

Original Article

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Adaptive-to-maladaptive gradient of emotion regulation tendencies are embedded in the functional–structural hybrid connectome

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Abstract

Background. Emotion regulation tendencies are well-known transdiagnostic markers of psychopathology, but their neurobiological foundations have mostly been examined within the theoretical framework of cortical–subcortical interactions.

Methods. We explored the connectome-wide neural correlates of emotion regulation tendencies using functional and diffusion magnetic resonance images of healthy young adults ($N = 99$; age 20–30; 28 females). We first tested the importance of considering both the functional and structural connectome through intersubject representational similarity analyses. Then, we employed a canonical correlation analysis between the functional–structural hybrid connectome and 23 emotion regulation strategies. Lastly, we sought to externally validate the results on a transdiagnostic adolescent sample ($N = 93$; age 11–19; 34 females).

Results. First, interindividual similarity of emotion regulation profiles was significantly correlated with interindividual similarity of the functional–structural hybrid connectome, more so than either the functional or structural connectome. Canonical correlation analysis revealed that an adaptive-to-maladaptive gradient of emotion regulation tendencies mapped onto a specific configuration of covariance within the functional–structural hybrid connectome, which primarily involved functional connections in the motor network and the visual networks as well as structural connections in the default mode network and the subcortical–cerebellar network. In the transdiagnostic adolescent dataset, stronger functional signatures of the found network were associated with higher general positive affect through more frequent use of adaptive coping strategies.

Conclusions. Taken together, our study illustrates a gradient of emotion regulation tendencies that is best captured when simultaneously considering the functional and structural connections across the whole brain.

Introduction

How individuals change the rise, maintenance, and decline of their affective experiences – the process of emotion regulation – has been widely recognized as a key process from normative functioning to psychopathology (Fernandez, Jazaieri, & Gross, 2016; Gross & Muñoz, 1995; Sheppes, Suri, & Gross, 2015). Studies have found that emotion regulation measures can lead to successful predictions of prospective mental health outcomes such as social functioning, well-being, internalizing symptoms, and externalizing symptoms (Berking, Wirtz, Svaldi, & Hofmann, 2014; Cameron & Overall, 2018; Kim & Cicchetti, 2010; Wirtz, Hofmann, Riper, & Berking, 2014). Moreover, recent studies highlight the role of emotion regulation in both the development and successful treatment of diverse dimensions of psychopathology (Aldao, Gee, De Los Reyes, & Seager, 2016; Fernandez et al., 2016; Sakiris & Berle, 2019; Sloan et al., 2017; Weissman et al., 2019).

Given its relevance in both normative and aberrant affective experiences, increasing number of neuroimaging studies sought to delineate the neural substrates of emotion regulation. In detail, decades of task-based experiments have culminated in relatively reliable meta-analytic mappings of emotion regulation circuits that encompass the amygdala, ventromedial prefrontal cortex, ventrolateral prefrontal cortex, dorsolateral prefrontal cortex, the insula, supplementary motor area, and the cingulate cortex (Buhle et al., 2014; Frank et al., 2014; Kohn et al., 2014; Morawetz, Bode, Derntl, & Heekeren, 2017). These empirical mappings are also in line with theoretical models that explain emotion regulation as a dynamic process that recruit multiple combinations of cortical–subcortical interactions to shape affective experiences (Braunstein, Gross, & Ochsner, 2017; Caballero, Nook, & Gee, 2022; Etkin, Büchel, & Gross, 2015; Ochsner, Silvers, & Buhle, 2012; Silvers & Moreira, 2019; Smith & Lane, 2015).

However, there are two important shortcomings in the relevant literature that need to be addressed: reliance on (1) laboratory-based tasks of emotion regulation and (2) *a priori* regions

of interest (ROIs) approaches. The first limitation of the emotion regulation literature is its heavy reliance on laboratory-based emotion regulation tasks to elucidate the neural substrates supporting successful implementation of certain emotion regulation strategies (Caballero et al., 2022; Silvers & Moreira, 2019). In other words, there is a relative paucity of neuroimaging research on emotion regulation *tendency*. Emotion regulation tendency refers to the habitual mode of emotion regulation in which individuals engage in when faced with naturalistic regulatory needs (Silvers & Moreira, 2019), and such tendencies cannot be fully captured in laboratory settings where subjects are given certain emotion regulation strategies to utilize. Numerous studies have demonstrated that dispositional patterns through which individuals deploy specific emotion regulation strategies can be especially informative in parsing psychopathology symptoms (Aldao, Nolen-Hoeksema, & Schweizer, 2010; Eftekhari, Zoellner, & Vigil, 2009; Naragon-Gainey, McMahon, & Chacko, 2017; Sheppes, Scheibe, Suri, & Gross, 2011), but few studies have investigated the neural underpinnings of such patterns. Though a number of studies investigated the neural mechanism behind emotion regulation tendency by giving individuals regulatory choices in experimental settings (Doré, Weber, & Ochsner, 2017; Fine, Schwartz, Hendler, Gonen, & Sheppes, 2022; Shafir, Schwartz, Blechert, & Sheppes, 2015; Shafir, Thiruchselvam, Suri, Gross, & Sheppes, 2016) or by probing the correlations between self-reported emotion regulation tendency and individual difference in brain activity magnitude (Che, Luo, Tong, Fitzgibbon, & Yang, 2015; Drabant, McRae, Manuck, Hariri, & Gross, 2009; Kanske, Heissler, Schönfelder, & Wessa, 2012; Kanske, Schönfelder, Forneck, & Wessa, 2015; Scult, Knodt, Swartz, Brigidi, & Hariri, 2017), studying diverse patterns across multiple emotion regulation strategies has been limited because these studies mainly focused on only one or two strategies in experimental settings.

The second limitation of the existing body of research is that the analyses were mostly limited to activations or functional connectivity patterns among *a priori* ROIs. Extracting neural phenotypes from emotion regulation circuits have led to promising models that predict symptoms or treatment responses (Fournier et al., 2021; Fresco et al., 2017; Klumpp et al., 2017; Wu et al., 2022). On the other hand, such models may be further improved by considering whole-brain data to understand the neural correlates of emotion regulation in a more comprehensive manner. Indeed, previous literature highlight that exploring outside the theoretically restricted ROIs contributes to building generalizable models of affective experience (Tejavibulya et al., 2022; Yarkoni & Westfall, 2017). Evidence that directly support this claim can be found where distributed patterns of activation across the entire brain showed better performance in capturing negative emotions than ROI activations (Chang, Gianaros, Manuck, Krishnan, & Wager, 2015), or where subjective fear was represented in distributed systems rather than conventionally defined ‘fear centers’ (Zhou et al., 2021). Taken together, a formal investigation of emotion regulation tendency in the context of whole-brain data is warranted.

One useful approach that would be able to address these issues is to investigate stable networks derived from whole-brain functional connections, or functional connectomes. Accumulating evidence suggest that although transitory states induce significant changes in functional connections (Finn & Bandettini, 2021; Geerligs, Rubinov, & Henson, 2015; Greene, Gao, Scheinost, & Constable, 2018), their network organizations are mostly stable

within individuals across time (Gratton et al., 2018; Horien, Shen, Scheinost, & Constable, 2019; Shen et al., 2017), making them suitable for inspecting trait-like individual differences such as sustained attention (Rosenberg et al., 2016), transdiagnostic psychopathology (Elliott, Romer, Knodt, & Hariri, 2018), or fluid intelligence (Finn et al., 2015). One prime example that emphasizes the utility of connectomes is a recent meta-analytic study using connectomics to find a convergence map that is clinically translatable to effective treatment targeting, which was unattainable when using regional activations (Cash, Müller, Fitzgerald, Eickhoff, & Zalesky, 2023).

On the other hand, structurally bound functional networks have been seldom studied despite its promise in highlighting stable trait-like features. Conceptually, if functional connectivity corresponds to the ‘observed amount of traffic’ between two ‘cities’, white matter structural connectivity derived from diffusion magnetic resonance imaging (dMRI), in turn, corresponds to the ‘highways’ that support the traffic (Amico & Goñi, 2018). Therefore, one can consider the possibility that stronger networks of highways shaping how traffics operate and include this dynamic in brain connectivity models. Of note, though stronger structural connectivity between two regions promotes functional connectivity between said regions (Sarwar, Tian, Yeo, Ramamohanarao, & Zalesky, 2021; Sporns, 2011; Suárez, Markello, Betzel, & Misic, 2020), the structural networks may influence spatially non-overlapping functional networks through facilitating or restricting network-level interactions (Amico & Goñi, 2018; Mišić et al., 2016).

To expand the emotion regulation literature through adopting such network-based approaches, we analyzed the functional connectome in tandem with the structural connectome to search for whole-brain functional–structural network correlates of emotion regulation tendency (Fig. 1). First, as a preliminary examination, we employed an intersubject representational similarity analysis (IS-RSA) framework to test whether individuals with similar functional and structural connectomes have similar emotion regulation tendencies across 23 regulatory strategies (Finn et al., 2020). The IS-RSA framework serves as a general test of relationship where statistical assumptions between the variables are minimal, and also retains the high resolution of information in the variables, which is especially helpful when analyzing a set of variables that may be comprised of qualitatively distinct subsets (e.g. 23 emotion regulation strategies). Then, we sought to pinpoint the structurally bound functional networks that represent individual differences in emotion regulation tendency. In detail, we applied independent component analysis (ICA) on the functional–structural covariant components that are reliably present across individuals (Amico & Goñi, 2018), then subjected these hybrid components to a canonical correlation analysis (CCA) to explore their relationship with emotion regulation tendencies (Smith et al., 2015). We hypothesized that multiple structurally bound functional networks would each be related to diversiform domains of emotion regulation tendency. Lastly, we sought to externally validate the results on a transdiagnostic sample of adolescents from the Healthy Brain Network (HBN; Alexander et al., 2017) to check if such structurally bound functional networks would also be important in the developmental stage where emotion regulation tendencies as well as psychopathology symptoms purportedly start to emerge (Ahmed, Bittencourt-Hewitt, & Sebastian, 2015; Casey, Getz, & Galvan, 2008; Lee et al., 2014; Silvers, 2022; Thompson, 1991).

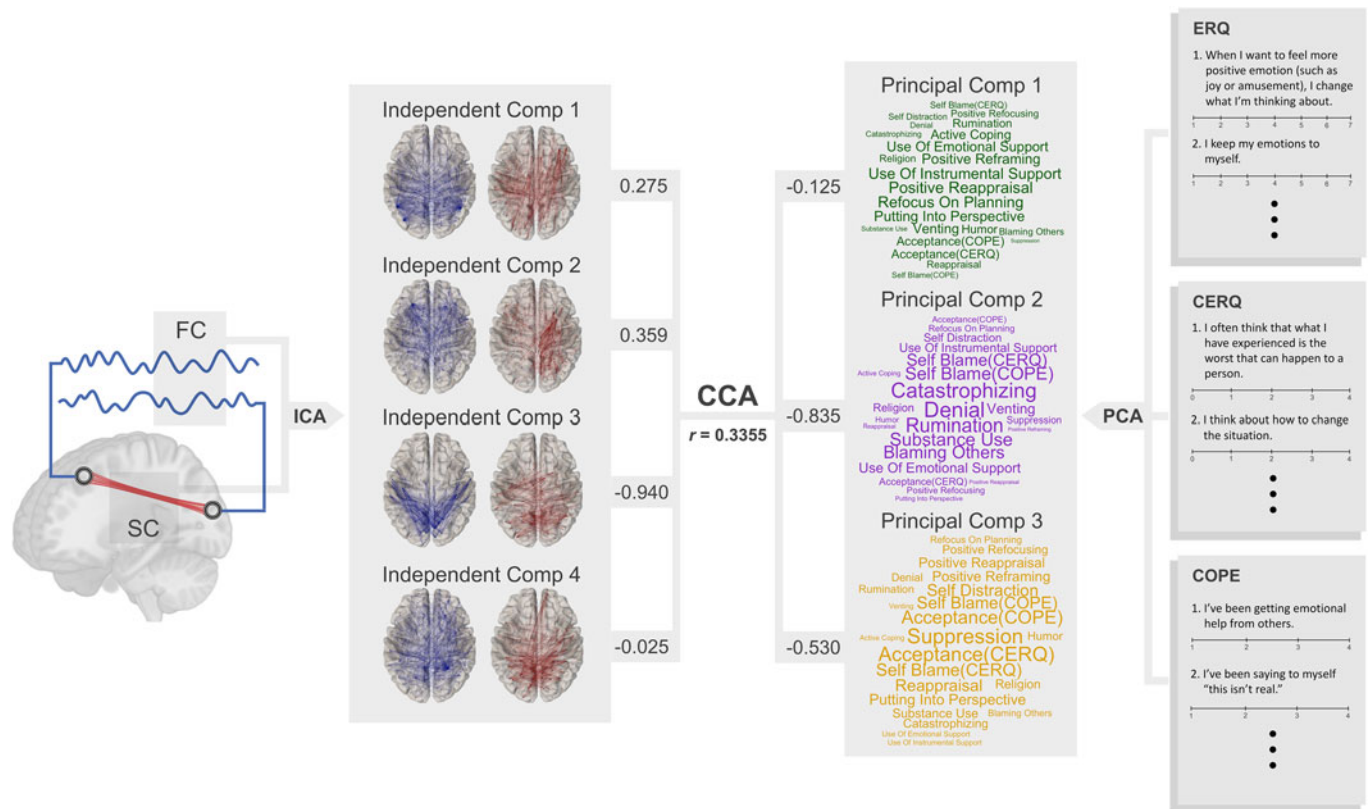


Figure 1. Schematic of the main analytic framework. The canonical correlation analysis involves the functional–structural hybrid connectome on one end and emotion regulation tendency on the other, both of which were each subjected to dimensionality reduction beforehand. Four independent components emerged from the 268 × 268 functional and structural connectomes, and three principal components were extracted from the 23 dimensions of emotion regulation tendency. Then, these sets of components were entered into the canonical correlation analysis framework to find the configuration of variable weights that determines maximal correlation between the two sets of variables.

Methods and materials

Participants

Data for this study were from the Max Planck Institute ‘Leipzig Study for Mind- Body-Emotion Interactions’ (LEMON) dataset (Babayan et al., 2019). The resulting sample comprised of 99 young German-speaking adults ($n = 59$ in age bracket 20–25, $n = 40$ in age bracket 25–30) among which 28 were female. Further details on the dataset are described in the online Supplementary Information.

Behavior measures

Data on emotion regulation tendency have been obtained from three different questionnaires (Emotion Regulation Questionnaire, ERQ; Cognitive Emotion Regulation Questionnaire, CERQ; Coping Orientations to Problems Experienced, COPE) to capture a broad range of individual difference in habitual emotion regulation. Details on these questionnaires can be found in the online Supplementary Information.

Connectome building

Image acquisition, preprocessing, and quality check as well as procedures on connectome construction are fully described in the online Supplementary Information. In brief, using the 268-node Shen atlas (Shen, Tokoglu, Papademetris, & Constable, 2013),

structural connectomes were derived from number of streamlines of probabilistic tractography on preprocessed dMRI images (Behrens, Berg, Jbabdi, Rushworth, & Woolrich, 2007), while functional connectomes were calculated from correlation coefficients between the mean timeseries of functional activations for each of the 268 regions from preprocessed resting-state functional images (Taylor & Saad, 2013).

Intersubject representational similarity analyses

IS-RSA via Mantel tests (Finn et al., 2020; Mantel, 1967) were performed to examine whether the joint consideration of functional and structural connectomes, compared to either connectome separately, offered better explanatory power for individual differences in emotion regulation tendencies. We therefore tested three intersubject similarity correlation models: (1) interindividual similarity of functional connectome and interindividual similarity of emotion regulation tendencies, (2) interindividual similarity of structural connectome and interindividual similarity of emotion regulation tendencies, and (3) interindividual similarity of functional–structural hybrid connectome and interindividual similarity of emotion regulation tendencies. Details are described in the online Supplementary Information.

Canonical correlation analysis

Given that the functional–structural hybrid connectome showed stronger correlation with emotion regulation tendencies than

either the functional or structural connectome by itself, the functional–structural hybrid connectome was further inspected to pinpoint the source of the correlation. Although CCA is a powerful multivariate analytic tool for capturing covariance between two sets of variables with high dimensionality (i.e. 268×268 brain variables and 23 behavior variables) (McPherson & Pestilli, 2021; Smith et al., 2015; Wang et al., 2020; Xia et al., 2018), concerns regarding its susceptibility to overfitting has been documented (Dinga et al., 2019; Mihalik et al., 2022). To circumvent this issue, we sought to reduce the dimensions of variables before they are entered into the CCA framework, which increases the stability and the reliability of CCA (Dinga et al., 2019; Mihalik et al., 2022; Wang et al., 2020). Crucially, considering the number of subjects of our study ($n=99$), the number of variables that would lead to reliable results is around 3–10 according to introductory texts (Pituch & Stevens, 2015; Tabachnick & Fidell, 2001) and less than 9 according to a recent methodological guide (Mihalik et al., 2022). Therefore, these standards were kept in mind when deciding the optimal number of dimensions, which are outlined in the online Supplementary Information. As a result, four independent components of functional–structural hybrid connectomes and three principal components of emotion regulation tendency were identified.

CCA takes two sets of variables and finds the optimal configuration of variable weights that maximizes the correlation between the two sets of variables. The analytic framework and the code for the CCA analysis followed a previous work (Smith et al., 2015), which also utilized CCA to pinpoint brain–behavior links after carrying out dimension reduction schemes on datasets to ensure reliability. First, for each participant, their weight for each of the four ICA components were found by averaging the weight values across the 1000 runs. Second, a covariate matrix was derived by aggregating and normalizing data on gender, age, height, weight, heart rate, resting-state EPI movement, and diffusion-weighted imaging movement for all subjects. Gender and age (in 5-year range brackets) were entered as binary dummy-codes, and data on height (cm) and weight (kg) were provided up to the first decimal figure. Heart rate data were collected during resting-state scans using BIOPAC MP150 acquisition system (BIOPAC Systems Inc., Goleta, CA, USA) and the acquisition software AcqKnowledge (Version 4.0, BIOPAC Systems Inc.), and the systole and the diastole signal at the brachial artery of the left arm were each used as covariates. Mean FD values during the resting-state acquisition and mean relative movement parameters during the diffusion image acquisition were also entered as covariates. Third, the covariate matrix was regressed out from both the functional–structural hybrid ICA components and the emotion regulation tendency PCA components. Fourth, CCA (*cancorr* function in Matlab) was run 10 000 times with the emotion regulation tendency PCA components randomly permuted across subjects each time. This formed the null distribution of CCA results, on which the non-parametric significance of the true CCA result could be tested. Lastly, the true CCA result was tested for significance with the $p < 0.05$ threshold after multiple test correction.

Control analyses

To account for possible alternate explanations for our results, we carried out multiple control analyses to test if the results were driven by (1) the functional connectome, (2) the structural connectome, or (3) the pure amount of data in the functional and

structural connectome. Details can be found in the online Supplementary Information.

External validation on transdiagnostic adolescent data

Based on prior literature that emphasize the role of adolescence in development of emotion regulation tendencies and psychopathology (Ahmed et al., 2015; Casey et al., 2008; Lee et al., 2014; Silvers, 2022; Thompson, 1991), the HBN dataset was used to probe if the results of our CCA analyses were generalizable to adolescent subjects with varying psychiatric diagnoses. As a direct correlate of emotion regulation tendency, we inspected coping strategies from the Children's Coping Strategies Checklist – Revised (CCSC-R1; Ayers et al., 1989). We additionally probed experience of positive affect as a possible consequence of emotion regulation, gauged by the Positive And Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988).

First, adolescent subjects with psychiatric diagnoses were selected from the HBN dataset Releases 7 through 10. Excluding subjects with insufficient data, no diagnosis, or with head movement above 0.2 mm in mean FD, the final sample consisted of 93 adolescents aged 11–19 years (34 females; mean age 14.39 ± 2.12). The sample was fully transdiagnostic as the adolescents were diagnosed with at least one psychiatric illness. According to diagnoses, the adolescents were further categorized into internalizing disorder ($n=38$; Generalized Anxiety Disorder, Major Depressive Disorder, Obsessive-Compulsive Disorder, Bulimia Nervosa, Persistent Depressive Disorder, Social Anxiety, and Specific Phobia), externalizing disorder ($n=2$; Conduct Disorder-Childhood-onset type and Alcohol Use Disorder), and neurodevelopmental disorder ($n=53$; ADHD-Combined Type, ADHD-Inattentive Type, Autism Spectrum Disorder, Borderline Intellectual Functioning, Intellectual Disability, Language Disorder, and Learning Disorder).

Functional connectomes of the adolescents were constructed following procedures reported in the online Supplementary Information. External validation was carried out by calculating network scores to explore the generalizability of the originally found network. We adopted this approach to discover a generalizable network model of emotion regulation tendencies that can aid further research without having to collect extensive emotion regulation tendency data or construct computationally expensive structural connectomes every time. One notable example is the sustained attention network model (Rosenberg et al., 2016), which has been leveraged to uncover novel findings pertaining to the nature of attention and related constructs – all based on a network predefined from a discovery sample (Jangraw et al., 2018; Kardan et al., 2022; Rosenberg et al., 2020). Nonetheless, as it is critical to also establish the replicability of our findings, we also constructed the structural connectomes and employed the same CCA framework in the adolescent dataset as described in the online Supplementary Information. Moreover, although not the primary aim of the validation analyses, we sought to confirm that the structural network found in the young adult dataset was also generalizable. We therefore calculated the structural network score by applying the methods described above to the structural connectomes of the adolescents and tested it for behavioral relevance.

We calculated the composite functional network score by first multiplying the weights of the final composite functional network from the young adult dataset with the functional connectomes of each subject in the adolescent dataset, and then aggregating the absolute values across the entire connectome to find single-value scores for each individual. These network scores would be higher

for subjects with stronger positive and negative connections across the composite functional network, and lower for subjects with overall weaker connections across the network. Notably, because individuals with stronger connections but with opposite signs (e.g. values of 3 and -2 for subject A and -3 and 2 for subject B) would be assigned the same absolute sum score (e.g. score of 5 for both subjects), we additionally calculated a positive and negative network score for each individual by aggregating across all positive or negative values only.

Then, Pearson correlations were conducted between these composite functional network scores and positive affects score and coping tendency score. Positive affect score was derived from 10 questions from the PANAS scale where subjects are prompted to answer the extent to which they generally feel a given emotion (e.g. 'Interested', 'Excited', 'Strong') on a 5-point Likert scale (PANAS; Watson et al., 1988). Coping tendency score was defined as the first principal component of the 13 coping strategies from the CCSC scale, which was found sufficient by the same criteria described above (Lüdecke, Ben-Shachar, Patil, & Makowski, 2020), explaining 46.0% of variance from the scale. Additionally, we have examined the relevance of our network feature with regards to psychiatric symptoms from the Child Behavior Checklist (CBCL; Achenbach, 1991).

Because the composite functional network absolute sum score was positively correlated with both behavioral measures, we also carried out a path analysis. In a path analytic framework, there is a direct path and an indirect path between an independent variable and a dependent variable. We reasoned that if the composite functional network can be replicated in the adolescent age, it will be correlated to the general experience of positive affect through promoting use of adaptive strategies. Therefore, a direct path from the composite functional network score to positive affect as well as an indirect path including the coping strategies principal component were tested. After finding evidence of indirect effects through linear modeling, bootstrapping of 5000 trials was conducted to measure the 95% confidence interval of the tests via the Causal Mediation Analysis package in R (Tingley, Yamamoto, Hirose, Keele, & Imai, 2014).

Results

Intersubject representational similarity analysis

The functional–structural hybrid connectome showed stronger correlation with emotion regulation tendencies than either the functional or structural connectome by itself, supported by various tests outlined in the online Supplementary Information.

Canonical correlation analysis

With three principal components of emotion regulation tendency and four independent components of functional–structural hybrid connectome as input, CCA resulted in one significant mode of correlation after 10 000 permutations ($r = 0.336$, $p = 0.025$ after correcting for multiple tests). The significant mode of correlation was between an adaptive-to-maladaptive gradient of emotion regulation tendency and the functional–structural network which mainly involved the functional and structural connections of the visual cortex. To elaborate, the three principal components of emotion regulation tendency with the weight of -0.125 , -0.835 , and -0.530 showed a canonical correlation with the four independent components of functional–structural hybrid connectome with the weight of 0.275,

Table 1. Composite emotion regulation tendency from the significant mode of canonical correlation

Emotion regulation strategies	Weight
Active coping	2.032
Positive reframing	1.316
Positive reappraisal	1.160
Humor	0.826
Refocus on planning	0.793
Reappraisal	0.784
Putting into perspective	0.758
Use of instrumental support	0.703
Positive refocusing	0.604
Venting	0.479
Use of emotional support	0.431
Religion	-0.010
Acceptance (COPE)	-0.194
Blaming others	-0.420
Suppression	-0.453
Self-distraction	-0.519
Acceptance (CERQ)	-0.690
Substance use	-0.975
Rumination	-1.059
Denial	-1.239
Catastrophizing	-1.344
Self-blame (CERQ)	-1.464
Self-blame (COPE)	-1.517

The 23 emotion regulation strategies are shown ordered by their canonical correlation weight.

0.359, -0.940 , and -0.025 . Each of these components, multiplied by their weights, was summed to create a comprehensive brain–behavior correlation that is interpretable.

As a result, the composite emotion regulation tendency mode revealed an adaptive-to-maladaptive gradient with active coping, positive reframing, and positive reappraisal on one end, and self-blame (both COPE and CERQ) and catastrophizing on the other (Table 1). The composite functional–structural hybrid model had pronounced functional connections concentrated in the motor network and the visual networks (Fig. 2a) as well as structural connections most heavily involving the subcortical–cerebellum network and the default mode network (Fig. 2b). In detail, the adaptive-to-maladaptive emotion regulation tendency gradient (1) negatively covaried with functional connections in the default mode network and the subcortical–cerebellum network, (2) positively covaried with functional connections involving the motor network and the visual networks, (3) negatively covaried with structural connections in the subcortical–cerebellum network and the default mode network, (4) positively covaried with structural connections among the motor network and the visual networks.

Control analyses

The results of the control analyses described in the online Supplementary Information ensured that the CCA results were

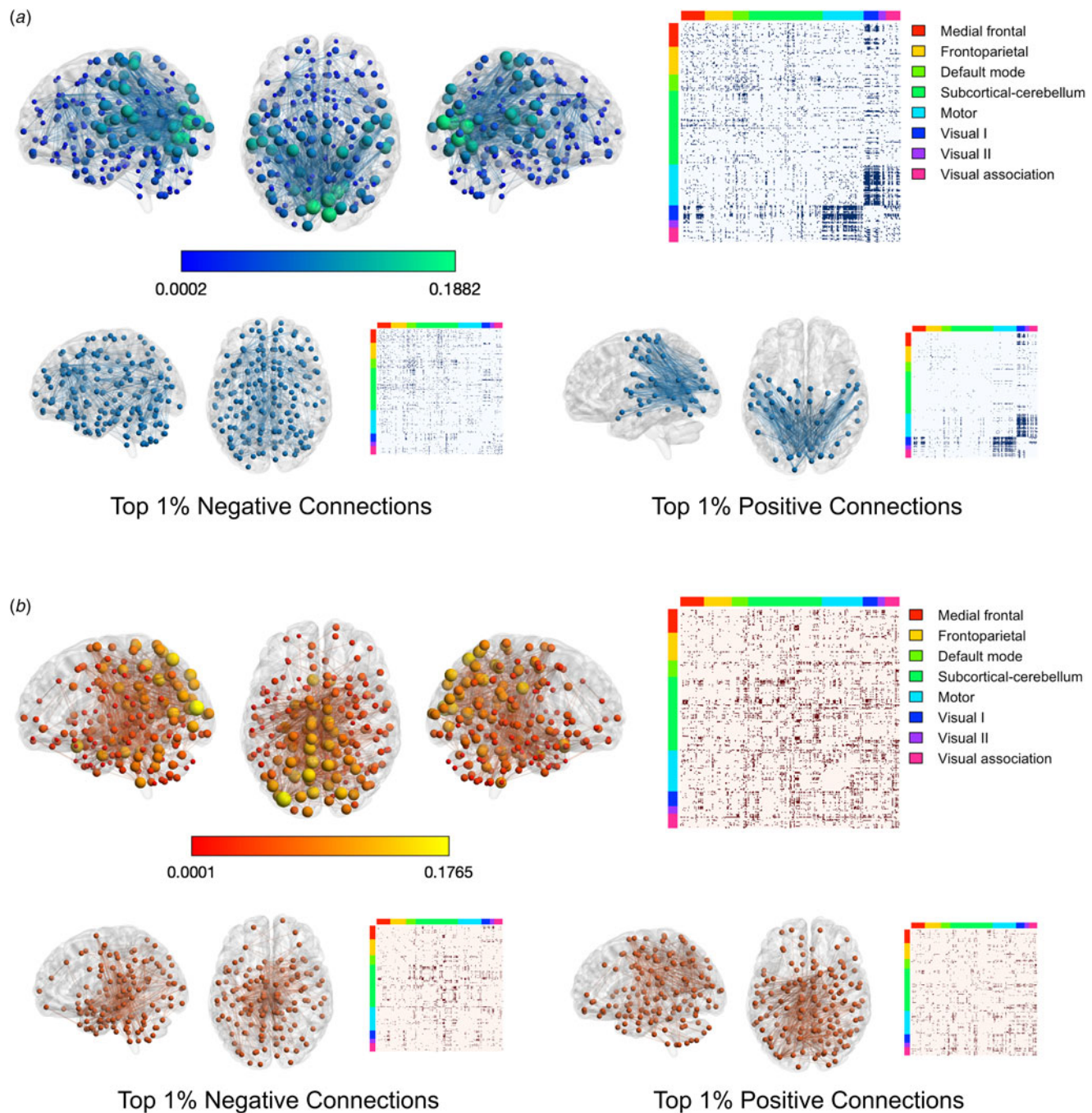


Figure 2. Composite functional and structural network properties from the significant mode of canonical correlation. (a) Functional connections of the significant mode reveal concentration in the motor network and the visual networks. Top left figure denotes important nodes with size and color scaled by eigenvector centrality, a metric of graph centrality emphasizing nodes that are connected to other nodes with high eigenvector centrality that was calculated via Brain Connectivity Toolbox (Rubinov & Sporns, 2010). Important connections that carry top 1% weight in either the positive or the negative direction are also shown. The same important connections are signified on the top right 268×268 matrix, ordered by eight network labels (Shen et al., 2013). Bottom left and right figures dissociate the connections that either positively covaries or negatively covaries with the adaptive-to-maladaptive gradient of emotion regulation tendency. (b) Structural connections of the significant mode illustrate relevance of subcortical-cerebellar structures and default mode network connections.

not solely dependent on (1) the functional connectome, (2) the structural connectome, or (3) the pure amount of data in the functional and structural connectome.

External validation on transdiagnostic adolescent data

We focused on the first principal component of the coping strategies that roughly followed an adaptive-to-maladaptive spectrum

from 'Cognitive Decision Making' and 'Optimistic Thinking' to 'Repression' and 'Avoidant Actions' (Table 2; accounting for 46.0% variance) and named this component the coping tendency score. The composite functional network score was positively correlated with this coping tendency score ($r = 0.236$, $p = 0.023$) as well as positive affect from the PANAS scale ($r = 0.270$, $p = 0.009$; Fig. 3a). Aside from the network absolute sum score used above, network positive value score and network negative

Table 2. One principal component of Children's Coping Strategy Checklist

Coping strategies	Weight
Direct problem solving	0.326
Control	0.325
Positivity	0.314
Cognitive decision making	0.312
Optimism	0.310
Support sought from peers	0.298
Seeking understanding	0.298
Wishful thinking	0.256
Support sought from mother/father/guardian	0.243
Avoidant actions	0.225
Support sought from siblings	0.221
Support sought from other adults	0.214
Religion	0.176
Repression	0.133

The 14 coping strategies are shown ordered by their principal component weight.

value score were also tested for correlation with positive affect and coping tendency score. The positive network score was positively correlated with coping tendency score ($r = 0.294$, $p = 0.004$) and positive affect ($r = 0.242$, $p = 0.019$), while the negative network score was not significantly correlated with coping tendency score ($p = 0.511$) or positive affect ($p = 0.153$). Despite the positive network score carrying heavier behavioral relevance, the absolute sum score was used for further analyses because it is conceptually more in line with our network property in which positive and negative connections work together. The structural network score was not significantly correlated to positive affect ($p = 0.711$) or the coping tendency score ($p = 0.114$). The functional composite network score was not correlated with the internalizing symptom score ($p = 0.193$) or the externalizing score ($p = 0.991$), and the same was true for the structural composite network score ($p = 0.560$; $p = 0.561$).

In the following path analysis, the effect of the composite functional network score on positive affect was fully explained by the coping tendency score (Fig. 3b). In other words, the path from the composite functional network score to coping tendency score ($B = 0.0005$, $p = 0.023$) and the path from coping tendency score to positive affect were both significant ($B = 1.6218$, $p < 0.001$), but the direct effect on positive affect from the composite functional network score ($B = 0.0020$, $p = 0.009$) was not significant anymore when considering the indirect path that included the coping tendency score ($B = 0.0012$, $p = 0.083$). Significance testing through 5000 trials of bootstrapping revealed that the indirect path was significant (indirect effects = 0.0008, 95% CI [0.00005–0.0016]), whereas the direct path was not (direct effects = 0.0012, 95% CI [–0.0001 to 0.0026]).

Discussion

In our study, IS-RSA and CCA have each demonstrated that individual differences in emotion regulation tendency can be gleaned from whole-brain functional and structural connections. First, IS-RSA showed that emotion regulation tendency is best captured

when investigating both the structural and the functional connectome. Second, CCA results associated an adaptive-to-maladaptive gradient of emotion regulation tendency with a network feature conveying noticeable contributions from motor network and visual network functional connections as well as default mode network and subcortical–cerebellum network structural connections. Together, our study advances the theoretical understanding of emotion regulation tendency by elucidating its neural foundations while also confirming multiple streams of clinical research on the transdiagnostic psychopathology factor.

First, our results provide affirmation as well as novel insights on the theoretical models of affective processes. Connections involving the visual network regions, motor network regions, and cerebellar regions, which are traditionally placed at the lowest end of the regulation hierarchy model (Smith & Lane, 2015), were most strongly correlated with the adaptive-to-maladaptive gradient of emotion regulation tendency. This implies that (1) individual differences in the network organization that oversees the somatosensory stages of emotion generation may cause downstream differences in voluntary emotion regulation tendency, or (2) adaptive-to-maladaptive emotion regulation tendency may be embedded in low-level networks. The former explanation is in line with the hierarchical models of emotion regulation, where the low-level functionalities of the human brain related to basic body states and movements form the building blocks of emotion generation that lead to downstream identification, choice, and implementation of regulatory goals (Gross, 2014; Sheppes et al., 2015; Smith & Lane, 2015). Within such frameworks, our result may indicate that individual differences in low-level processes that are ostensibly devoid of affective value can bring on differences in habitual emotion regulation tendency down the line. The latter, on the other hand, relates to relatively recent findings that affective information such as valence (Bo et al., 2021; Kragel et al., 2021; Xu et al., 2023), fear learning (Li & Keil, 2023; You, Brown, & Li, 2021), distinct emotion categories (Kragel, Reddan, LaBar, & Wager, 2019), and even emotion down-regulation (Bo et al., 2023) is processed at the rudimentary visual perception stage. Building on such empirical evidence, we may speculate that early stages of affective experience may already contain information on regulatory tendency that spans an adaptive-to-maladaptive gradient. Though both accounts are plausible, our study demonstrates a clear link between low-level network features and high-level emotion regulation tendencies, speaking to the importance of conceptualizing the emotion regulation process as an integrated and dynamic system instead of a segregated and unidirectional system that follows a strict hierarchy (Pessoa, 2017; Underwood, Tolmeijer, Wibroe, Peters, & Mason, 2021).

Second, our network property also aligns well with a burgeoning literature on neural correlates of the transdiagnostic factor of psychopathology. On one hand, adaptive or maladaptive emotion regulation tendency has been consistently implicated with multiple psychopathology symptoms across diagnoses (Aldao et al., 2010; Eftekhari et al., 2009; Fernandez et al., 2016; Naragon-Gainey et al., 2017). On the other, studies aiming to locate the neural basis of general psychopathology have also been accumulating evidence supporting the involvement of regions and networks prominently featured in the present data. In detail, while abnormal connectome-wide functional connectivity of the visual association cortex and default mode network have been found to be indicative of transdiagnostic psychopathology features (Doucet et al., 2020; Elliott et al., 2018; Whitfield-

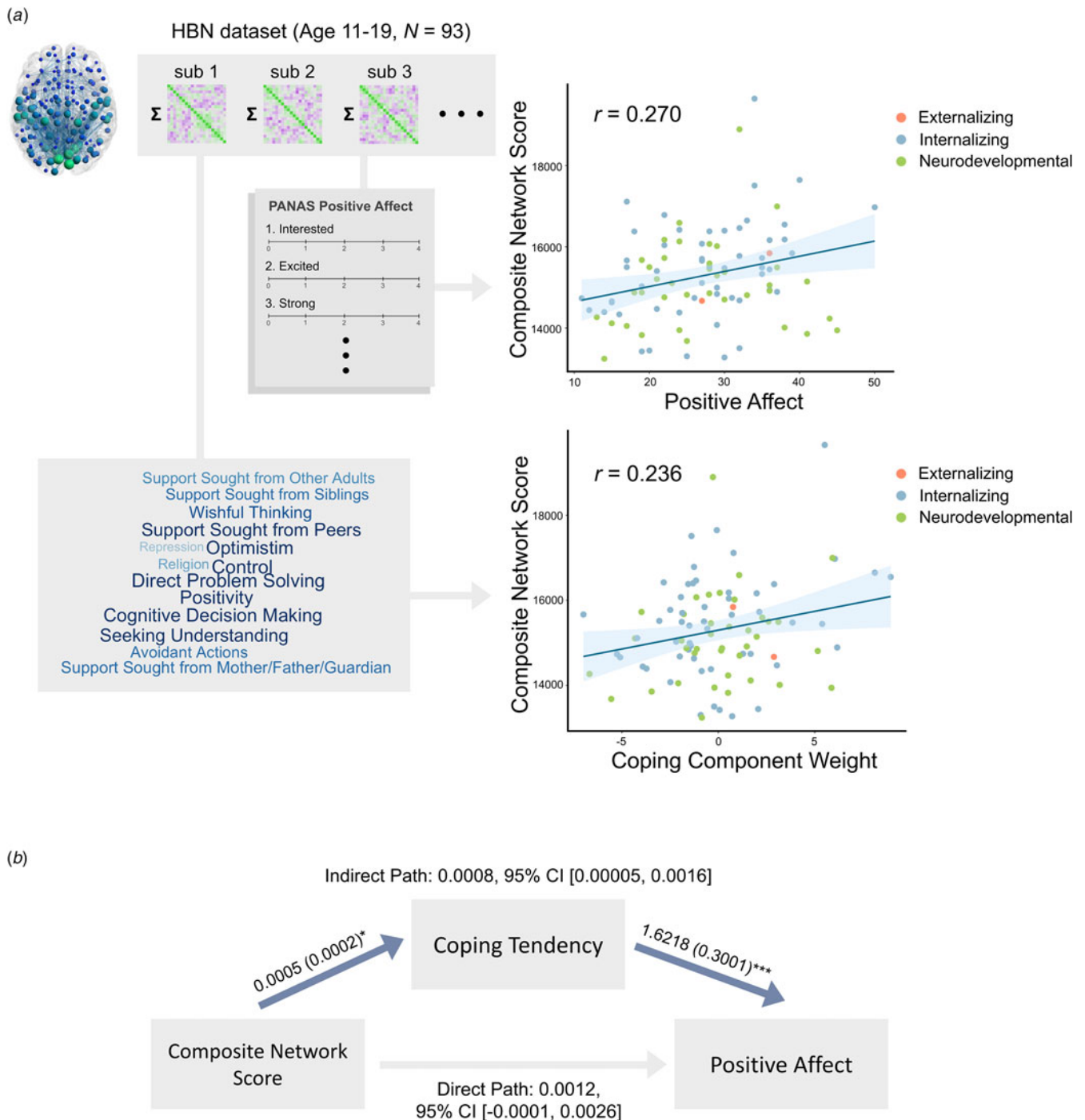


Figure 3. External validation on a transdiagnostic adolescent dataset. (a) Composite functional network score is positively correlated with positive affect and coping tendency. Composite functional network score was calculated by multiplying the weights from the network property of the young adult dataset with the connectomes of the adolescents and then finding the sum of the absolute values across each connectome. Positive affect was assessed via PANAS scale, and coping tendency score was defined from extracting the first principal component of the CCSC Questionnaire. The adolescents were categorized into internalizing, externalizing, or neurodevelopmental disorders according to their diagnoses, indicated as colors of dots on scatterplots. (b) The effect of the composite functional network score on positive affect is fully explained by the coping tendency in transdiagnostic adolescents. 95% Confidence intervals that do not include zero signify statistical significance. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Gabrieli & Ford, 2012), functional connectivity disruptions of somatosensory-motor network both within and across networks have been documented as transdiagnostic signatures of psychopathology (Kebets et al., 2019). Moreover, general psychopathology features related to structural connectivity and gray matter

volume alterations of cerebellar circuitry and visual cortices have been demonstrated and replicated with large transdiagnostic datasets (Moberget et al., 2019; Romer et al., 2018, 2021b). Although these studies did not explicitly connote emotion regulation tendency as a transdiagnostic risk factor, maladaptive

regulatory goals have been pointed out as the primary consequence of such transdiagnostic neural aberrations (Romer, Hariri, & Strauman, 2021a). To sum up, our network property that is correlated with an adaptive-to-maladaptive gradient of emotion regulation tendency resembles previous findings that highlight brain-wide functional and structural connectivity anomalies as signatures of transdiagnostic psychopathology.

Finally, our composite network related to emotion regulation tendency was externally validated in a transdiagnostic sample of adolescents aged 11–19. In detail, adolescents with stronger signatures of the composite functional network from the young adult sample had higher general experiences of positive affect through more frequent use of adaptive coping strategies such as ‘Direct Problem Solving’ or ‘Positivity’. As emotion regulation tendencies that start to be fully fleshed out in adolescence can act as risk or resilience toward psychopathology, locating a neural marker of emotion regulation tendency has implications for preventive and early intervention (Cracco, Goossens, & Braet, 2017; Silvers, 2022; Young, Sandman, & Craske, 2019). It is also noteworthy that such effects were found in a sample of adolescents with distinct psychiatric diagnoses that span internalizing, externalizing, and neurodevelopmental disorders. One potentially fruitful avenue of translational research is to target our network related to emotion regulation tendency as a neural marker of resilience in pediatric psychiatric patients that may be associated to positive affect through use of more adaptive coping strategies, which in turn could mitigate symptoms (Davis & Suveg, 2014; Gilbert, 2012).

Together, our results imply that the whole-brain network that was extracted from young adults that was linked to an adaptive-to-maladaptive spectrum of emotion regulation tendencies starts to take shape as early as adolescence. That said, carrying out the identical CCA analyses on the adolescent dataset produced a network that had different configurations of important connections though the connections similarly involved the visual networks and the subcortical–cerebellar network. At least three possible explanations exist for this. First, the specific configurations of connections critical to the adaptive-to-maladaptive emotion regulation tendency may manifest differently for individuals at distinct developmental stages or mental health states. Second, the sub-critical connections in the network may cumulatively explain the adaptive-to-maladaptive emotion regulation tendency, given the fact that the young adult network was generalized to the adolescents despite differences in their most important connections. Third, the CCSC scale may not have captured the full extent of the adaptive-to-maladaptive emotion regulation tendency spectrum that was originally acquired from three different questionnaires. While these possibilities remain open, future work could leverage the generalizable network found in our study to explore such outstanding questions.

There are still limitations to our study. First, our network feature that represents an adaptive-to-maladaptive emotion regulation tendency was defined at a whole-brain scale, but multiple subsystems could theoretically be present within this network feature. This prospect adheres to a phenomenon well-documented regarding the default mode network where multiple functionally segregated subsystems were found to be embedded within the network (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Buckner & DiNicola, 2019). Such a possibility also aligns with our ICA results where robust independent components reached a plateau at four and then at 16, which could imply that the four components were recapitulated as fragmented

representations. Although our study was not designed to pinpoint individual differences at such minute scale, whether the fine-grained subsystems within our network related to emotion regulation tendency could aid in parsing heterogeneity in emotion regulation and psychopathology is a question that remain unexplored. Second, our measure of emotion regulation tendency depends on cross-sectional self-report questionnaires, which may not thoroughly cover the dynamic nature of emotion regulation tendency that persist throughout daily life (Lincoln, Schulze, & Renneberg, 2022). That said, we used a conglomerate of three different emotion regulation strategy questionnaires to extract coherent patterns from expansive repertoires of strategies. Future studies could use ecological momentary assessment to track multiple features of emotion regulation such as frequency or flexibility in relation to the neural foundations of emotion regulation (Colombo et al., 2020). Third, females were underrepresented in our main sample of young adults (<30%). Despite including gender as a covariate in the main analytic framework, our analyses were likely ill-equipped to determine potential effects of gender, which have been reported to exist in diverse facets of emotion regulation (Nolen-Hoeksema, 2012). We therefore remain cautious in terms of making claims about the generalizability of our results across genders. Collecting ample sample size across genders would be a crucial goal for future studies, as gender-related differences in neural activity have also been documented in the traditional cortical–subcortical pathways (Mak, Hu, Zhang, Xiao, & Lee, 2009). Fourth, the relatively low loadings on the emotion regulation tendency principal components in the young adult sample as well as the coping strategy principal component in the adolescent sample suggests that the strategies are not as highly correlated as expected. While employing as many variables as possible and preserving the multivariate nature of the emotion regulation strategies could lead to more exhaustive explanations of the possible brain–behavior relationships, we chose to adhere to parsimonious models that would prevent overfitting while maximizing generalizability. That said, we note that replacing the single coping tendency component with the first three principal components increased the effect in the generalization analyses (i.e. better model fit), accounting for the full variability of the emotion regulation tendencies and the coping strategies without any dimensionality reduction may yield stronger and clearer effects. Though comparing the performance between similar multivariate methods falls outside the aim of the current study, more refined dimensionality reduction or regularization methods that retain the most amount of meaningful variability such as domain-driven dimension reduction may grant supplementary insights (Liu, Whitaker, Smith, & Nichols, 2022; for comparison among methods, see also Mihalik et al., 2022). Lastly, only the functional composite network score was generalized to the transdiagnostic adolescent sample, and not the structural composite network score. This may indicate that the functional and structural connectomes in the transdiagnostic adolescent sample are not coupled in an identical manner as the young adults, and also that only the functional network is generalizable to the coping strategies and positive affect of the adolescents. It is noteworthy that previous literature suggest that adolescence may be a time that structural–functional coupling goes through cortex-wide changes to support functional development (Baum et al., 2020; Park et al., 2022). However, formal tests using a healthy adolescent sample and a young adult sample with psychiatric symptoms may need to take place to fully flesh out such interpretations.

Conclusion

Our study demonstrates the existence of a network related to an adaptive-to-maladaptive gradient of emotion regulation tendency that span the entire brain of functional and structural connections. Elucidating the topology of this network system can inform existing theories on affective experiences while also expanding our understanding of the neural mechanisms underlying pediatric psychopathology. Together, our findings complement theory-driven neural schematics of emotion regulation with a network feature identified through a data-driven approach.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0033291724000473>

Data availability. The MPI-LEMON dataset (<https://www.nitrc.org/projects/mpilmbb>) (<https://doi.org/10.18112/openneuro.ds000221.v1.0.0>) is publicly available. The HBN dataset is also publicly available (http://fcon_1000.projects.nitrc.org/indi/emi_healthy_brain_network/). Analytical pipeline and scripts have been deposited in GitHub (<https://doi.org/10.5281/zenodo.7885176>).

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