness, deliberate mindfulness experience, mind wandering, and demographic information. IES was evaluated for validity within the sample. A partial correlation was performed between AAMS mindfulness facets and 2-back working memory variables controlling for mindfulness experience.

Neuroimaging data was analyzed using the Statistical Parametric Mapping 12 (SPM12) toolbox in MATLAB 2019a. To correct for motion, the Artifact Detection Tool (ART; NITRC 2008) was used. Motion outliers were volumes with scan-to-scan motion of > 0.5 mm in either the *x*, *y*, or *z* plane, 0.02 radians in either the roll, pitch, or yaw rotation, or mean global signal (z) ≥ 2.0. Frequency of overall and task block motion outliers did not correlate to dispositional mindfulness or working memory variables. Participants were excluded from neuroimaging analyses if 25% or more of task volumes had outliers (4.8%, $n = 4$). One participant was excluded due to an image acquisition error and another due to a recent concussion, leaving $n = 77$.

Functional images were normalized to Montreal Neurological Institute (MNI) standardized stereotactic space using the SPM EPI template and spatially smoothed with an 8-mm Gaussian filter, Full-Width Half Maximum (FWHM). For each participant, a first-level general linear model (GLM) was constructed in SPM with regressors for the 2-back and 0-back conditions as well as the six motion parameters and censored volumes as covariates of no interest. Contrasts were generated for 2-back compared to 0-back and entered in a group analysis at the second level with dispositional mindfulness as a covariate. Separate models were computed for each AAMS facet.

Based on right-lateralization of visuospatial working memory (Nagel et al., 2013), we conducted a priori analyses restricting the search space to the right dlPFC and vlPFC. The right dlPFC mask was defined as voxels activated during working memory (2-back vs 0-back contrast, $p < 0.001$ uncorrected) within the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002) right middle frontal gyrus (MFG) and right superior frontal gyrus (SFG). The right vlPFC mask was defined as voxels activated during working memory (2-back vs 0-back contrast, $p < 0.001$ uncorrected) within the AAL atlas (Tzourio-Mazoyer et al., 2002) right IFG. Both masks were created using WFU_pickatlas (Maldjian et al., 2003).

Psychophysiological interaction (PPI; O'Reilly et al. 2012) analyses tested the extent to which task-dependent connectivity of the right dlPFC and right vlPFC with the whole brain during the 2-back versus 0-back conditions vary as a function of dispositional mindfulness. Exploratory analyses were also performed with seeds in the right ACC and right superior parietal lobule (SPL), as these are key nodes of the working memory network activated by the N-back task used in this study (Barch et al., 2013). Regions were defined as the above with voxels activated during the N-back task (2-back vs 0-back contrast, $p < 0.001$ uncorrected) within AAL atlas regions in the right ACC and right SPL.

Considering a possible influence of deliberate mindfulness experience on brain activation, we performed all analyses with and without this variable as a covariate of no interest. Inferences were drawn using an uncorrected peak $p \leq 0.001$ threshold and cluster-wise family wise error (FWE) correction of $p < 0.050$, Bonferroni-corrected for two comparisons (i.e., the dlPFC and vlPFC seeds; $0.050/2 = 0.025$). Coordinates are reported in MNI coordinate space. Images were created using MRIcroGL (Rorden et al., 2007).

Results

Associations Between Dispositional Mindfulness and Behavioral Data

Table 1 displays descriptive statistics and zero-order correlations among study variables. Age and sex had no associations with dispositional mindfulness facets, working memory variables, or BOLD signal in the right dlPFC and right vlPFC. Household income correlated positively to Self-Acceptance. Parental education was positively correlated to 2-back accuracy. Controlling for household income and parental education did not significantly affect results; thus, they were not included in analyses. Self-reported mind wandering during the fMRI scan was negatively correlated to Nonreactivity and Self-Acceptance. Accuracy on the 2-back task was not significantly correlated to 2-back RT and had a mean of 60.8%, which together did not meet the validity requirements for IES (Bruyer & Brysbaert, 2011; Vandierendonck, 2017). IES was therefore not well-suited for the sample. No other working memory performance variable was significantly associated with dispositional mindfulness, irrespective of deliberate mindfulness experience (Table 2).

Most participants either reported no meditation experience (43.4%, $n = 36$) or indicated meditating once or twice in their lifetime (25.3%, $n = 21$). The remaining participants reported meditating at least once per month for less than a year (20.4%, $n = 17$) or had a weekly to daily meditation practice for longer than a year (10.8% $n = 9$). The sample either had no yoga experience (33.7%, $n = 28$), had practiced

Table 1 Bivariate correlation table of study variables and descriptive statistics

	1	2	3	4	5	6	7	8	9	10	11	12
1. Attention and Awareness	1											
2. Nonreactivity	−.36**	1										
3. Nonjudgment	−.57**	.49**	1									
4. Self-Acceptance	−.18	.55**	.59**	1								
5. 2-Back Accuracy	.15	−.11	−.16	.09	1							
6. 2-Back RT	.01	.17	.08	.04	−.17	1						
7. Mindfulness Experience	.28*	−.06	−.22*	−.24*	.14	.12	1					
8. Mind Wandering	−.03	−.30**	−.16	−.32**	−.21	−.04	−.04	1				
9. Age	.17	−.09	−.08	−.05	−.09	−.15	.07	.04	1			
10. Sex	−.02	.09	−.06	.15	.09	−.12	−.22*	−.20	.22*	1		
11. Household Income	−.10	.08	.17	.26**	.15	.08	−.11	−.24	−.32**	.14	1	
12. Parental Education	.01	−.11	−.05	.01	.23*	.07	.08	−.16	−.18	.01	.40**	1
Mean	28.68	9.39	12.96	11.47	60.80	1096	5.19	2.21	13.75	1.43	4.63	4.31
SD	7.39	3.10	3.82	2.99	19.01	157.6	4.96	1.23	1.56	0.50	2.20	1.60

*$p < .050$; **$p < .010$

Reaction time (RT) in ms; female = 1, male = 2; the mean of 4.63 on Household Income is approximately $100,000; the mean of 4.31 on Parental Education is between a trade/technical/vocational diploma and undergraduate degree

Table 2 Partial correlation of AAMS dispositional mindfulness with working memory performance variables controlling for mindfulness experience ($n = 81$)

	1	2	3	4	5	6
1. Attention and Awareness	1					
2. Nonreactivity	−.33**	1				
3. Nonjudgement	−.55**	.48**	1			
4. Self-Acceptance	−.09	.54**	.56**	1		
5. 2-Back Accuracy	.11	−.11	−.14	.12	1	
6. 2-Back RT	−.04	.18	.11	.07	−.20	1

*$p < .050$; **$p < .010$

RT reaction time

yoga once or twice in their lifetime (31.3%, $n = 26$), had been practicing yoga at least monthly for less than a year (22.9%, $n = 19$), or had been practicing yoga at least weekly for a year or more (12.0%, $n = 10$). Deliberate mindfulness experience (i.e., the aggregate score of meditation and yoga experience questions) was significantly higher in females (female = 1, male = 2; $t(79) = 1.99$, $p = 0.050$). Deliberate mindfulness experience was positively correlated to Attention and Awareness and negatively correlated to Self-Acceptance and Nonjudgment. Based on these results and previous research linking deliberate mindfulness training to frontal cortical recruitment (Wheeler et al., 2017), neuroimaging analyses were performed with and without deliberate mindfulness experience as a control to examine its influence on patterns of associations between dispositional mindfulness and working memory neural correlates.

Associations Between Dispositional Mindfulness and Working Memory Neural Correlates

Consistent with prior research, bilateral dlPFC, vlPFC, parietal cortex, and cerebellum showed increased BOLD signal during the 2-back versus 0-back working memory task (Supplementary Table 1; Supplementary Fig. 1). There was no significant associations between the 2-back compared to 0-back BOLD response with Nonreactivity, Nonjudgment, or Self-Acceptance. Higher Attention and Awareness was associated with significantly lower BOLD signal in the right vlPFC (pars opercularis IFG), controlling for deliberate mindfulness experience (Table 3, Figs. 2a, and 3a). Although the overall pattern of associations did not change, the right vlPFC did not survive Bonferroni correction for two comparisons when not controlling for deliberate mindfulness experience ($\alpha = 0.025$, FWE$p = 0.031$; Table 3, Figs. 2b, and 3b). Dispositional mindfulness did not significantly correlate to right dlPFC BOLD signal (Table 3).

Higher levels of Nonreactivity were associated with lower functional connectivity between the right vlPFC and a cluster with peak coordinates in the right dorsomedial PFC (dmPFC), or medial SFG (mSFG) based on the AAL atlas, during 2-back versus 0-back when controlling for deliberate mindfulness experience (Table 3; Figs. 2c, and 3c) and when not controlling for deliberate mindfulness experience (Table 3; Figs. 2d, and 3d). Much of the cluster is situated in the right supplementary motor area (SMA; Fig. 2c), and without controlling for deliberate mindfulness experience, extends to the left dmPFC (Fig. 2d). These findings did not survive Bonferroni correction for two comparisons. No

Table 3 Neural correlates of AAMS facets during 2-back compared to 0-back N-back task ($n = 77$)

Dependent variable	Control variable	Region (H)	AAL atlas	MNI coordinates *x*	*y*	*z*	Cluster *k*	FWE*p*
		<u>Neural BOLD signal after small volume correction</u>						
Attention and Awareness	Mindfulness Experience	dlPFC (R)	MFG	48	10	48	6	.139
	Mindfulness Experience	vlPFC (R)	Oper. IFG	44	12	30	112	.011*
	None	vlPFC (R)	Oper. IFG	44	12	30	35	.031*
Nonreactivity		<u>Functional connectivity with right vlPFC</u>						
	Mindfulness Experience	dmPFC (R)	mSFG	4	20	44	283	.039*
	None	dmPFC (R)	mSFG	4	20	44	320	.026*

*$p \leq .050$; **$p \leq .001$

H hemisphere (*R* = right), *dlPFC* dorsolateral prefrontal cortex, *vlPFC* ventrolateral prefrontal cortex, *dmPFC* dorsomedial prefrontal cortex, *AAL* automated anatomical labeling, *MFG* middle frontal gyrus, *IFG* interior frontal gyrus, *mSFG* medial superior frontal gyrus, *MNI* Montreal Neurological Institute, *k* number of voxels, *FWEp* family-wise error corrected *p*-value

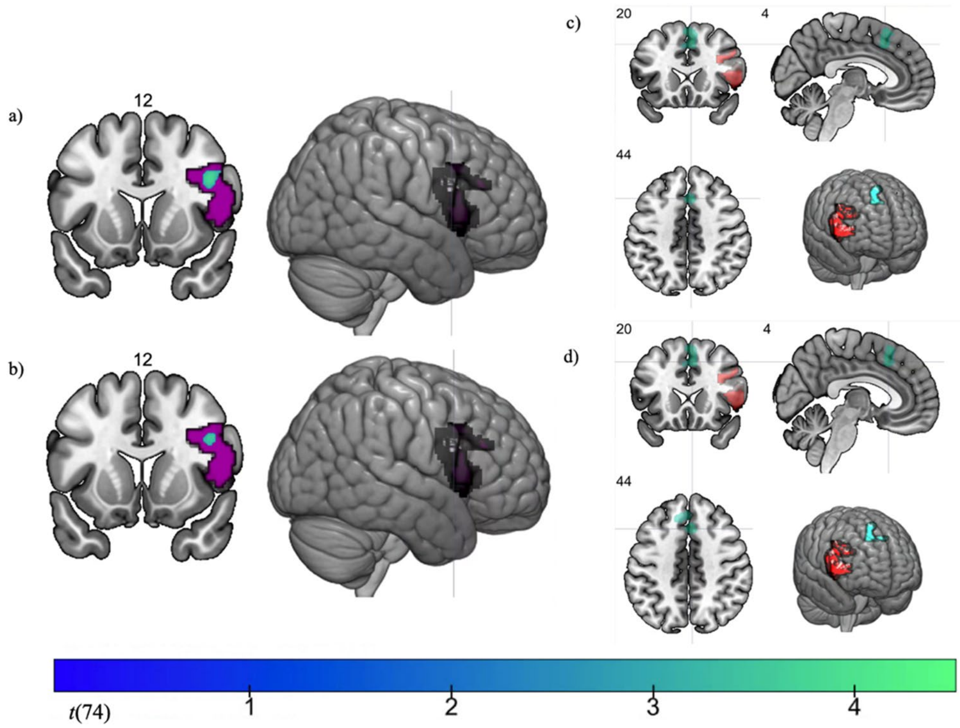

Fig. 2 Right vlPFC associations of AAMS facets during 2-back compared to 0-back task ($n=77$). *Note:* Right ventrolateral prefrontal cortex (vlPFC) was defined as voxels activated during 2-back vs 0-back contrast ($p<.001$ uncorrected) within the right inferior frontal gyrus (IFG) from the Automatic Anatomical Labeling (AAL) atlas. (a) BOLD signal in right vlPFC (purple) negatively correlated to Attention and Awareness, controlling for deliberate mindfulness experience [$t(74)=3.93$, FWE$p=.011$, $k=112$]. (b) Results from (a) without controlling for deliberate mindfulness experience [$t(74)=3.62$, FWE$p=.031$, $k=35$]. (c) Negative functional connectivity between right vlPFC (red) and right dorsomedial PFC (dmPFC; blue) at FWE$p<.050$ correlated to high Nonreactivity, controlling for deliberate mindfulness experience [$t(74)=4.27$, FWE$p=.039$, $k=283$]. (d) Results from (c) without controlling for deliberate mindfulness experience [$t(74)=4.23$, FWE$p=.026$, $k=320$]. $k=$number of voxels; FWE$p=$family-wise error corrected peak-level activation

associations were found between AAMS facets and N-back functional connectivity with seed regions in the right dlPFC, right ACC, or right SPL.

Discussion

As mindfulness-based interventions become more prominent among youth (Zenner et al., 2014), characterizing the neural correlates of dispositional mindfulness in the adolescent brain may be important for understanding the mechanism of change and therapeutic benefit of such interventions. We examined the association between dispositional mindfulness and BOLD neural activity and functional connectivity during an N-back task, as well as between dispositional mindfulness and working memory in a sample of adolescents. In support of our hypotheses, higher levels of Attention and Awareness were associated with less BOLD signal in the right vlPFC during a high cognitive load compared to a low cognitive load (i.e., 2-back vs 0-back), controlling for mindfulness experience. Furthermore, the vlPFC showed lower functional connectivity with a cluster within the right dmPFC (mSFG) and SMA during the 2-back versus 0-back condition in adolescents with high levels of Nonreactivity, although this finding did not survive correction for multiple comparisons. We did not find a significant association between dispositional mindfulness and N-back working memory performance, dlPFC BOLD signal, or functional connectivity.

Working Memory Neural Associations

Decreased BOLD response within the right vlPFC (pars opercularis IFG) during working memory was significantly correlated to higher levels of Attention and Awareness. The right pars opercularis IFG is strongly implicated in inhibition, including the stopping of actions via inhibition of the basal ganglia (Aaron 2007), inhibiting irrelevant memories from entering working memory by downregulating the

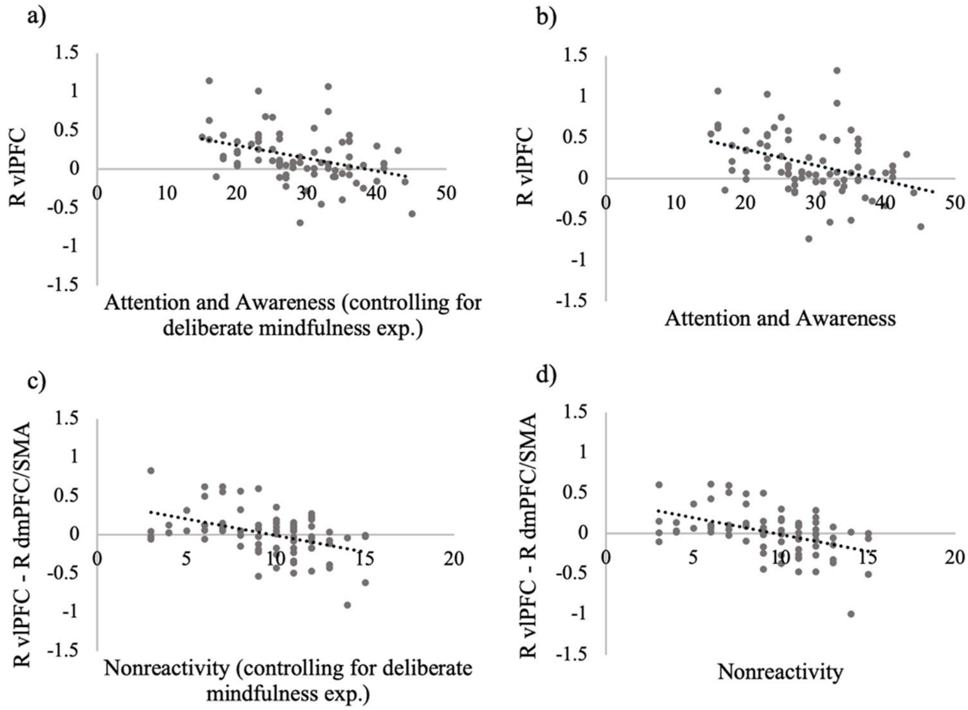

Fig. 3 Scatterplot for the association between AAMS facets, BOLD neural signal, and functional connectivity during N-back task, 2-back versus 0-back. *Note:* R = right; vlPFC = ventrolateral prefrontal cortex; dmPFC = dorsomedial prefrontal cortex; SMA = supplementary motor area. **a** Attention and Awareness and right vlPFC BOLD activity controlling for deliberate mindfulness experience ($r = -.378$, $p = .001$; cluster-wise FWE$p = .011$). **b** Attention and Awareness and right vlPFC BOLD activity without controlling for deliberate mindfulness experience ($r = -.382$, $p = .001$; cluster-wise FWE$p = .031$). **c** Nonreactivity and right vlPFC–right dmPFC/SMA functional connectivity controlling for deliberate mindfulness experience ($r = -.448$, $p < .001$; cluster-wise FWE$p = .039$). **d** Nonreactivity and right vlPFC–right dmPFC/SMA functional connectivity without controlling for deliberate mindfulness experience ($r = -.465$, $p < .001$; cluster-wise FWE$p = .026$)

hippocampus (Anderson & Levy, 2009), and cognitive control over emotional distractors by deactivating the amygdala (Dolcos & McCarthy, 2006). Thus, findings may indicate that more observant adolescents require less cognitive effort to inhibit prepotent responses and internal distractors from disrupting working memory.

Previous research has found that naïve yoga practitioners had greater vlPFC BOLD activation during a Stroop Task when negative emotionally valenced compared to neutral distractors were presented (Froeliger et al. 2012), and beginner meditators showed increased vlPFC activation during affect labeling after a mindfulness-based intervention (Hölzel et al., 2013). Results from the current study are consistent with the neural activation pattern found in regular meditators, which show decreased activity in frontal cortical regions during executive functioning (Kirk et al., 2011; Kozasa et al., 2012). Indeed, the pattern of frontal cortical engagement during meditation and executive functioning is thought to follow an inverted U-shaped pattern dependent on deliberate mindfulness experience (Wheeler et al., 2017).

The relationship survived only when deliberate mindfulness experience was controlled for. Drawing on Brefczynski-Lewis et al. (2007), Wheeler et al. (2017) defined novice practitioners as having fewer than 8 weeks of training and 100 h of personal practice, experienced/intermediate practitioners as having more than 8 weeks of training and fewer than 44 000 h of personal practice, and expert mindfulness practitioners as having more than 44,000 h of personal practice. Adolescents with deliberate mindfulness experience within our sample would therefore be considered novice to intermediate. As such and consistent with prior research presented above, adolescents with intermediate levels of experience may have recruited greater right vlPFC BOLD activity, although deliberate mindfulness experience did not significantly correlate to BOLD signal in the 2-back compared to 0-back condition. It should be noted that intermediate levels of deliberate mindfulness experience in our sample was low, with only 4 participants (4.8%) having reported more than 2 years of personal practice. Thus, there was likely a lack of variance in deliberate mindfulness experience in the sample to provide an adequate test for this possibility. Further research is required to examine the association between deliberate mindfulness experience and working memory in adolescents.

Working Memory Functional Connectivity Associations

Elevated Nonreactivity was associated with decreased functional connectivity of the right vlPFC with the right dmPFC/SMA during the 2-back versus 0-back. Interpretations of this finding, however, should be made with caution, as this finding did not survive correction for multiple comparisons. The right dmPFC is a region within the DMN and is involved in a range of cognitive functions including autobiographical memory (Bado et al., 2013). Reduced functional connectivity between the right vlPFC and dmPFC in adolescents with high Nonreactivity may indicate that adolescents less prone to elaborative processing were able to shift away from self-referential thinking or mind wandering during the task. This possibility is consistent with the finding that Nonreactivity and Self-Acceptance were inversely related to mind wandering, as reported in a post-scan questionnaire, indicating that adolescents that were more accepting of their environment and themselves were able to stay on task during the scan. A similar relationship was found in adults during a resting state fMRI study, such that higher FFMQ total was associated with decreased functional connectivity between the central executive network (CEN) and the dmPFC (Parkinson et al., 2019). Furthermore, in a study looking at dynamic neural states of meditation-naïve children and adolescents, high intrinsic dispositional mindfulness (i.e., CAMM; Greco et al., 2011) was related to decreased functional connectivity between the DMN and CEN (Marusak et al., 2018). In the current study, the cluster also extended to the right and left SMA, which is associated with control and inhibition of actions (Nachev et al., 2008). While the exact mechanisms underpinning links between Nonreactivity and functional connectivity of the vlPFC with the dmPFC/SMA cannot be gleaned from the current study, the negative functional connectivity between the right vlPFC and SMA in adolescents with higher Nonreactivity may suggest less cognitive effort to inhibit button presses to incorrect responses during the working memory task in adolescents that were more versus less accepting of the present moment.

Working Memory Performance

No association was found between dispositional mindfulness and working memory performance in our sample. This is inconsistent with previous findings that report associations between greater intrinsic MAAS levels and better self- and parent-reported updating, inhibition (Geronimi et al., 2019; Riggs et al., 2015), and task shifting components of executive function in youth (Geronimi et al., 2019) and better visuospatial working memory performance in adults (Jaiswal et al., 2018). Deliberate mindfulness training has also been found to improve working memory performance in adults (see Jha et al., 2019) and adolescents (see Dunning et al., 2018).

As some studies show improvements on N-back task performance immediately after deliberate mindfulness training (Zeidan et al., 2010), Jha et al. (2019) speculate that enhancements in working memory performance may relate to temporary state effects of meditation rather than lasting trait changes from cognitive training and strengthening of working memory networks. This, however, would not explain the trait-like functional differences in vlPFC BOLD activation during the working memory task observed in adolescents with high levels of Nonreactivity in our sample. Highly Nonreactive individuals may require less cognitive effort during an N-back task to perform as well as others. Alternatively, considering the role of vlPFC in inhibition (Nyberg & Eriksson, 2015), a task that more explicitly tests inhibition may have produced a stronger effect. Indeed, Gallant (2016) reviewed 12 mindfulness meditation studies and found inhibition to be the most consistent component of executive function improved from deliberate mindfulness training.

Limitations and Future Directions

There are several important limitations to note. First, although comparable to other neuroimaging studies, the sample size was somewhat modest for correlation analyses, which may have impacted the ability to detect significant results between other facets of dispositional mindfulness and working memory previously reported in attention (e.g., Maltais et al., 2020) and working memory tasks (e.g., Ruocco & Direkoglu, 2013). Second, the cross-sectional nature of the study did not allow for causal inferences to be drawn or the examination of changes in working memory performance as a result of dispositional mindfulness over time, or vice versa. It also cannot establish the direction of effects as dispositional mindfulness and working memory may have bidirectional effects. Third, the AAMS does not include a facet similar to FFMQ *Acting with Awareness*, defined as the opposite of running on automatic pilot (Baer et al., 2006). Thus, specific effects related to Acting with Awareness and working memory were not examined in this study. Fourth, younger adolescents may not have been able to adequately identify their ability to observe thoughts, feelings, and bodily sensations the same way an adult or older adolescent is capable. Nonetheless, the AAMS was originally validated in youth as young as 11 and age was not correlated to any of the study variables. Lastly, there was, on average, 2 months between assessment of mindfulness variables (i.e., the AAMS and deliberate mindfulness experience measures) and behavioral and neuroimaging working memory data (i.e., N-back). While it is possible that some participants may have gained mindfulness experience during this period, dispositional mindfulness is a relatively stable trait (Brown et al., 2007) and our sample had generally low levels of deliberate mindfulness experience. Thus, it is unlikely that subjects, on average, developed substantially higher levels of dispositional mindfulness between visits.

More research is needed to understand the cognitive and neural bases of dispositional mindfulness, especially in youth. The lack of a significant association between dispositional mindfulness and dlPFC BOLD signal and functional connectivity is potentially due to participant reliance on maintenance rather than manipulation strategies during the task, as the dlPFC is typically recruited in executive manipulation when cognitive demands are high (Nyberg & Eriksson, 2015). Since the 0-back task measures sustained attention with little to no working memory demand (Miller et al., 2009), future work may consider varying the cognitive load in the N-back by incorporating a 1-back or 3-back condition to allow further examination of the neural correlates of mental manipulation and their association with dispositional mindfulness. Future research should also employ large diverse samples with varying level of deliberate mindfulness experience and longitudinal designs to disentangle directions of effects and determine the neural mechanisms underlying deliberate mindfulness training. Future research may also test the effects of dispositional mindfulness and vlPFC-mediated inhibitory control using clinical samples and mindfulness intervention experimental studies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12671-021-01785-4.

Acknowledgements This research was supported by funding from Social Sciences and Humanities Research Council of Canada, the Natural Sciences and Engineering Research Council of Canada, the Canadian Institutes of Health Research, and the Brain and Behavior Research Foundation, awarded to Dr. Daniel Kopala-Sibley. Jade Stein was supported by a Branch Out Neurological Foundation Master's Grant and Natural Sciences and Engineering Research Council of Canada Master's Scholarship.

Author Contribution J. A. S. designed and executed the study, performed data analyses, and wrote the manuscript. S. B. collaborated with the design and analyses. F. P. M. and L. T. M. collaborated with the study design. D. C. K. S. designed the study and collaborated with analyses and writing of the manuscript. All authors contributed to editing the final manuscript.

Data Availability The datasets generated and analyzed in the current study are available from the corresponding author on reasonable request.

Declarations

Ethics standards Ethics approval for all procedures performed in the study was obtained from the institutional Conjoint Health Research Ethics Board (CHREB), REB17-2377. Informed consent was obtained from all participants and parents of minor participants.

Conflict of Interest The authors declare no competing interests.

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