Association between emotional intelligence and effective brain connectome: A large-scale spectral DCM study

Sahil Bajaj,a,∗William D. S. Killgore,a

a Social, Cognitive and Affective Neuroscience Laboratory (SCAN Lab), Department of Psychiatry, College of Medicine, University of Arizona, Tucson, AZ, USA
b Multimodal Clinical Neuroimaging Laboratory (MCNL), Center for Neurobehavioral Research, Boys Town National Research Hospital, 14015 Flanagan Blvd. Suite #102, Boys Town, NE 68010, USA

A B S T R A C T

Introduction: Emotional Intelligence (EI) is a well-documented aspect of social and interpersonal functioning, but the underlying neural mechanisms for this capacity remain poorly understood. Here we used advanced brain connectivity techniques to explore the associations between EI and effective connectivity (EC) within four functional brain networks.

Methods: The Mayer-Salovey-Caruso Emotional Intelligence Test (MSCEIT) was used to collect EI data from 55 healthy individuals (mean age = 30.56±8.3 years, 26 males). The MSCEIT comprises two area cores – experiential EI (T1) and strategic EI (T2). The T1 core included two sub-scales – perception of emotions (S1) and using emotions to facilitate thinking (S2), and the T2 core included two sub-scales – understanding of emotions (S3) and management of emotions (S4). All participants underwent structural and resting-state functional magnetic resonance imaging (rsfMRI) scans. The spectral dynamic causal modeling approach was implemented to estimate EC within four networks of interest – the default-mode network (DMN), dorsal attention network (DAN), control-execution network (CEN) and salience network (SN). The strength of EC within each network was correlated with the measures of EI, with correlations at p<0.05 considered as significant.

Results: There was no significant association between any of the measures of EI and EC strength within the DMN and DAN. For CEN, however, we found that there were significant negative associations between EC strength from the right anterior prefrontal cortex (RAPFC) to the left anterior prefrontal cortex (LAPFC) and both S2 and T1, and significant positive associations between EC strength from LAPFC to RAPFC and S2. EC strength from the right superior parietal cortex (SPC) to RAPFC also showed significant negative association with S4 and T2. For the SN, S3 showed significant negative association with EC strength from the right insula to RAPFC and significant positive association with EC strength from the left insula to dorsal anterior cingulate cortex (DACC).

Conclusions: We provide evidence that the negative ECs within the right hemisphere, and from the right to left hemisphere, and positive ECs within the left hemisphere and from the left to right hemisphere of CEN (involving bilateral frontal and right parietal region) and SN (involving right frontal, anterior cingulate and bilateral insula) play a significant role in regulating and processing emotions. These findings also suggest that measures of EC can be utilized as important biomarkers to better understand the underlying neural mechanisms of EI.

1. Introduction

Emotional intelligence (EI) refers to the competencies or abilities of individuals to effectively monitor, understand and process emotional information, and further use these abilities to guide one’s thinking, actions, and to solve social and emotional problems (Mayer et al., 2001). Trait EI (TEI) and ability EI (AEI) are the two predominant approaches to measure EI. TEI is typically measured through self-reported questionnaires and has been reported to be helpful in predicting the quality of social interactions (Lopes et al., 2005). AEI is measured through the performance of individuals during specific cognitive tasks and has been reported to be helpful in predicting life satisfaction (Gannon and Ranzijn, 2005) and social competence (Brackett et al., 2006). The phenomenon of EI is distinct from other human characteristics such as temperament and measured cognitive intelligence, and has been proposed as its own form of intelligence (Mayer et al., 2001). One aspect of EI involves affective self-regulation, which is a very relevant component to physical health. For example, individuals who are unable to effectively control or suppress their negative emotions such as anger and hostility are more susceptible to heart related diseases (Vlachaki and Maridaki Kassotaki, 2013; Vlachakis et al., 2018), abnormal blood pressure (Brownley et al., 1996; Zysberg and Raz, 2019) and even cancer (Gross, 1989; Mirzaei et al., 2019; Rey et al., 2013). Therefore, it becomes important to stay emotionally strong in terms of intelligent and appropriate emotional self-management and expressions to avoid developing negative health consequences. Moreover, EI can also be the key to the future. Experts believe that in the near future, artificial intelligence (AI) may begin to take the place of humans in the workplace. However, factors such as meaningful human connection, positive working atmosphere, creativity and productivity can only be created by growing EI.

∗ Corresponding author at: Multimodal Clinical Neuroimaging Laboratory (MCNL), Center for Neurobehavioral Research, Boys Town National Research Hospital, 14015 Flanagan Blvd. Suite #102, Boys Town, NE 68010, USA.
E-mail address: sahil.bajaj@boystown.org (S. Bajaj).

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through social skills, self-awareness, empathy and emotional regulation. In the job market as well, prospective employers are not only attentive towards an individual’s education or business skill set, but also towards empathy, ability to work with others, integrity, an individual’s abilities to monitor their own and others’ emotional responses, and even guide or influence others’ emotions to achieve positive outcomes.

Despite the known significance of EI across a variety of fields, the underlying neural mechanisms explaining EI have yet to be clearly established. Bar-On and colleagues proposed a model suggesting that a hypothesized emotional decision-making network (Damasio, 1996), known as the Somatic Marker Circuitry (SMC), can be used to understand the underlying neural substrates comprising EI (Bar-On et al., 2003; Bechara and Damasio, 2005). The Somatic Marker Hypothesis (SMH) explains the phenomenon of learning from emotional experiences by using somatically processed experiential knowledge to make decisions (Damasio, 1994). As per the SMH, this phenomenon involves three primary brain structures, including the amygdala (AMG), insula (INS) and ventromedial prefrontal cortex (vmPFC), which play crucial roles in the development of these somatic signals. In addition, the anterior cingulate cortex (ACC) may also play a significant role in regulating emotions (Etkin et al., 2011). Functional neuroimaging studies showed significant negative association between measures of EI from the Mayer-Salovey-Caruso Emotional Intelligence Test (MSCEIT) – an ability measure of EI (Mayer et al., 2002), and activation within the prefrontal cortex (PFC) (Reis et al., 2007). Scores on the Bar-On Emotional Quotient Inventory – a trait measure of EI have also been reported to be negatively correlated with activation within the vmPFC and INS (Killgore and Yurgelun-Todd, 2007a). Structural neuroimaging studies also showed significant positive associations between measures of EI and grey-matter volume (GMV). Killgore and colleagues reported a significant positive association between scores on MSCEIT and greater GMV of the left INS, as well as between strategic EI scale of MSCEIT and GMV of the left vmPFC and INS (Killgore et al., 2012). However, in that study, the investigators did not report significant role of AMG in predicting the measures of EI. Another study based on the analysis of GMV correlates across perceived EI showed that lower scores on mood repair were associated with lower volume in the left ACC (Koven et al., 2011). Damage to selective brain structures that are crucial in processing social information, e.g., within the frontal and parietal lobes comprising the right orbitofrontal cortex (OFC) and the left inferior and superior parietal cortices (IPC/SPC), have been reported to be associated with impairments in EI (Barbay et al., 2014). Cerebral lateralization also plays a crucial role in processing emotions. One theory, known as the Valence-Specific Hypothesis (VSH), suggests that the left cerebral hemisphere is more specialized for processing positive emotions while the right hemisphere tends to dominate for processing of negative emotions (Adolphs et al., 2001). A second theory, known as the Right Hemisphere Hypothesis (RHH), suggests that the right cerebral hemisphere tends to be dominant for processing all the emotions, regardless of affective valence (Borod et al., 1998). In a study by Killgore and colleagues, it was shown that VSH and RHH are not necessarily mutually exclusive, both may both fit the data under certain circumstances, suggesting the simultaneous operation of independent underlying neural mechanisms comprising a set of complex and diverse emotion processing networks (Killgore and Yurgelun-Todd, 2007b). The preceding findings based on the associations between measures of EI and underlying neural effort suggest that higher EI may require functional neural effort within a specific hemisphere. These findings also support the notion of potential existence of a diverse set of brain regions explaining the phenomenon of EI and suggest that the complex intra- and inter-hemispheric functional interactions among these regions may be associated with the measures of EI.

Previously, total scores on MSCEIT have been reported to be unrelated to functional connectivity of the anterior default-mode network (DMN), but negatively related to functional connectivity within the posterior DMN - which involved emotion processing structures such as the AMG, INS and OFC, as well as within the basal ganglia/limbic network – which again involved emotion processing regions such as the vmPFC, INS, AMG and lateral OFC (Killgore et al., 2017). Here, functional connectivity between regions that are less commonly ascribed to the processing of emotions, such as the medial temporal pole, middle temporal cortex (MTC), hippocampus, prefrontal/tertiary cingulate cortex (PCC) and SPC was also negatively correlated with total MSCEIT. Another functional connectivity study showed that (i) higher scores on a trait EI intrapersonal scale was associated with stronger anticorrelation between the medial PFC and anterior dorsolateral PFC (DLPFC), (ii) higher scores on the trait EI interpersonal scale were positively associated with stronger connectivity between the medial PFC and lingual gyrus, and (iii) total trait EI was positively associated with stronger connectivity between the medial PFC and PCC, as well as between the left anterior INS and middle right DLPFC (Takeuchi et al., 2013). These findings suggest a reliable association between measures of EI and the strength of functional connectivity between emotionally related regions of interest. However, more advanced brain connectivity techniques still need to be employed to better understand the underlying neural mechanisms displaying effective interactions among key brain areas associated with EI.

Interestingly, a number of options are available for effective connectivity (EC) analysis, including network-wise inferences such as the directed functional connectivity (Granger causality, GC) approach, the structural equation modeling (SEM) approach and the dynamic causal modeling (DCM) approach, as well as pairwise inferences such as pairwise likelihood ratios (Bielczyk et al., 2019). Network-wise inferences usually do not pose any constraints on the connectivity structure of nodes of interest. Methods such as GC and SEM also do not require one to define a specific hypothesis or pose any limit to the size of the network of interest. On the other hand, traditional DCM (based on state-space models) requires a limited number of predefined causal structures of networks – in terms of models (model space) and uses a model comparison tool to determine the ‘winning’ model within the space (Friston et al., 2003). Recent advancements in DCM – implemented in spectral DCM (spDCM) makes it possible to model resting-state functional MRI (fMRI) data and invert large-scale models (~ 32–64 regions) with low computational complexity (Razi et al., 2017). Therefore, spDCM can be used within a large model space when there is a lack of prior knowledge, and predefined hypotheses cannot be limited within a narrow range. On the other hand, the use of the GC approach to fMRI data has been a topic of debate recently, where signal non-stationarity and time-lag in fMRI data have been broadly discussed to indicate that they do not meet the underlying assumptions of GC approach (Stokes and Purdon, 2017). However, prior work on validation of GC also shows that despite such limitations, GC is still applicable for fMRI data (Roebroeck et al., 2005; Seth et al., 2013), and both GC and DCM can be reliable for resting-state fMRI data (Bajaj et al., 2016). Second, SEM relies on expressing the time-series data of every region of interest within a network as a linear combination of all the time-series and with an addition of noise. Therefore, causal inferences made from SEM rely on a number of assumptions, including criteria of omitted variables, lower-order model components and models of fitting. Moreover, both GC and SEM are resilient to confounds only within an isolated system with all variables of interest taken into account. Third, the causal inference from the pairwise method involves assumptions on the pair of nodes only, i.e., it does not involve any assumptions on the global patterns of connectivity at the network-level. Here, the overall uncertainty associated with causal inference at a network level is larger, and it grows as the number of regions increases within a network. A more detailed comparison of various brain connectivity techniques can be found in one of the recent studies by Bielczyk and colleagues (Bielczyk et al., 2019). Therefore, we believe that given the current framework of our data structure and exploratory goals of our study, the spDCM approach, which is one of the latest and most popular approaches for causal inference, is more suitable than any other approaches.
In our current study, we implemented the spDCM approach to estimate the strength of EC within four resting-state networks of interest – the default mode network (DMN), dorsal-attention network (DAN), control-execution network (CEN), and salience network (SN) (Raichle, 2011). The exploratory focus of the present study is to determine the association between measures of EI and EC within each of these four resting-state networks involving both intra- and inter-hemispheric interactions. We expect a significant association between measures of EI and the EC strength among regions which are known to process information related to emotions, such as insula and areas within the PFC in particular.

2. Materials and methods

2.1. Participants

Fifty-five healthy individuals aged between 18-45 years (all righthanded with mean age = 30.56±8.3 years, 26 males) were recruited from the New England area and screened via a comprehensive telephone interview. Detailed demographics data are provided in Table 1. Individuals with no history of psychiatric, neurological, or significant medical problems, current use of psychotropic medications, or current use of illicit substances were included. Participants were all primary native English speakers. All of the participants provided written informed consent prior to enrollment. The study protocol was approved by the Institutional Review Boards of McLean Hospital and Partners Healthcare, and the U.S. Army Human Research Protections Office. Other behavioral data and structural estimates from this sample have been reported elsewhere (Bajaj et al., 2019, 2018, 2017; Bajaj and Killgore, 2020; Killgore et al., 2013), but the resting-state brain connectivity measures and their associations with measures of EI reported in this study are novel and have not been previously reported.

2.2. Data acquisition

2.2.1. Emotional intelligence (EI)

Leading theories of EI include trait, mixed, and ability models. Each of these approaches has practical and theoretical implications. For this project, we focused on EI as a set of abilities that can be measured via objective responses to emotion-related problems, an approach known as the Ability Model (Daus, 2006; Mayer et al., 2002). The construct of Ability EI was assessed by using one of the most prominent and widely used measures, the Mayer-Salovey-Caruso Emotional Intelligence Test (MSCEIT) (Daus, 2006; Mayer et al., 2002). This test consists of two area cores – emotional EI and strategic EI, which are each comprised of two branch scores. Experiential EI includes the branches of perception of emotion (S1) and using emotion to facilitate thinking (S2), while strategic EI includes the branches of understanding of emotion (S3) and management of emotion (S4) (Brackett and Salovey, 2006).

- Perception of emotion (S1) represents the ability to perceive emotions in oneself as well as in others, including objects, art, stories and music.
- Using emotion to facilitate thinking (S2) represents the ability to generate, use, and feel emotions to communicate/employ feelings.
- Understanding of emotion (S3) represents the ability to understand, combine and appreciate emotions to progress through relationship transitions.
- Management of emotion (S4) represents the ability to be open to feelings and modulate the feelings in oneself and others to effectively promote personal understanding.

As described in greater detail in the test manual (Mayer et al., 2002), each of the four branch scores is derived by summing the individual items that contribute to that branch based on consensus scoring, and then scaling the summed index score relative to the sex-based normative sample to obtain a scaled score with a mean of 100 and a standard deviation of 15. The overall experiential, strategic and total MSCEIT scores are represented by T1, T2 and T3 respectively. Essentially, each summary score (T1-T3) was calculated by summing the individual item scores for all items corresponding to that particular domain, then scaling the score to the sex-matched normative group. Specifically, the total Experiential score (T1) is the sum of all individual items for S1 and S2, scaled to the normative group. The total Strategic score (T2) is the sum of all individual items that comprise S3 and S4, scaled to the normative group. Finally, the total MSCEIT score is the sum of all items on the test, scaled to the normative group (Mayer et al., 2002). Mean scores and their corresponding standard deviations (SD) for each scale and sub-scale are reported in Table 1. Associations between MSCEIT sub-scales and scales for the present sample were calculated using Pearson’s correlation analysis. Brackett and Mayer showed that the full-test MSCEIT over a three week interval had a test-retest reliability of r(59) = 0.86 (Brackett and Mayer, 2003). The area scores reliabilities for experiential and strategic EI were reported to be 0.90 and 0.90 for consensus scoring and 0.88 and 0.86 for expert scoring respectively (Mayer et al., 2003).

2.2.2. Resting-state functional magnetic resonance imaging (MRI) and neuroanatomical data

Resting-state functional MRI and neuroanatomical data from all of the participants were recorded using a 3T Siemens TIM Trio whole-brain MR scanner. The scanner was located at the McLean Hospital Imaging Center. During both the scans, participants were instructed to remain still with minimum body movements. The resting-state scan lasted for 6 minutes. Participants were asked to keep their eyes open and to let their mind wander. Data were acquired using a T2*-weighted echoplanar imaging (EPI) sequence, which consisted of 180 frames (voxel resolution = 3.5 × 3.5 × 3.5 mm³, field of view (FOV) = 384 mm) with TR/TE/FA of 2000 ms/30 ms/90°. Neuroanatomical (T1-weighted) data were acquired using a 3D magnetization-prepared rapid acquisition gradient echo sequence which consisted of 128 sagittal slices (voxel resolution = 1.33 × 1 × 1 mm³, field of view (FOV) = 256 mm) with TR/TE/FA/inversion time of 2100 ms/2.25 ms/12°/1100 ms.

2.3. Data analysis

2.3.1. Image preprocessing

The current sample underwent initial image quality check in our previously published work (Killgore et al., 2017). During quality check, any subject who met any of the following two conditions was not included in the current sample: (i) if there was greater than one voxel motion in

| Table 1. Demographics and measures of EI. |
|------------------------------------------|
|        |  
| Total (N) | 55  |
| Males/Females (N) | 26/29 |
| Mean Age (SD) | 30.56 (8.3) |
| Mean Education (SD) | 15 (2.2) |
| Race (%) |  
| Caucasian | 67.3 |
| African American | 16.4 |
| Asian | 9.1 |
| Other | 3.6 |
| More than one | 3.6 |
| Mean MSCEIT (SD) |  
| Experiential EI |  
| S1 Perception | 105.76 (14.5) |
| S2 Facilitate | 105.33 (13.7) |
| T1 Total Experiential EI | 106.60 (14.9) |
| Strategic EI |  
| S3 Understand | 101.51 (11.6) |
| S4 Manage | 96.62 (8.6) |
| T2 Total Strategic EI | 99.20 (9.5) |
| Total EI |  
| T3 MSCEIT Total | 101.56 (11.7) |
any direction, or (ii) if the raw functional MRI data showed variations in image intensity across the axial planes (e.g. intensity rolling due to interactions of motion with radio-frequency pulses) (Killgore et al., 2017). Data were preprocessed using the default-pipeline implemented in CONN Toolbox (V.18.a) (https://www.nitrc.org/projects/conn) based on SPM12 (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/) in MATLAB R2018a (MathWorks, Inc., MA, USA). Standard preprocessing included functional realignment (all scans were registered and resampled to a reference image (first scan) using b-spline interpolation), slice-time correction (correction of temporal misalignment between different slices of the functional data), outlier identification and motion-correction (new reference image for functional data was created by averaging over all scans except potential outlier scans which were identified if the framewise displacement was above 0.9 mm or global signal change was above 5 standard deviations), direct segmentation and normalization (separate normalization of the functional and structural volumes to standard MNI-space and segmentation into grey matter, white matter, and CSF tissue classes), Gaussian spatial smoothing at 6 mm full width at half maximum, and band-pass filtering (0.008–0.09 Hz, default). During the direct segmentation and normalization step, data were also resampled with 2 mm isotropic voxels for functional data and 1 mm for structural data, using 4th order spline interpolation.

2.3.2. Networks and regions of interest (ROIs)

Our goal here was to compare EC findings associated with EI to past work on connectivity of large-scale networks. Therefore, to minimize network size, we selected the four dominant cognitive networks described previously as our networks of interest (Almgren et al., 2018; Esménio et al., 2019; Raichle, 2011; Sharaev et al., 2016). EC measures within four networks (N1-N4), namely the default-mode network (N1: DMN), dorsal-attention network (N2: DAN), control-execution network (N3: CEN), and salience network (N4: SN), were calculated. ROIs within each network were defined with a spherical radius of 8 mm. N1 – DMN involved four regions, namely posterior cingulate cortex (R1: PCC), medial prefrontal cortex (R2: MPFC), left and right lateral parietal cortex (R3: LLPc and R4: RLPC). N2 – DAN involved eight regions, namely left and right frontoparietal eye field (R1: LFEF and R2: RFEF), left and right posterior intraparietal sulcus (R3: LIPS and R4: RIPS), left and right anterior intraparietal sulcus (R5: LAIpS and R6: RAIpS), and left and right middle temporal cortex (R7: LMTc and R8: RMTc). N3 – CEN involved five regions, namely dorsal medial prefrontal cortex (R1: DMPFC), left and right anterior prefrontal cortex (R2: LAPPc and R3: RAPPc), and left and right superior parietal cortex (R4: LSPPc and R5: RSPc). N4 – SN involved seven regions, namely dorsal anterior cingulate cortex (R1: DACC), left and right anterior prefrontal cortex (R2: LAPPc and R3: RAPPc), left and right insula (R4: LI and R5: RI), and left and right lateral parietal cortex (R6: LLPC and R7: RLPC). Spatial location of each ROI on standard MNI template is shown in Fig. 1. Central MNI co-ordinates of each ROI (identical across participants) were selected based on previously published studies (Raichle, 2011; Raaij et al., 2017), and are reported in Table 2. For EC analysis, time-series from each ROI was corrected for head motion and physiological noise. For this purpose, the nuisance regressors included the six head-motion parameters, cerebrospinal fluid (extracted from left ventricle), and white matter (extracted from pons). The idea here was to account for signals associated with artifacts that we were not interested in. To create head-motion regressors, the motion in all three directions (i.e., X, Y and Z) were recorded at each time-point. In case of cerebrospinal fluid and white matter, the average time course across each tissue was calculated. Inclusion of this data as nuisance regressors helped correcting time-series while restricting any effects to grey matter only. While testing the efficacy of our current approach to correct the time-series in comparison to more advanced methods (e.g., compared to recommendations proposed in Parkes et al., 2018) (Parkes et al., 2018) is beyond the scope of this study, our current strategy is strongly supported by recent literature on DCM analysis that used similar approaches for time-series/head-motion correction (Almgren et al., 2018; Esménio et al., 2019; Preller et al., 2019; Sokolov et al., 2020; Voigt et al., 2020). Low-frequency signal drifts were filtered using a 128-s high-pass filter.

2.3.3. Network-wise EC and its association with measures of EI

The spDCM approach (spm_dcm_fmri_check.m implemented in DCM12/SPM12, revision 7487) with default shrinkage priors (Friston et al., 2014) was used to estimate the EC within each network. For each network, explained variance was determined using model fit (spm_dcm_fmri_check.m in SPM12) as a diagnostic tool. We found that the mean explained variance for DMN (N1), DAN (N2), CEN (N3) and SN (N4) were 97.11%, 98.53%, 97.18% and 98.05% respectively. Individual connectivity parameters for each network across all the participants were modeled at the group-level using a Bayesian general linear model (GLM) with a regressor for group’s mean value

Fig. 1. Networks and regions of interest. Here we show the spatial locations of regions of interest for each of the four networks on standard MNI template – the default-mode network (N1: DMN) (A), dorsal-attention network (N2: DAN) (B), control-execution network (N3: CEN) (C), and salience network (N4: SN) (D), which were used to estimate the strength of EC. L/R: Left/Right.
per connection. At the group level, we used parametric empirical Bayes (PEB) — a between-subjects hierarchical or empirical Bayesian model over parameters — which models how individual (within-subject) connections relate to group or condition means. This hierarchical model treats intrinsic connectivity as a random (between-subjects) effect, which is modeled by adding a random Gaussian component to subject-specific parameters; that is, a GLM of between subject effects generates the parameters of a within subject dynamic causal model. This random effect modeling is important because, unlike a classical test (e.g., t-test), it uses the full posterior density over the parameters from each subject’s DCM – both the expected strength of each connection and the associated uncertainty (i.e., posterior covariance) – to inform the group-level result (i.e., group means). The group-level parameters were used as empirical priors to finesse subject-wise parameter estimation (Zeidman et al., 2019). To evaluate how regions in the network of interest interact, we used Bayesian model comparison to explore the space of possible hypotheses (or models), where each hypothesis assumed that a different combination of the connectivity parameters could characterize all the participants. Candidate models were obtained by removing one or more connections to produce nested or reduced forms of the full model. With x (y regions times y regions) intrinsic connections (or parameters) of the fully connected model, there is large number of possible nested models in the model space. To address this we used Bayesian model reduction (BMR) that enables the evidence and parameters of nested models to be derived from a full model in a matter of seconds, enabling an efficient (greedy) search of the model space by scoring (based on the log model-evidence or free energy) each reduced model. More details can be found in one of the recently published papers by Friston and colleagues (Friston et al., 2016). In addition, the search algorithm used BMR to prune connection parameters from the full model, until there was no further improvement in model-evidence. The parameters of the best 256 models from this search procedure were then averaged, weighted by their model evidence (Bayesian Model Averaging) (Penny et al., 2010). Because the intrinsic self-connections cannot be pruned, therefore, the self-connections were not interpreted. To estimate the associations between EC strength and measures of EI, subject-wise connectivity values for each connection within each network were extracted. The Spearman’s partial correlation approach, with mean centered ‘age’, ‘sex’, ‘education’ and ‘race’ as covariates, was used to determine the associations between strength of EC and EI. Any data-point on the scatter plot with Cook’s distance greater than four times the mean was considered as outlier and was excluded from the analysis. The correlations with p < 0.05 (FDR-corrected using Benjamini & Hochberg procedure (Benjamini and Hochberg, 1995)) were considered as significant. Here FDR-correction was performed separately for each network, which involves correlations between connectivity strength of each connection within a network and four sub-scales (S1-S4) of EI.

### 3. Results

#### 3.1. Associations between MSCEIT sub-scales and scales

Pearson’s correlation coefficients between MSCEIT sub-scales (S1-S4) and scales (T1-T3) are reported in **Table 3**.

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**Table 2. Networks and regions of interest.**

| # | Region                                                                 | Abbreviation | MNI coordinates (X, Y, Z) |
|---|-----------------------------------------------------------------------|--------------|---------------------------|
| N1 Network 1: Default-mode network (DMN)                               |              |                           |
| R1 | Posterior cingulate cortex/Precuneus                                  | PCC          | 0, -52, 27                |
| R2 | Medial prefrontal cortex                                             | MPFC         | -1, 54, 27                |
| R3 | Left lateral parietal cortex-1                                       | LLPC         | -46, -66, 30              |
| R4 | Right lateral parietal cortex-1                                      | RLPC         | 49, -63, 33               |
| N2 Network 2: Dorsal attention network (DAN)                            |              |                           |
| R1 | Left frontal eye field                                               | LFEF         | -29, -9, 54               |
| R2 | Right frontal eye field                                              | RFEF         | 29, -9, 54                |
| R3 | Left posterior intraparietal sulcus                                  | LPIPS        | -26, -66, 48              |
| R4 | Right posterior intraparietal sulcus                                 | RPIPS        | 26, -66, 48               |
| R5 | Left anterior intraparietal sulcus                                   | LAPS         | -44, -39, 45              |
| R6 | Right anterior intraparietal sulcus                                  | RAPS         | 41, -39, 45               |
| R7 | Left middle temporal cortex                                          | LMTC         | -50, -66, -6              |
| R8 | Right middle temporal cortex                                         | RMTC         | 53, -63, -6               |
| N3 Network 3: Control-execution network (CEN)                           |              |                           |
| R1 | Dorsal medial prefrontal cortex                                       | DMPPC        | 0, 24, 46                 |
| R2 | Left anterior prefrontal cortex-1                                    | LAPPFC       | -44, 45, 0                |
| R3 | Right anterior prefrontal cortex-1                                    | RAPPFC       | 44, 45, 0                 |
| R4 | Left superior parietal cortex                                        | LSFC         | -50, -51, 45              |
| R5 | Right superior parietal cortex                                       | RSFC         | 50, -51, 45               |
| N4 Network 4: Salience network (SN)                                     |              |                           |
| R1 | Dorsal anterior cingulate cortex                                      | DACC         | 0, 21, 36                 |
| R2 | Left anterior prefrontal cortex-2                                    | LAPFC        | -35, 45, 30               |
| R3 | Right anterior prefrontal cortex-2                                   | RAPFC        | 32, 45, 30                |
| R4 | Left insula                                                           | LI           | -41, 3, 6                 |
| R5 | Right insula                                                          | RI           | 41, 3, 6                  |
| R6 | Left lateral parietal cortex-2                                       | LLPC         | -62, -45, 30              |
| R7 | Right lateral parietal cortex-2                                      | RLPC         | 62, -45, 30               |

**Table 3. Pearson’s Correlation between MSCEIT sub-scales and scales.**

|          | S1   | S2   | S3   | S4   | T1   | T2   | T3   |
|----------|------|------|------|------|------|------|------|
| S1       | 0.56*| 0.22 | 0.04 | 0.89*| 0.15 | 0.66*|      |
| S2       |      | 0.49*| 0.35*| 0.87*| 0.49*| 0.84*|      |
| S3       |      |      | 0.29*| 0.41*| 0.81**| 0.71**|      |
| S4       |      |      |      | 0.20 | 0.77**| 0.55**|      |
| T1       |      |      |      |      | 0.36**| 0.86**|      |
| T2       |      |      |      |      |      | 0.77**|      |
| T3       |      |      |      |      |      |      | 0.73**|

**Abbreviations:** Perception of emotion (S1); Using emotion to facilitate thinking (S2); Understanding of emotion (S3); Management of emotion (S4); Experiential EI (T1); Strategic EI (T2); Total MSCEIT (T3).

* p < 0.05,
** p < 0.01.
3.2. Associations between EC strength and EI (four-branch model)

Below we report the associations observed between EC strength for each network and scores on each sub-scale of four-branch model (S1-S4) of EI:

3.2.1. DMN and MSCEIT sub-scales (S1-S4)

In Fig. 2, we report the correlation coefficient strength (colorbar) between four sub-scales of MSCEIT (S1-S4) and the EC strength of each connection within N1 (DMN). Corresponding p-values (FDR-corrected) are displayed within the cells. Here $C_{ab}$: $a$→$b$ represents the connections from $a$ to $b$, where $a$ and $b$ represent regions from 1 to 4 i.e., R1 to R4 within N1 (DMN) (self-connections are avoided). At $p_{FDR} < 0.05$, there was no significant association between EC strength for any connection and any of the four sub-scales of MSCEIT.

3.2.2. DAN and MSCEIT sub-scales (S1-S4)

In Fig. 3, we report the correlation coefficient strength (colorbar) between four sub-scales of MSCEIT (S1-S4) and the EC strength of each connection within N2 (DAN). Corresponding p-values (FDR-corrected) are displayed within the cells. Here $C_{ab}$: $a$→$b$ represents the connections from $a$ to $b$, where $a$ and $b$ represent regions from 1 to 8 i.e., R1 to R8 within N2 (DAN) (self-connections are avoided). At $p_{FDR} < 0.05$, there was no significant association between EC strength for any connection and any of the four sub-scales of MSCEIT.

3.2.3. CEN and MSCEIT sub-scales (S1-S4)

In Fig. 4, we report the correlation coefficient strength (colorbar) between four sub-scales of MSCEIT (S1-S4) and the EC strength of each connection within N3 (CEN). Corresponding p-values (FDR-corrected) are displayed within the cells. Here $C_{ab}$: $a$→$b$ represents the connections from $a$ to $b$, where $a$ and $b$ represent regions from 1 to 7 i.e., R1 to R7 within N3 (CEN) (self-connections are avoided). The cells representing the significant correlations at $p_{FDR} < 0.05$ are indicated by ‘∗’ and the corresponding scatter plots are shown in Fig. 5.

We observed that there was significant (i) positive correlation between EC strength for the connection – LAFPC to RAPFC ($C_{23}$) and facilitate sub-scale (S2) ($\rho = 0.45$, $p_{FDR} = 0.027$) (Fig. 5A), (ii) negative correlation between EC strength for the connection – RAPFC to LAPFC ($C_{32}$) and facilitate sub-scale (S2) ($\rho = 0.67$, $p_{FDR} = 0.002$) (Fig. 5B), and (iii) negative correlation between EC strength for the connection – RSPC to RAPFC ($C_{33}$) and manage sub-scale (S4) ($\rho = 0.60$, $p_{FDR} = 0.002$) (Fig. 5C).

3.2.4. SN and MSCEIT sub-scales (S1-S4)

In Fig. 6, we report the correlation coefficient strength (colorbar) between four sub-scales of MSCEIT (S1-S4) and the EC strength of each connection within N4 (SN). Corresponding p-values (FDR-corrected) are displayed within the cells. Here $C_{ab}$: $a$→$b$ represents the connections from $a$ to $b$, where $a$ and $b$ represent regions from 1 to 7 i.e., R1 to R7 within N4 (SN) (self-connections are avoided). The cells representing the significant correlations at $p_{FDR} < 0.05$ are indicated by ‘∗’ and the corresponding scatter plots are shown in Fig. 7.

We observed that there was significant (i) positive correlation between EC strength for the connection – LLI to DACC (C_{41}) and the understanding sub-scale (S3) ($\rho = 0.47$, $p_{FDR} = 0.041$) (Fig. 7A), and (ii) negative correlation between EC strength for the connection – R1 to RAPFC
Fig. 4. Spearman’s correlation matrix between the strength of EC within the CEN (N3) and four sub-scales (S1-S4) of EI. Here we show the correlation matrix between EC strength of each connection within the N3 (CEN) and each of the MSCEIT sub-scales (S1-S4). Strength of the correlation coefficients are shown along the color-bar. Corresponding p-values (FDR-corrected) are displayed within the cells. Cells marked with ‘∗’ represent the significant correlation coefficients at $p_{FDR} < 0.05$.

![Correlation Matrix](image)

Connections ($C_{a\rightarrow b}$) for N3 (CEN)

$\rho = 0.45^{∗}$

$\rho_{FDR} = 0.027$

$\rho = 0.54^{∗}$

$\rho_{FDR} = 0.002$

Fig. 5. Scatterplots of EC strength within the CEN and MSCEIT sub-scales. Here we show the scatterplots for residualized EC strength from LAPFC to RAPFC (A) and RAPFC to LAPFC (B) with residualized scores on abilities to use emotions to facilitate thinking (facilitate EI) (A-B), and for residualized EC strength from RSPC to RAPFC with residualized scores on abilities to manage emotions (manage EI) (C). All of these associations (A-C) are significant at $p_{FDR} < 0.05$.

![Scatterplots](image)

Fig. 6. Spearman’s correlation matrix between the strength of EC within the SN (N4) and four sub-scales (S1-S4) of EI. Here we show the correlation matrix between EC strength of each connection within the N4 (SN) (A-B) and each of the MSCEIT sub-scales (S1-S4). Strength of the correlation coefficients are shown along the color-bar. Corresponding p-values (FDR-corrected) are displayed within the cells. Cells marked with ‘∗’ represent the significant correlation coefficients at $p_{FDR} < 0.05$.

![Correlation Matrix](image)

Connections ($C_{a\rightarrow b}$) for N4 (SN)

$\rho_{FDR} < 0.05$
Fig. 7. Scatterplots of EC strength within the SN and MSCEIT sub-scales. Here show the scatterplots for residualized EC strength from LI to DACC (A) and RI to RAPFC (B) with residualized scores on abilities to understand emotions (understand EI) (A-B). All of these associations (A-B) are significant at $p_{FDR} < 0.05$.

Fig. 8. Scatterplots of EC strength within the CEN and total scores on MSCEIT. Here show the scatterplots for residualized EC strength from RAPFC to LAPFC (A) and RSPC to RAPFC (B) with residualized total experiential EI (A) and residualized total strategic EI (B). All of these associations (A-B) are significant at $p_{FDR} < 0.05$.

($C_{53}^{5}$) and the understanding sub-scale ($S_3$) ($\rho = -0.46, p_{FDR} = 0.041$) (Fig. 7B).

3.3. Associations between EC strength and EI (two area cores: T1-T2)

At $p_{FDR} < 0.05$, none of the connections within the DMN (N1), DAN (N2) or SN (N4) showed a significant association between EC strength and either of T1 or T2. However, for the CEN (N3), there was significant negative correlation between EC strength for (i) the connection – RAPFC to LAPFC ($C_{32}$) and total experiential EI (T1) ($\rho = -0.47, p_{FDR} = 0.012$) (Fig. 8A), and (ii) the connection – RSPC to RAPFC ($C_{53}$) and total strategic EI (T2) ($\rho = -0.51, p_{FDR} = 0.005$) (Fig. 8B).

3.4. Associations between EC strength and total EI (T3)

At $p_{FDR} < 0.05$, none of the connections within any of the networks (N1-N4) showed a significant association between EC strength and T3.

3.5. Associations between EC strength and EI after accounting for the effect of the other (remaining) (sub)scales/scales of EI

We calculated the associations between EC and (sub)scales (S1-S4)/scales (T1-T2) of EI after accounting for the effect of the other (remaining) (sub)scales/scales of EI. However, we believe that the sub-scales (S1-S4) have their own unique variance (Brackett and Sa-lovey, 2006) and therefore, are usually not covaried while drawing conclusions/interpretations (Emmer et al., 2012; Howe et al., 2014; Killgore et al., 2017; Lishner et al., 2011; Vidal et al., 2010). Moreover, by covarying them, it essentially removes any potentially common aspects of EI that are shared across them and simply interpreting the specific connectivity patterns that are not shared with the others. Therefore, these additional findings are reported in Supplementary Section, but are not further interpreted in the Discussion section.

4. Discussion

In this study, we investigated the associations between EC strength within four functional brain networks and measures of EI. Below we discuss our findings in detail.

We reported that for the CEN, there was significant negative association between EC strength for the connection from the RAPFC to the LAPFC and both abilities to facilitate emotions and total scores on experiential EI. However, there was significant positive association between EC strength for the same connection but in the opposite direction (RAPFC to LAPFC) and abilities to facilitate emotions. The EC strength for the connection from the RSPC to RAPFC also showed sig-
nificant negative association with abilities to manage emotions and total scores on trait EI. Previously, the distinct neural substrates of the prefrontal cortex (PFC), particularly the ventromedial and dorsolateral PFC, have been known to play a crucial role in understanding and managing emotionally relevant information (Krueger et al., 2009). A study investigating the association between EI and performance in Wisconsin Card Sorting Test (WCST) – a neuropsychological test to evaluate functioning of frontal lobe, showed that the differences in PFC function may lead to differences between WCST performances of high and low EI groups (Alipour et al., 2011). More specifically, the anterior PFC has been reported to be critically involved in moral cognition and sensitivity (Moll et al., 2005, 2002), socio-emotional judgements (Karim et al., 2010; Raine and Yang, 2006), and emotionally loaded moral behaviors (Greene et al., 2001). The neural substrates associated with the impairments in EI scores include areas which are known to process social information, i.e., frontal and parietal areas, including the right orbitofrontal and both left inferior and superior parietal cortices (Barbey et al., 2014). Our findings showing greater involvement of the RSFPC in stronger abilities to understand and manage emotions, in conjunction with previous findings showing the association between cortical activity within the right parietal cortex and positive emotional experience (Horton, 1988), appear to converge to suggest similar neural mechanisms underlying abilities to process some aspects of emotional information.

For the SN, we reported that there was significant negative association between EC strength for the connection from the RI to RAPFC and abilities to understand emotions, and significant positive association between EC strength for the connection from the LI to DACC and abilities to understand emotions. These findings indicate that the EC between RAPFC and RI, and between DACC and LI plays crucial role in the ability to understand emotions. Despite the fact that our data involved only resting state fMRI data, we identified clear distinct roles of left and right insula associated with measures of EI. Previous studies reported that insular responses may be emotion specific. Quarto and colleagues reported positive association between EI and left insular activity during social judgement of fearful faces, but a negative association between the two during social judgement of angry faces (Quarto et al., 2016). In one of the studies from our laboratory, we reported an association between higher levels of EI and reduced left insular responses to masked angry presentations (Alkozai and Killgore, 2015). Consistent with our previous findings, the right insular regions in the present study were closely associated with abilities to understand feelings. A meta-analysis study by Fan and colleagues reported that the affective forms of empathy are more likely to activate the right insular regions, whereas the left insula appears to be involved in both affective and cognitive empathy (Fan et al., 2011). The anterior cingulate cortex (ACC), which is an integral part of the limbic network, processes both cognitive and emotional information through two distinct major sub-divisions – the dorsal cognitive division and the rostral-ventral affective division (Devinsky et al., 1995). Our findings show that directed interaction from the insula to ACC leads to greater response of the ACC, which in turn, contributes to greater abilities to understand emotions—a finding that is also in line with previous studies. Previously, lesions within the ACC have been associated with symptoms such as difficulties in social interactions and impairments in the ability to identify and understand emotions (Hornak et al., 2003). The functional response of the ACC to emotions and experiential processing may be useful as a method to measure an individual’s abilities to understand emotions (Lane et al., 1998). Similarly, functional connectivity analysis also showed that during resting-state, the insula and portions of both anterior and posterior cingulate cortices form a network which might be responsible for integrating and processing information associated with emotional salience (Taylor et al., 2009). Our findings extend the findings reported in previous articles by specifying the association between individual brain areas within the CEN and SN and the levels of EI, and also indicate that the measures of EC can be considered as reliable biomarkers to identify the interactions among distributed brain areas to clarify the conceptual details of the underlying mechanisms of EI.

For the DMN and DAN, we did not observe significant associations between any of the connections within any of these networks and any of the EI scales or subscales. Prior published work has shown significant associations of the DMN that included the ventral medial PFC, orbitofrontal cortex, temporal pole, middle temporal cortex, anterior cingulate cortex, precuneus/PCC, and superior parietal regions (where parietal and middle temporal areas also part of the DAN) with measures of EI (Killgore et al., 2017; Ling et al., 2019; Takeuchi et al., 2013). However, absence of significant associations between EC strength of any of the connections within the DMN/DAN and EI in the current study doesn’t indicate that the current findings are contradictory to previous literature. For instance, in the study by Killgore and colleagues, independent component analysis (ICA) was performed to decompose the fMRI data into distributed set of brain regions (called ‘independent components’) (Killgore et al., 2017). This resulted in a set of cortical and sub-cortical brain regions that were spatially different from the regions included in the current study. Moreover, in the current study, as a first step, we chose to quantify the EC strength within well-established cognitive networks described previously. This could be the reason that despite having frontal (i.e., medial PFC) and parietal (i.e., lateral parietal) areas as important components of the DMN in the current study, we found EC between the frontal (i.e., anterior prefrontal cortex) and parietal areas (i.e., superior parietal) of the control-execution network associated with EI. In the other two studies (i.e., one by Ling and colleagues and the other by Takeuchi and colleagues), whole-brain functional connectivity maps were evaluated using a specific region as a seed region rather than limiting the analysis to a particular network (Ling et al., 2019; Takeuchi et al., 2013). This might have allowed the authors to reveal unexpected resting-state functional correlates of EI. (Takeuchi et al., 2013). However, in the study by Ling and colleagues, authors found that the functional network architecture of the left superior parietal lobe is associated with EI (Ling et al., 2019). This was consistent with our current findings showing an association between EC strength between regions that involved the superior parietal cortex (i.e., within the control-execution network) and EI. In sum, we believe that some of the inconsistencies between our current findings and the findings reported in prior literature could just be due to different methodological approaches used in respective studies (e.g., large-scale spectral DCM approach for pre-defined cortical networks vs. ICA/whole-brain functional connectivity). Therefore, caution should be exercised while drawing conclusions within and across network-wise connectivity correlates of EI.

To summarize our findings, we observed that EC from the left to right anterior regions of the prefrontal cortex is associated with greater EI abilities. In contrast, EC in the opposite direction between these two regions is associated with lower EI abilities. In addition, right lateralized EC from the RI to RAPFC contributes to lower ability to understand emotions, whereas left lateralized EC from LI to DACC is associated with greater abilities to understand emotions. These findings suggest that the dominant negative EC within the right hemisphere and from the right to left hemisphere, and dominant positive EC within the left hemisphere and from the left to right hemisphere of CEN and SN may be indicative of mechanisms underlying EI. A tentative model of effective brain interactions underlying the measures of EI is shown in Fig. 9. These findings suggest a specific role of each hemisphere in processing emotions and advance our knowledge on potential associations between hemispheric asymmetry and complex abilities to understand emotions. In previous work, hemispheric lateralization and asymmetric involvement of frontal brain areas have been associated with the EI. In particular, greater involvement of the right hemisphere in processing information appears to be linked to greater difficulties in regulating emotions (Gupta et al., 2011), which we find may be consistent with lower levels of EI. Also, there is prior evidence of a positive association between trait EI abilities and resting electroencephalographic
(EEG) frontal activation within the left hemisphere (Mikolajczak et al., 2010). In early work, Nestor and Safer reported an association of tendencies to express emotions with right hemisphericity, and tendencies to inhibit emotions with left hemisphericity (Nestor and Safer, 1990). In another early study, right hemispheric individuals were reported to be tense and suspicious, possessed negative attitude towards themselves, and had less self-control over their impulses, where left hemispheric individuals were less tense and suspicious, more imaginative, possessed greater self-control over their impulses and had greater positive attitude towards themselves (Vingiano, 1989). Consistent with these previous reports, our findings suggest a systematic hemispheric organization of the brain which is associated with the levels of EI, i.e., greater negative EC within right and from right to left hemisphere, but greater positive EC within left and from left to right hemisphere are associated with greater levels of EI.

5. Limitations and future directions

Our findings should be interpreted in consideration of a few limitations. First, this study involved resting-state fMRI data of moderate resolution from a moderate sample size. Future studies would benefit from the use of high-resolution fMRI data from a relatively larger sample size. Second, our study involved interactions among different regions based on only resting-state fMRI data and their associations with emotional intelligence. Task-based fMRI data and morphometry analysis were not explored in this study. It would be of great importance for future work to identify and clarify the associations between emotional intelligence and task-based effective functional characteristics and morphometry measures such as cortical thickness, area and volume. Third, despite the fact that lower EL has been consistently observed across a variety of conditions affecting cognition or mental health, including individuals with autism spectrum disorders (Brady et al., 2014), depression (Downey et al., 2008), personality disorders (Lizeretti et al., 2014) and suicidal behavior (Dominguez-Garcia and Fernandez-Berrocal, 2018), this initial study focused on emotional intelligence of only healthy individuals. Future studies would benefit by expanding their focus beyond healthy cohorts to also include groups with various forms of psychopathology or neuropathology. With due consideration to these limitations, this is the first study which utilized the spectral DCM technique to explore the large-scale effective brain connectome to better understand the underlying mechanisms of EI.

These findings have potential to impact future research aimed at assessing strategies to improve intervention approaches for individuals with mood disorders or other forms of affective psychopathology, as well as efforts to facilitate a healthy juncture between emotion and cognition. The current findings also provide a foundation for future studies to focus on applications of EI in the job market, where EI is often considered as one of the strongest predictors of success. The present findings provide concrete neural systems that could be targeted for strengthening to potentially enhance the capacity for empathy, emotional reasoning, motivation, resilience, stress management, better communication, and to effectively resolve social conflicts, and may provide an objective method for assessing the effects of interventions on the brain systems that underlie these capacities.

6. Conclusions

A network of distributed brain regions within the control-execution and salience networks, and both inter- and intra-hemispheric directed interactions appear to provide important neural underpinnings of emotional intelligence. Our findings suggest that effective interactions among frontal, parietal, cingulate and insular regions are closely associated with individual emotional processing abilities. Hemispheric asymmetry of the effective interactions appeared to be significantly associated with emotional intelligence abilities. These findings suggest that measures of effective connectivity may potentially be utilized as important biomarkers to further understand the complex neural interactions underlying EI and may prove useful for assessing the outcomes of interventions aimed at strengthening EI abilities. A significant amount of work still remains to be done to establish the reliability of large-scale effective connectivity measures in this context.

Data availability statement

Any data associated with this article will be made available by reasonable request to senior author WDSK. Most of the data analyses scripts used in our manuscript are freely available in open access toolboxes CONN, SPM and SPM/Parametric Empirical Bayes (PEB). Any scripts associated with large-scale DCM data analysis will be made available by reasonable request to first author SB.

Disclosure statement

None

Credit author statement

SB analyzed the data and wrote the initial draft. WDSK obtained the funding, designed the study, collected the data, supervised all aspects of the study, and contributed to data analysis and writing of the manuscript.
Supplementary materials

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