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Predicting individual differences in behavioral activation and behavioral inhibition from functional networks in the resting EEG

Alana J. Anderson *, Sammy Perone

Department of Human Development, Washington State University, USA

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ABSTRACT

The behavioral activation system (BAS) and behavioral inhibition system (BIS) are thought to underly affective dispositions and self-regulatory processes. The BAS is sensitive to reward and involved in approach behaviors, and the BIS is sensitive to punishment and involved in avoidance behaviors. Trait BAS and BIS relate to distinct behavioral profiles and neural activity, but little is known about how trait BAS and BIS relate to functional networks in EEG. We applied a data-driven method called connectome predictive modeling (CPM) to identify networks relating to trait BAS and BIS and tested whether the strength of those networks predicted trait BAS and BIS in novel subjects using a leave-one-out cross-validation procedure. Adult participants ($N = 107$) completed a resting state task with eyes closed and eyes open, and trait BAS and BIS were measured via Carver and White's (1994) BIS and BAS scales. We hypothesized distinct positive (more synchronization) and negative (less synchronization) networks would relate to trait BAS and BIS. For eyes closed, we identified two negative networks, one in theta and one in alpha predicted BIS. We identified three positive networks, one in theta and one in beta predicted Fun Seeking and one in theta predicted Drive. For eyes open, negative theta and alpha networks predicted BIS, a positive theta network predicted Fun Seeking, and a negative gamma network predicted mean BAS. Visualization of the networks are presented. Discussion centers on the observed networks and how to advance application of CPM to EEG, including with clinical implications.

Approach and avoidance are motivational processes involved in regulating thoughts, emotions, and behavior and are governed by the activity of the behavioral activation system (BAS) and behavioral inhibition system (BIS), respectively (Gray, 1981; Pickering & Corr, 2008). While both approach and avoidance are important processes for healthy human functioning, a consistent use of one or the other to self-regulate is associated with mental and behavioral health problems. A large literature has shown individual differences in trait BAS and BIS are linked to neural activity in the electroencephalogram (EEG), the primary focus of which has been measures based on EEG power. Little research has examined how trait BAS and BIS relate to functional connectivity in the EEG. This was the aim of the current study. Specifically, we used a data-driven approach called connectome predictive modeling (CPM; Shen et al., 2017) to identify functional networks in the resting state EEG that relate to trait BAS and BIS measured via self-report. The goal of CPM is to identify networks in one set of subjects that can predict behavior in novel subjects. We used a built-in cross-validation procedure to test whether the strength of BAS and BIS networks identified in one set of subjects and extracted from novel subjects could predict their self-report BAS and BIS scores.

1. Behavioral activation and behavioral inhibition

The BAS and BIS are two systems involved in emotion regulation as described in Gray's Reinforcement Sensitivity Theory (Gray, 1981; Pickering & Corr, 2008). In the original formulation of the theory, the BAS was described as sensitive to reward cues and underlying approach behaviors, and the BIS was described as sensitive to punishment cues and underlying avoidance and withdraw behaviors (Gable et al., 2018; Pickering & Corr, 2008). Healthy daily functioning requires use of both approach and avoidance, such as use of approach to engage in social interactions and avoidance when encountering uncertain or dangerous situations. However, mental and behavioral health problems can arise from overactivity of the BAS or BIS. For example, individuals high in trait BAS are more likely to be highly social, seek stimulating activities (e.g., skydiving; Wagner & Houlihan, 1994; Zuckerman, 1994; see Roberti, 2004 for review), and engage in more risk behaviors (e.g., drug use, Franken & Muris, 2006). Individuals high in trait BIS are more likely

* Correspondence to: 501 Johnson Tower, Pullman, WA 99164, USA.
E-mail address: alana.anderson@wsu.edu (A.J. Anderson).

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to experience depression or anxiety (Carver & White, 1994; Jorm et al., 1998; Reniers et al., 2016).

Trait BAS and BIS are commonly measured using the BAS/BIS scales developed by Carver and White (1994). The scales included are a BIS scale and three BAS subscales. The BIS scale measures sensitivity to punishment cues. Higher ratings on the BIS scale are associated with negative affect (Gable et al., 2000), a lower likelihood of engaging in aggressive behavior (Wingrove & Bond, 1998), and a higher likelihood of experiencing anxiety and depression (Quay, 1988). The BAS scales measure different aspects of reward sensitivity and include Drive, Reward Responsiveness, and Fun Seeking. Drive measures a tendency to engage in goal-directed behaviors, Reward Responsiveness measures the positive responses to the anticipation or receipt of reward, and Fun Seeking measures impulsive sensation seeking, or reward seeking behaviors. People high in BAS measured via a composite score also have greater positive affectivity (Gable et al., 2000), are more likely to engage in aggressive behavior (Wingrove & Bond, 1998), and have a greater potential for addiction (Zohreh & Ghazal, 2018). Higher levels of composite BAS are also associated with higher rates of impulsivity measured via self-report as well as risky decision making (e.g., drinking and driving; Braddock et al., 2011) and personality traits such as psychopathy and narcissism (Stenason & Vernon, 2016).

The BAS scales are thought to measure two different components of approach behaviors: responses to rewards and impulsivity. The Reward Responsiveness and Drive scales have been shown in psychometric studies to be more closely related to other potential markers of reward-sensitivity (e.g., goal-directedness, extraversion, reward-expectancy) whereas the Fun Seeking scale has been shown to be associated with novelty seeking, impulsiveness, and psychoticism (Caseras et al., 2003; Knyazev et al., 2004; Smillie et al., 2006; Zelenski & Larsen, 1999). The Reward Responsiveness and Drive scales predicted reactions to reward in an experimental setting, whereas Fun Seeking did not (Carver & White, 1994). The BAS scales have also been shown to be related to different behaviors. For example, higher Reward Responsiveness is associated with psychological well-being and resilience (Taubitz et al., 2015). A study by Voigt and colleagues found Reward Responsiveness was associated with lower levels of risk behaviors, such as alcohol and drug use, safe sex practices, and general safety (e.g., seatbelt use), whereas higher Fun Seeking has been associated with higher levels of risk behaviors, including drug and alcohol use, risky sex practices, and less use of general safety practices (Voigt et al., 2009). Additionally, while the BAS scales are often considered as separate fine-grained measures, there is evidence of an overarching BAS factor that accounts for much of the variance in each of these subscales (Kelley et al., 2019), suggesting that the BAS scales can also be considered together as they may be capturing an larger BAS construct. A large body of evidence indicates resting EEG activity relates to individual differences in BAS and BIS activity. We provide an overview of resting state EEG and this literature next.

2. Resting state EEG

Resting state tasks measure the intrinsic dynamics of the brain while participants perform no assigned task. A typical resting state task involves asking participants to remain still and relaxed with eyes closed or while maintaining attention on a fixation cross. Resting brain activity is associated with performance and behavioral tendencies observed in other contexts (e.g., Karamacoska et al., 2017; Perone et al., 2018; Rogala et al., 2020; for a review, see Anderson & Perone, 2018) and the study of resting activity has shed light on the neural basis of mental health conditions, such as major depression (Greicius et al., 2007), and neurodegenerative diseases, such as Alzheimer's Disease (Linkenkaer-Hansen et al., 2005; Stam et al., 2009). EEG is a continuous recording of electrical activity in cortex measured at electrode sites placed over the scalp. EEG records the oscillatory behavior of neural populations firing together across a range of frequencies. One common measure extracted from the EEG is power, higher levels of which reflect more neurons firing together within a given frequency. EEG power is typically averaged across frequency into distinct bands, named theta (4–8 Hz), alpha (8–13 Hz), beta (13–30 Hz), and gamma (30–50 Hz). The current study focuses on functional connectivity which is a measure of the statistical dependencies between the EEG in each frequency at recording sites placed over the scalp. The strength of connectivity between all electrode pairs creates site-by-site connectivity matrices which can be computed for each frequency band. Functional networks are patterns of connectivity within the matrix extracted in an a priori or data-driven fashion.

Resting brain activity is often viewed as reflecting the dynamics of brain networks specifically active at rest or those networks that are engaged while completing specific tasks (Damoiseaux et al., 2006; Gusnard & Raichle, 2001; Raichle, 2010). A large literature has shown resting EEG power is associated with individual differences in trait-level indicators of the BAS and BIS. Much of this literature has focused on frontal alpha asymmetry which is a measure of relative levels of alpha activity recorded at left and right sites over the frontal region of the brain. People who exhibit more relative left frontal alpha activity at rest also exhibit more approach-oriented behaviors and have a positive affective disposition, whereas those who exhibit more relative right frontal alpha activity exhibit more avoidance-oriented behaviors and have a negative affective disposition (e.g., Harmon-Jones & Allen, 1997; Tomarken et al., 1990; see Allen et al., 2018 for review). Individual differences in frontal alpha activity have also been linked to scores on the BIS and BAS subscales. For example, a composite of the BAS subscales is associated with greater relative left frontal alpha activity (Coan & Allen, 2003; Harmon-Jones & Allen, 1997; Krmpotich et al., 2013), and the BIS scale is associated with greater right frontal alpha activity (Balconi & Mazza, 2009; Shackman et al., 2009; Sutton & Davidson, 2000). Relations between resting EEG power in other bands and processes thought to rely on BAS and BIS activity have also been observed. For example, higher levels of frontal theta power relate to reward sensitivity as measured in the Iowa Gambling Task (Massar et al., 2014), a higher frontal theta to beta ratio relates to top-down regulation over emotional cues in a response inhibition task (Putman et al., 2010), and more right (sourced) prefrontal theta power relates to more risk taking in a gambling task (Studer et al., 2013). Some evidence indicates theta and beta may be involved in distinct aspects of reward processing. For example, Marco-Pallares et al. (2008) observed higher levels of beta upon reward but higher levels theta upon loss. Less research has focused on functional connectivity in the EEG as it relates to the BAS and BIS, which is the focal point of the current study.

3. Functional connectivity

Nunez et al. (2015) proposed functional connectivity reflects state-dependent dynamics across spatially distributed brain regions, creating global networks that are thought to be involved in integration of information processing across local networks and essential for healthy cognition. Much of our understanding of functional networks as it relates to BAS and BIS activity is based on studies using fMRI (e.g., Bramson et al., 2020), many of which have examined resting functional connectivity as it relates to trait levels of BAS and BIS activity using self-report. For example, Adrián-Ventura et al. (2019) found individual differences in reward sensitivity were associated with functional connectivity in areas involved in conflict resolution and monitoring, such as anterior cingulate cortex, and reward processing, such as ventral medial prefrontal cortex. Huggins et al. (2018) found individual differences in harm avoidance were inversely related to functional connectivity involving anterior insula and other areas, such as dorsal anterior cingulate cortex, and Caulfield et al. (2016) found that more behaviorally inhibited individuals exhibited higher levels of functional connectivity between left dorsal lateral prefrontal cortex and dorsal anterior cingulate cortex as well as between right dorsal lateral prefrontal cortex

and cerebellum.

General patterns of results from the fMRI literature can help in setting some expectations for the current study. For example, we might expect to observe distinct networks to relate to scores on the BIS and BAS subscales. Prior studies have shown different networks were active depending on whether participants were asked to make an approach or avoidance response (Leitão et al., 2022), and a large body of behavioral evidence indicates activity of the BIS and BAS relate to distinct behavioral profiles (e.g., Franken & Muris, 2006; Jorm et al., 1998; Reniers et al., 2016; Zuckerman, 1994). We might also expect to observe networks positively and negatively relating to BIS or BAS subscales. Prior studies have shown different coping styles to be related to more synchronization of some resting networks and desynchronization of others. Specifically, Santarnecchi et al. (2018) studied avoidance-oriented coping, problem-oriented coping, and social-support-oriented coping styles. They found distinct networks inversely related to social-support-oriented and avoidance-oriented coping styles, whereas a different network positively related to a problem-solving-oriented coping style. CPM simultaneously tests for the presence of positive and negative networks relating to behavioral measures.

4. Connectome predictive modeling

CPM is founded on the idea a common network relates to specific behaviors across individuals, and what varies across individuals is the relationship between the strength of the network and the behavior (Rosenberg et al., 2017). CPM is used to identify common networks that relate to behavior and test whether individual differences in the strength of those networks predict behavior in novel subjects using a built-in cross-validation procedure. The general CPM method is shown in Fig. 1. The starting point is computing connectivity matrices for each individual and pairing those with the scores on a behavioral measure for all subjects (step 1). One subject is set aside, and correlations are computed between functional connectivity for all possible electrode pairs (referred to as edges) and behavioral scores for *n*-1 subjects, called the training set (step 2). Positive and negative correlations are treated separately to identify networks where stronger connectivity relate to higher ratings on the BAS/BIS scale (positive networks) or weaker connectivity relate to higher ratings on the BAS/BIS scale (negative networks). Statistically significant edges are selected (step 3), and the magnitude of the correlation is discarded prior to computing network strength by summing the connectivity of the significant edges (step 4). The behavioral data is then regressed onto network strength for the training set (step 5). The coefficients from this linear model are used to predict behavior in the subject set aside using their network strength extracted from the same network identified in the training set. This yields a predicted and observed score for the behavioral measure (step 6). This process is repeated until all subjects have been left out and a predicted and observed score for the behavioral measure is obtained. Pearson's *r* is used to characterize the fit between observed and

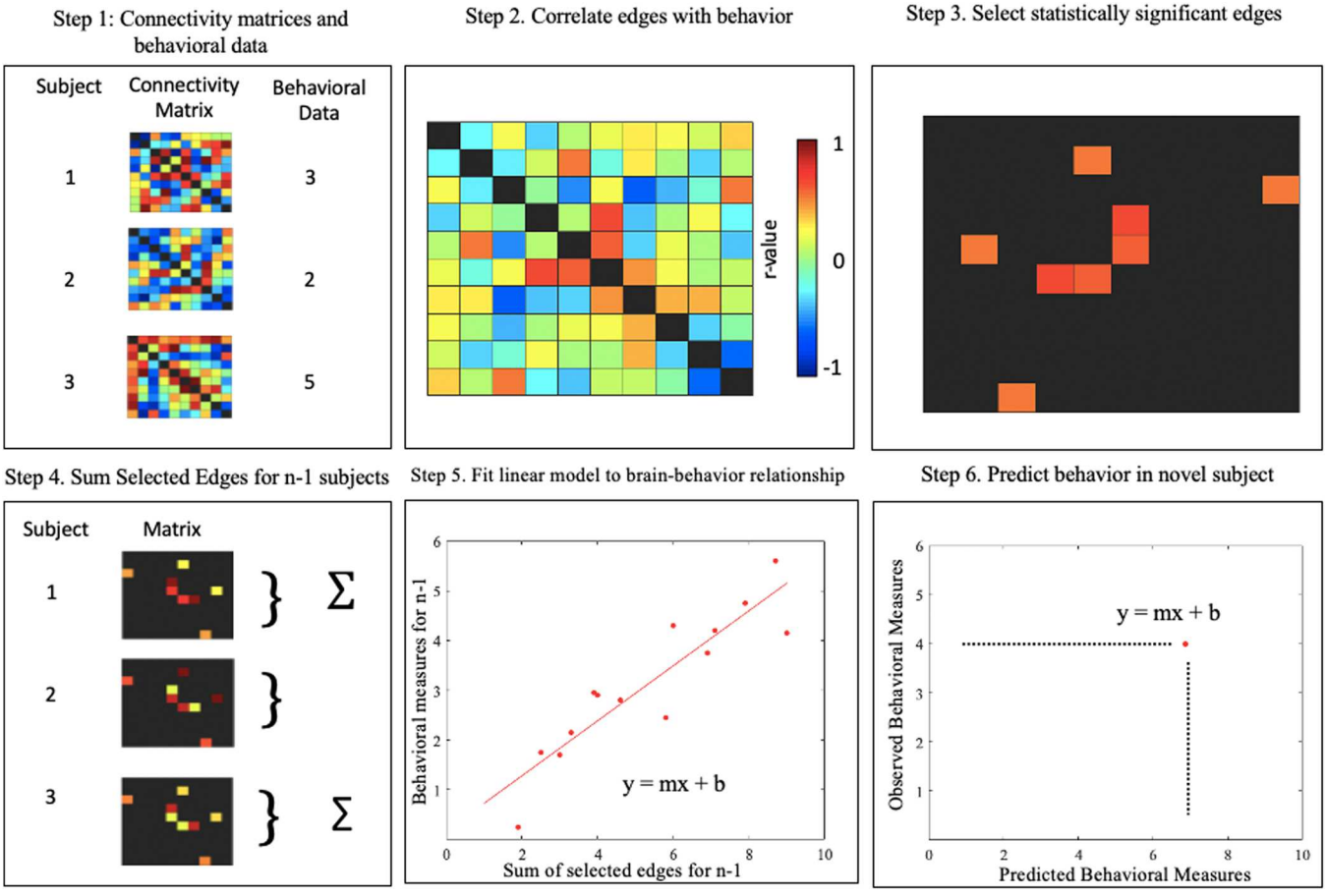

Fig. 1. Step-by-step overview of Connectome Predictive Modeling. Figure based on method as depicted by Shen et al. (2017). Connectivity matrices and BIS and BAS subscale scores for the training set (n-1 subjects) are selected (step 1), and Pearson's r is computed for all site-by-site connectivity strengths (edges) and the behavioral measure (step 2). Significant ($p < .05$, two-tailed) edges are selected (step 3). Positive and negative correlations were treated separately. The magnitude of the r statistic is discarded, and network strength is computed by summing the edges relating to the behavioral measure of the training set (step 4). The behavioral measure is regressed onto network strength for the training set (step 5). Using a built-in cross-validation procedure, the coefficients from the training are used to construct a predictive model using the network strength from the subject set aside to predict their score on the scale (step 6). This process was repeated in an iterative fashion until a predicted and observed score was obtained for all subjects.

predicted scores, and the statistical significance of the *r* statistic is determined using random permutation testing.

Numerous CPM studies using resting fMRI have identified networks relating to task-based performance, such as fluid intelligence (Finn et al., 2015) and attention (Rosenberg et al., 2016). These studies have identified both positive and negative networks relating to performance such that more synchronization of the positive networks relate to better task performance and more synchronization of negative networks relate to poorer task performance. CPM has been used with resting fMRI to predict scores on self-report instruments as well. However, the capacity of positive and negative networks to predict self-report scores in novel subjects has not always been observed. For example, Hsu et al. (2018) found positive and negative networks predicted extroversion and neuroticism, Wang et al. (2021) found only a negative network predicted trait anxiety, and Feng et al. (2019) found only a positive network predicted loneliness.

5. Current study

The goal of the current study was to apply CPM to resting EEG and test whether functional networks related to trait BAS and BIS and could predict individual differences in scale scores. A large literature has shown trait BAS and BIS are associated with distinct behavioral profiles (Carver & White, 1994; Roberti, 2004; Zuckerman, 1994) and patterns of neural activity relate to individual differences in use of these systems (Bramson et al., 2020) as well as trait levels of BAS and BIS activity (Hsu et al., 2018; Meyer et al., 2018; Wang et al., 2021). Thus, the general hypothesis guiding this research was distinct networks underlie the BAS and BIS. We expected to observe networks positively and negatively relating to BIS or BAS scales. This expectation is based on prior studies showing different coping styles relate to more synchronization of some networks and desynchronization of others at rest (Santarnecchi et al., 2018). However, we did not have scale specific predictions. We also did not have band specific predictions. Reasonable band predictions are difficult to make because multiple bands often are shown to relate to similar constructs, and different constructs are often shown to relate to multiple bands (El-Badri et al., 2001; Perone et al., 2021; for a review, see Anderson & Perone, 2018). Nevertheless, a body of evidence indicates theta and beta relate to top-down regulation over reward cues (Knyazev & Slobodskoy-Plusnin, 2009; Marco-Pallares et al., 2008; Massar et al., 2014; Putman et al., 2010) and alpha relates to approach and avoidance behaviors (Balconi & Mazza, 2009; Coan & Allen, 2003; Harmon-Jones & Allen, 1997; Krmpotich et al., 2013; Sutton & Davidson, 2000). We might expect theta and beta to relate to the BAS scales and alpha to relate to the BIS and BAS scales.

6. Method

6.1. Participants

The full sample consisted of 114 undergraduate students who received extra credit for participation. Seven participants were excluded due to excessive artifacts in the EEG ($n = 1$) or because their head size was larger than the EEG cap ($n = 6$). The final sample consisted of 107 undergraduate students who received extra credit for participation ($M_{age} = 20.31$, $SD_{age} = 1.46$, 84 females). Participants self-identified as White (50.5%), Asian (16.8%), Hispanic/Latino (11.2%), African American/Black (3.7%), Native/Indigenous (3%), and multiracial (16.8%).

6.2. Design and procedure

Participants completed the BIS/BAS scales prior to being fitted with the EEG cap. Resting state EEG was recorded in a dimly lit room across four 2-minute trials of alternating eyes closed and eyes open conditions resulting in 4 min in each condition. For both conditions, participants were instructed to remain still and relaxed. During the eyes open condition, participants were also instructed to look at a fixation cross displayed on a computer monitor.

6.3. EEG data collection and processing

EEG data was collected using a 128-channel HydroCel net manufactured by Electrical Geodesics, Inc. Impedance levels were set below 80 kΩ and typically below 50 kΩ. The EEG was monitored prior to recording, and electrodes were reset if needed to ensure high-quality data collection. EEG was recorded using the NetAmp 400 at 1000 Hz, referenced to Cz, and high-pass filtered at 0.1 Hz online. The EEG was processed in Matlab using functions from EEGLab (Makeig & Delorme, 2004), ERPLab (Lopez-Calderon & Luck, 2014), FieldTrip (Oostenveld et al., 2011), and the CSD toolbox (Kayser & Tenke, 2006). The continuous EEG was re-sampled at 500 Hz and high-pass filtered at 1 Hz with a 60 Hz notch filter. Excessively noisy electrodes were identified via visual inspection and removed ($M = 3.08$, $SD = 3.44$, Range = 0–18). A small number of electrodes that exceeded + /− 250 microvolts for more than 10 s were also flagged as excessively noisy and removed ($M = 0.15$, $SD = .45$, Range = 0–3). Independent Components Analysis was used to identify and correct ocular artifacts. Blinks and horizontal eye movements were identified via visual inspection of both components and channel activations. Components capturing ocular artifacts were removed. The corrected EEG was confirmed via visual inspection. Missing electrodes were interpolated, and the EEG was referenced to the average of all electrodes and divided into 1 s epochs with 75% overlap which is within the range typically used in the literature (Cohen, 2014; Luck, 2014; for examples, see Black et al., 2014; Park et al., 2021; Perone et al., 2019). Epochs containing 1 or more electrodes with voltage exceeding 150 microvolts for more than 100 ms were marked for rejection. The average number of epochs used for analysis in the eyes closed condition was 925.90 (97.05%, $SD = 0.052$), and the average number of epochs used for analysis in the eyes open condition was 897.16 (94.04%, $SD = 0.10$). The EEG was Laplacian transformed to increase the topographical localization of the signal. Laplacian transformation was done using the CSD toolbox with default parameters ($m = 4$, head radius = 10, $\lambda = 0.00001$). Time-frequency decomposition using Fast Fourier transform (FFT) was performed on artifact-free epochs using a Hanning window.

Functional connectivity was measured using Phase Lag Index (PLI) computed in FieldTrip. PLI measures the degree to which two signals consistently lead or lag each other over time and ranges from 0 (no synchrony) to 1 (perfect synchrony). PLI was computed for all electrode pairs in each frequency. For each pair of electrodes, the average PLI was computed across frequencies to create theta (4–8 Hz), alpha (8–13 Hz), beta (13–30 Hz), and gamma (30–50 Hz) bands. Electrodes on the face and the outer ring of electrodes on the posterior were removed (Calbi et al., 2019) leaving a 110 × 110 PLI connectivity matrix for analysis (Fig. 2). PLI values for each band at each pair of electrodes were winsorized such that values outside of 10% and 90% percentile were replaced with the most extreme remaining value within that range. This step was important to prevent extreme values from driving correlations between scales and connectivity.

6.4. Behavioral inhibition and activation

Trait BIS and BAS was measured using Carver and White's (1994) 20-item self-report scale. Each item is rated on a 4-point scale ranging from very true (1) to very false (4). Mean values were calculated from 4 subscales: BIS ($M = 3.04$, $SD = 0.53$), BAS Reward Responsiveness ($M = 3.54$, $SD = 0.58$), BAS Drive ($M = 2.79$, $SD = 0.62$), and BAS Fun Seeking ($M = 3.03$, $SD = 0.59$), and a composite BAS score which was the mean of all BAS items ($M = 3.15$, $SD = 0.46$). Cronbach's alpha indicated acceptable to good internal consistency for all scales (range = 0.73–0.86). Four scores for Reward Responsiveness were deemed outliers because they were 3 SD away from the mean and had no

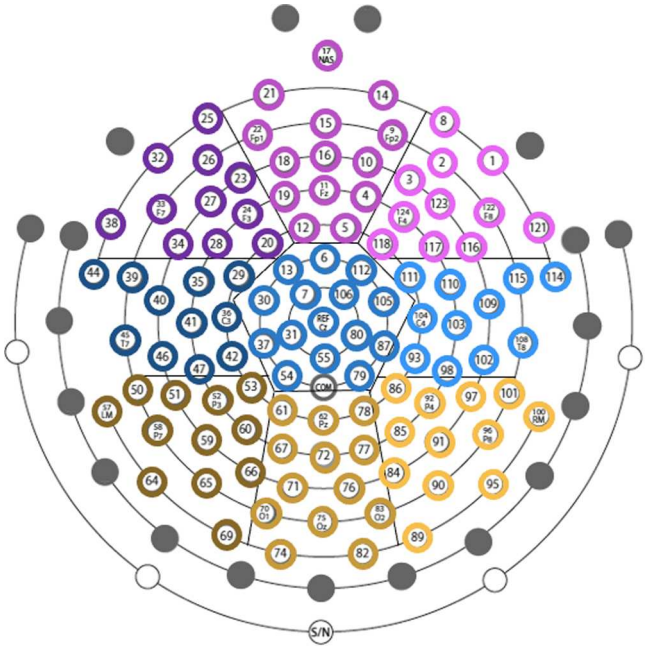

Fig. 2. EGI 128 channel scalp map. 110 electrodes were included in analysis (all colored electrodes). Nine different regions were used for visualizing and describing networks. Each hue shows a different region, including frontal (magenta), central (blue), and posterior (gold). For each hue, the darkest (e.g., dark gold) indicates the left-most region on the scalp while the lightest (e.g., light gold) indicates the right-most region on the scalp.

neighboring values within 1 SD, which was confirmed via visual inspection. These scores were winsorized to the closest non-outlying score.

6.5. Connectome predictive modeling

CPM was used to identify functional networks relating to BIS and BAS scales. CPM was performed for condition (eyes closed, eyes open), each band (theta, alpha, beta, and gamma), and BIS and BAS scales separately. We tested whether the strength of these networks could predict scores on the scales in novel subjects using the leave-one-out built-in cross-validation method outlined in Shen et al. (2017) and illustrated in Fig. 1. Specifically, the connectivity matrices for a given band for the training set consisting of *n*-1 subjects were selected (step 1), and Pearson's *r* was computed for all edges for a given BIS or BAS scales (step 2). Significant ($p < .05$, two-tailed) edges were selected (step 3). Positive and negative correlations were treated separately. The magnitude of the *r* statistic was discarded, and network strength was computed by taking the sum of edges relating to the BIS or BAS scales for n-1 subjects (step 4). Scores on each scale were then regressed onto network strength for the training set (step 5). Using a built-in cross-validation procedure, the coefficients from the training set were used to construct a predictive model using the network strength from the subject set aside to predict their score on the scale (step 6). Importantly, the network strength computed for the novel subject was extracted from the same network identified in the training set. Thus, CPM tests whether networks identified in one set of subjects can predict behavior in novel subjects. This process was repeated in an iterative fashion until a predicted and observed score was obtained for all subjects.

The capacity of the predictive model to reproduce the observed BIS or BAS scores was evaluated by computing Pearson's *r* between the observed and predicted scores. The statistical significance of the *r* statistic was determined using random permutation testing for all *r* statistics greater than zero because they indicate the predictive model generated scores in the same direction as the observed scores. Specifically, the score for the BIS or BAS scale for all participants were shuffled to break the link between the connectivity matrix of a given subject and their scale score. All steps 1–6 in Fig. 1 of CPM were performed across 5000 iterations of random pairings, creating a null distribution of the *r* statistic if the brain-behavior relation was observed by chance. The statistical significance of the true *r* statistic was computed by dividing the number of randomly generated *r* values exceeding the true *r* by the size of the null distribution. Only *r* statistics with $p < .05$ were considered significant.

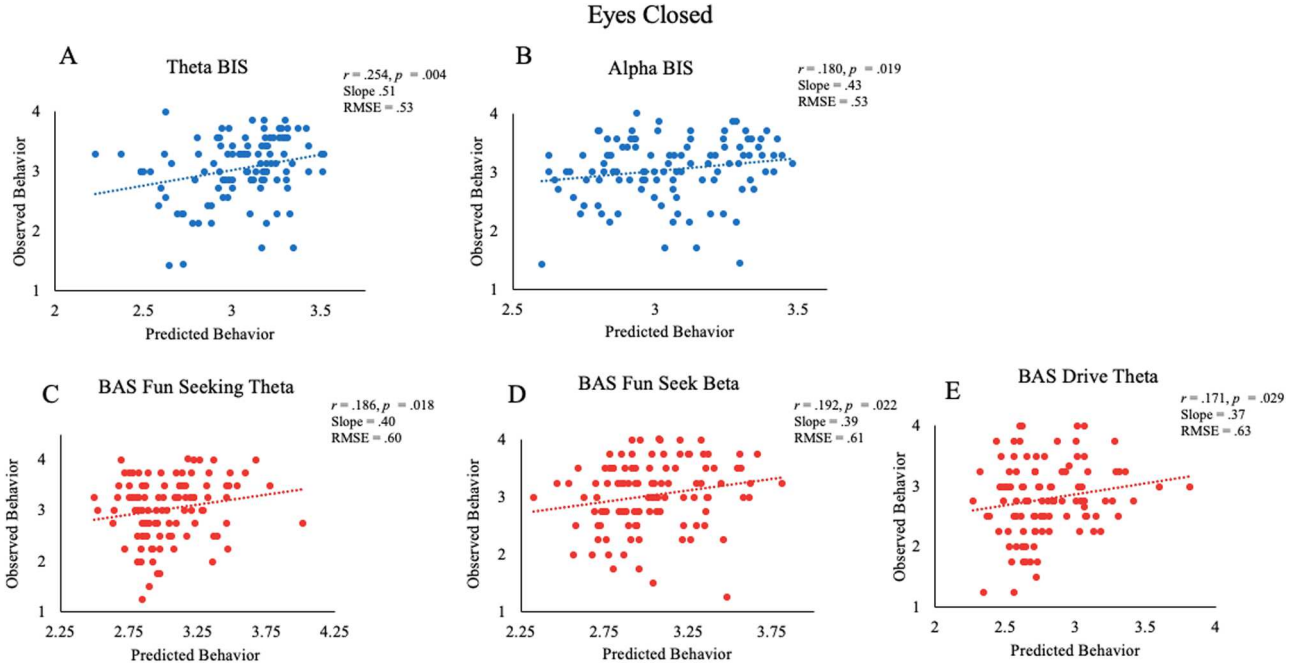

Fig. 3. Shows fits for the eyes closed condition between observed and predicted scores on the BIS (top row) for theta (A) and alpha (B) and BAS subscales (bottom row) including Fun Seeking for theta (C), Fun Seeking for beta (D), and Drive for beta (E).

7. Results

The results are presented in two sections. The first section presents the main results which is the capacity of the predictive models to reproduce scores on the BIS and BAS scales, which we present separately for each scale and band across conditions. The second section presents visualizations and descriptive statistics to characterize the networks used in the models we found to fit the behavioral data well.

7.1. Model fits

For the eyes closed condition, five models were able to predict observed scale scores at levels exceeding chance. Fig. 3 shows the relation between the observed and predicted scale scores for each of the models. Negative networks relating to BIS scores were observed for theta, $r = 0.254$, $p = .004$ (3 A) and alpha, $r = 0.180$, $p = .019$ (3B), indicating less synchronized activity in these networks relate to lower levels of behavioral inhibition. Positive networks predicting Fun Seeking were observed for theta, $r = 0.186$, $p = .018$ (3 C), and beta, $r = 0.192$, $p = .022$ (3D), as well as Drive for theta, $r = 0.171$, $p = .029$ (3E). As can be seen in Fig. 3, the range of predicted scores were narrower than the range of observed scores. To characterize the fit between the observed and predicted scores for each scale, we computed Root Mean Squared Error (RMSE) and slopes. The RMSE ranged from 0.53–0.63, indicating the predictive models produced scores that were inaccurate by about one-half of a score on the rating scale. Slopes were consistently below 1, indicating the predictive models consistently underestimated observed scores.

For the eyes open condition, four models were able to predict observed scores at levels exceeding chance. Fig. 4 shows the relation between the observed and predicted scores for each of the models. Three of these models were also observed for the eyes closed condition, including negative networks relating to BIS for theta, $r = 0.199$, $p = .017$ (4 A), and alpha, $r = 0.200$, $p = .014$ (4B), as well as a positive network relating to Fun Seeking for theta, $r = 0.208$, $p = .011$ (4 C). A negative network relating to mean BAS for gamma, $r = 0.215$, $p = .012$ (4D) was also observed. Like the networks for the eyes closed condition, the range of predicted scores were narrower than the range of observed scores. The RMSE ranged from 0.45–0.60, indicating the predicted models were inaccurate by about one-half of a score on the rating scale, and the slopes were consistently below 1, indicated the predictive models underestimated the observed scores.

7.2. Network characterization

Networks identified using data-driven methods such as CPM can be large and complex. To aid in characterizing networks, we created visualizations of their topography. The visualization of the networks identified for the eyes closed condition are shown in Fig. 5. The top row of Fig. 5A-B shows the networks relating to BIS in theta (5 A) and alpha (5B). The circles show electrode sites. More interconnected sites are depicted by larger circles, and each of the lines shows the connection (edge) related to BIS scores. To describe connectivity within and across regions, we carved the electrode map depicted in Fig. 2 into nine regions based on Calbi et al. (2019) consisting of left, midline, and right sections over frontal, central, and posterior regions. The second row shows a connectivity matrix for the total number of connections within and between regions. The third row shows the total number of connections involving each region. The bottom row shows the total number of connections within more coarsely divided regions, consisting of all sites within the frontal, central, and posterior regions. For the negative theta BIS network, short-range frontal and mid-range frontal-central connectivity was most salient. For the negative alpha BIS network, short-range frontal, mid-range frontal-central, mid-range central-posterior, and long-range frontal-posterior connectivity were prevalent. Fig. 5C-E shows the visualization of networks relating to the BAS subscales, including positive theta Fun Seeking (5 C), beta Fun Seeking (5D), and theta Drive (5E) networks. The topographies of the Fun Seeking networks were similar. Mid-range frontal-central, mid-range central--posterior, and long-range frontal-posterior connectivity were most prevalent. For the theta Drive network, however, mid-range central--posterior connectivity was most prevalent.

The visualizations of the networks identified in the eyes open condition are shown in Fig. 6. The topography of the networks that were observed for the eyes closed and eyes open condition were similar, especially those relating to BIS. For the negative theta BIS network, short-range frontal and mid-range frontal-central connectivity was most prevalent (6 A), and for the negative alpha BIS network, short-range frontal, mid-range frontal-central, mid-range central-posterior, and long-range frontal-posterior connectivity were prevalent (6B). The positive theta Fun Seeking network was also similar to the same network observed under the eyes closed (6 C), especially prevalence of mid-range frontal-posterior and long-range frontal-posterior connectivity. For the mean BAS gamma network, short-range posterior and mid-range central-posterior connectivity was most salient. In the General Discussion, we draw on the extant literature to shed light on the networks we identified.

8. General discussion

One goal of human neuroscience is to understand how individual differences in brain function relate to behavior. Network activity reflects communication within and between brain regions thought to underlie cognition, and disruptions to networks may underlie dysregulation (Nunez et al., 2015). Networks underlying specific behavioral tendencies are not always known or are too large and complex to be specified a priori. We used CPM to identify networks in the resting EEG under eyes closed and eyes open conditions relating to trait BIS and BAS in a data-driven fashion. Using a built-in cross-validation procedure, we tested whether the strength of these networks predicted trait BIS and BAS as measured by the BIS and BAS scales developed by Carver and White (1994). For the eyes closed condition, we were able to predict trait levels on the BIS from a negative theta and negative alpha network, Fun Seeking from a positive theta and positive beta network, and Drive from a positive theta network. For the eyes open condition, we also were able to predict trait levels on the BIS from a negative theta and negative alpha network and Fun Seeking from a positive theta network. A negative gamma network predicted mean BAS scores under these conditions as well. Prior studies have applied CPM to fMRI. Our study shows CPM can successfully be applied to EEG to identify networks relating to the BAS and BIS, which are well-studied systems involved in self-regulation and thought to underlie affective dispositions and self-regulatory processes (Gray, 1976, 1981; Pickering & Corr, 2008). The use of CPM with EEG can advance our understanding of resting EEG networks and may have clinical implications.

The most striking finding from the eyes closed condition was *only* negative networks related to BIS and *only* positive networks related to Fun Seeking and Drive. A similar pattern of results was observed for eyes open except a negative mean BAS gamma network was also observed. For BIS, negative resting networks in theta and alpha were observed when eyes were closed and open, indicating the more these networks synchronize the less sensitive the individual is to punishment cues. Prior studies using simultaneous fMRI-EEG have shown theta and alpha activity are associated with amygdala activity and BIS-related processes. For example, Sperl et al. (2019) used a fear-conditioning task in which a face was paired with electrical stimulation and found frontal-central theta activity and amygdala activity were both higher during recall of non-extinguished fear cues. Other studies have found alpha connectivity over the frontal region also relates to BIS-related processes. For example, Zotev et al. (2016) used a neurofeedback design based on amygdala activity to guide depressed individuals to think about happy memories. They found those with higher levels of depression also exhibited an

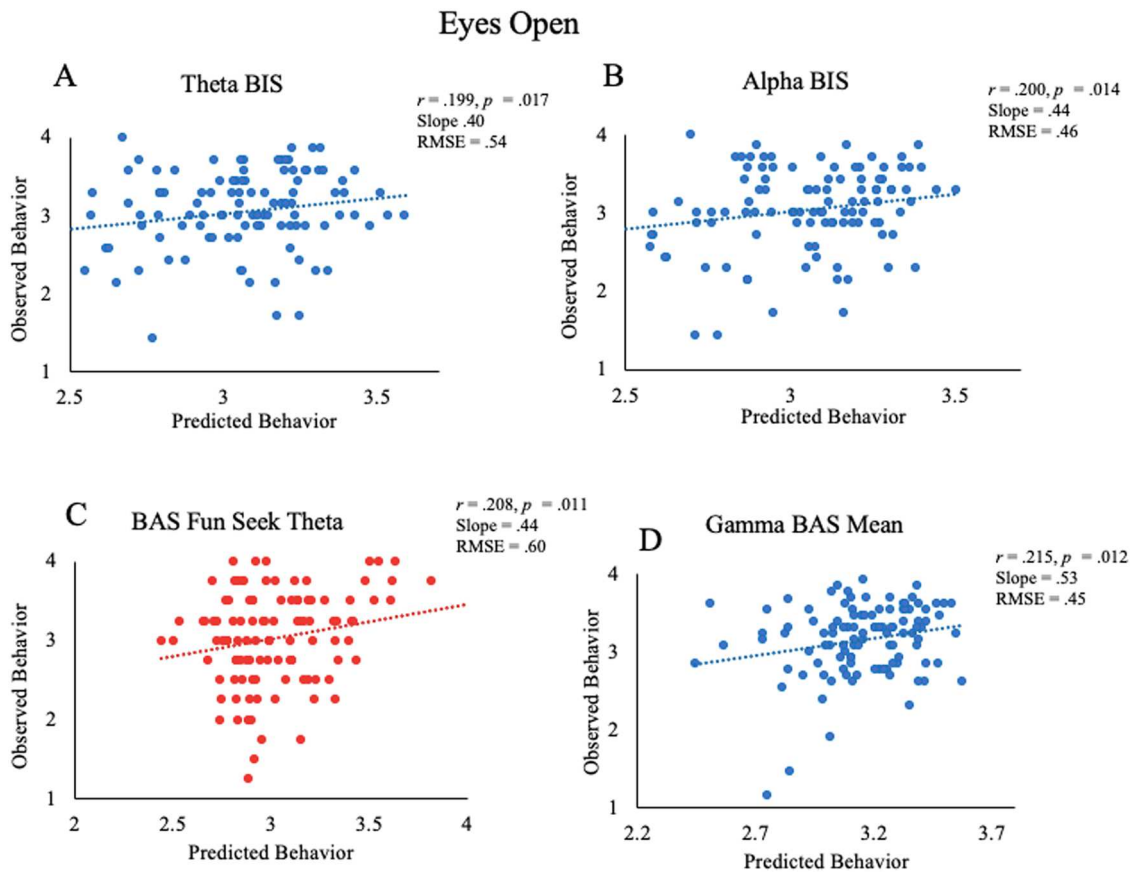

Fig. 4. Shows fits for the eyes open condition between observed and predicted scores on the BIS for theta (A) and alpha (B) and Fun Seeking for theta (C) and BAS Mean for gamma (D).

increase in alpha connectivity over left frontal-temporal regions across trials. Alpha connectivity over frontal regions has also been observed while people process emotional expressions. For example, Balconi and Mazza (2009) observed the highest levels of right frontal-central alpha connectivity while processing fear, anger, and surprise. We also observed connectivity in the BIS alpha network over left, right, and central frontal regions to be especially interconnected. Together, these studies point to network activity recorded over these regions to be especially important to the BIS.

Only positive networks related to Fun Seeking and Drive, indicating the more these networks synchronize, the more sensitive the individual is to aspects of reward. Fun Seeking reflects pursuit of reward and relates to novelty seeking, impulsiveness, and more risk behaviors (Caseras et al., 2003; Knyazev et al., 2004; Smillie et al., 2006; Zelenski & Larsen, 1999). For Fun Seeking, we found a positive theta network when eyes were closed and open and positive beta network when eyes were closed. These networks had strikingly similar topographies that involved long-range frontal-central, fontal-posterior, and central-posterior connectivity. Prior studies indicate long-range theta connectivity is involved in top-down regulatory processes (Anguera et al., 2013; Mizuhara et al., 2004; Sauseng et al., 2005). It is possible the networks we observed are involved in control over reward processing. Some evidence indicates theta and beta activity are involved in distinct aspects of processing reward and punishment. For example, high-beta activity is associated with reward processing, whereas theta activity is associated with processing of losses, especially over frontal-central regions (Marco-Pallares et al., 2008). Using simultaneous fMRI-EEG during a gambling task, Andreou et al. (2017) also observed high-beta activity was associated with processing of reward and theta activity was associated with processing losses. Additionally, they found theta and beta were associated with distinct networks. Theta was associated with brain regions involved in conflict monitoring, such as anterior cingulate cortex, whereas beta was associated with areas involved in reward processing, such as ventral striatum. We also found a positive theta network relating to Drive when eyes were closed which reflects goal-directedness, extraversion, and reward expectancy (Carver & White, 1994). Notably, several studies have also found relations between brain activity and Drive. For example, Putman et al. (2010) found frontal theta/beta activity related to Drive, and Knyazev and Slobodskoy-Plusnin (2009) found frontal theta activity increased upon reward notification in those high in Drive.

The extant literature on beta activation as it relates to motor functioning and motivation can also shed light on our findings. Beta power has been shown to be stronger when motor movement is resisted or suppressed (Androulidakis et al., 2007; Lalo et al., 2007; Zhang et al., 2008), to decrease in preparation and during completion of a goal (Pfurtscheller, 1997; Pogosyan et al., 2009), and that decreases in beta activity at rest over motor control regions related to higher composite BAS scores (Threadgill & Gable, 2018). Beta has also been shown to decrease more on reward trials relative to non-reward trials (Meadows et al., 2016) and when participants are told that a trial would be more difficult relative to trials that were anticipated to be easier (Wilhelm et al., 2021), suggesting that beta is involved in motivation based on reward as well as motivation to complete a difficult task. We found higher levels of Fun Seeking were predicted from a beta network during a resting state task in which participants were instructed to remain still and calm with their eyes closed. Participants who are higher in Fun Seeking may have a greater propensity to engage in impulsive behaviors and motivated by reward, and thus a resting state task that asks participants to sit quietly with eyes closed may require greater control to complete for individuals higher in Fun Seeking than those who are lower in Fun Seeking. It is possible the beta network we observed during the

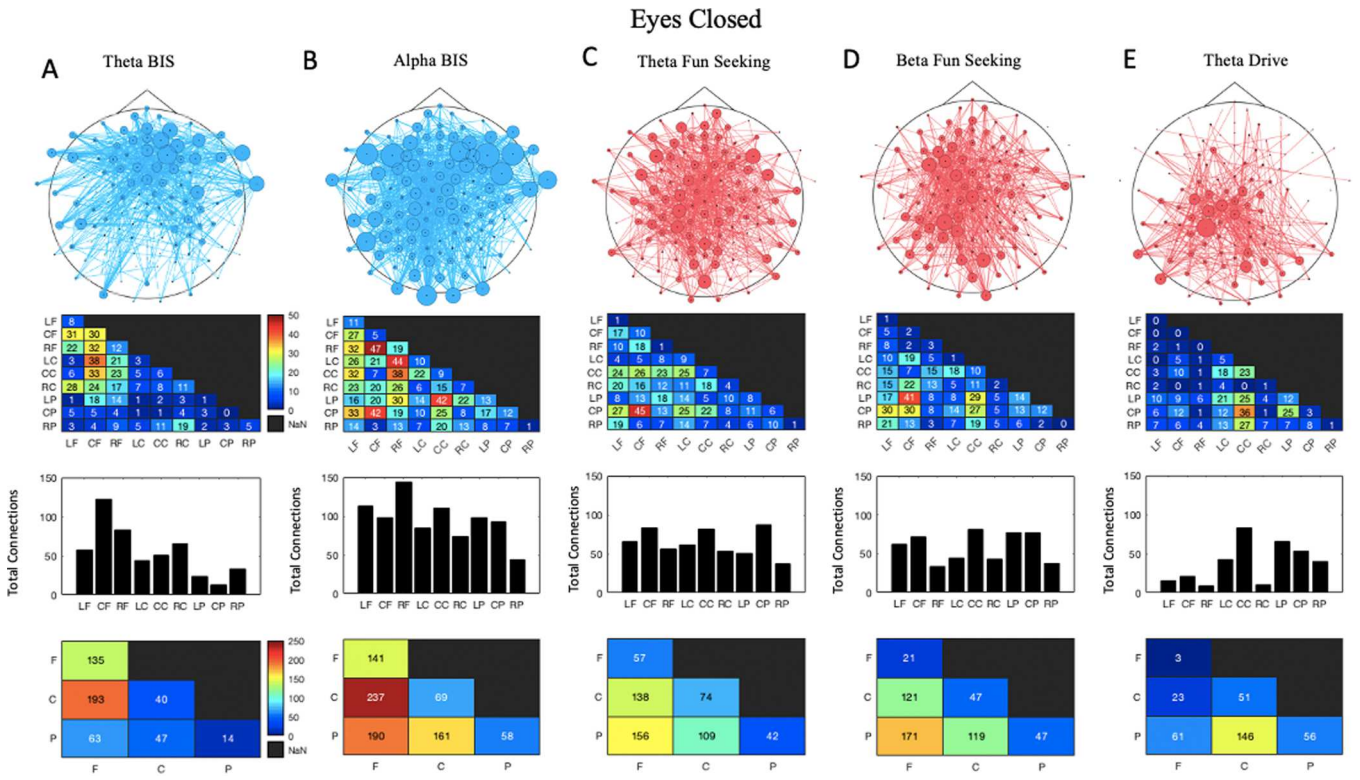

Fig. 5. Shows visualizations of predictive networks for the eyes closed condition. The top row shows the topography for predictive networks that fit the behavioral data well. Networks shown depict connectivity shared by 95% of iterations for the leave-one-out cross-validation procedure. Negative networks are shown in blue (A-B) and positive networks are shown in red (C-D). The second row shows a connectivity matrix depicting the number of connections (warmer colors, more connections) within and between regions over the scalp as shown in Fig. 2, including left frontal (LF), central frontal (CF), right frontal (RF), left central (LC), central central (CC), right central (RC), and left posterior (LP), central posterior (CP), right posterior (RP). The third row shows the total number of connections involving each region. The bottom row shows a connectivity matrix depicting the number of connections within coarsely divided regions into frontal (F), central (C), and posterior (P) regions.

eyes closed condition to relate to Fun Seeking is involved in these control processes.

Studies using CPM with fMRI have primarily reported networks identified when participants rest with their eyes closed (Feng et al., 2018, 2019; Lu et al., 2019; Wang et al., 2021). A contribution of this study is it applied CPM to resting EEG under eyes closed and eyes open conditions. These conditions are associated with distinct topographies and levels of EEG power, which may be due in part to the need to maintain attention on a visual stimulus during the eyes open condition (Barry et al., 2007; Perone et al., 2019; for a review, see Anderson & Perone, 2018). Consistent with this hypothesis, lower levels of the theta / beta ratio have been observed during eyes open relative to eyes closed (Perone et al., 2019), which is a neural correlate of engaged attention (van Son et al., 2019). The pattern of results observed herein is also consistent with this hypothesis. We found more synchronization of a gamma network over the posterior related to lower levels of mean BAS only in the eyes open condition. Posterior gamma activity is involved in visually attending to a stimulus (Müller et al., 2000). People low in mean BAS are less impulsive (Braddock et al., 2011) and may be able to maintain attention control in the eyes open condition well, as indicated by more synchronization of the posterior gamma network. Some effects present in the eyes closed condition were absent from the eyes open condition, including the positive theta Drive and positive beta Fun Seeking networks. We speculate that these relations emerge when eyes are closed due to engaged control processes that are allocated elsewhere in the eyes open condition when there is a need to maintain attention on a visual stimulus. More research investigating the ongoing processes across resting conditions is crucial to more fully understand why some relations are observed in one condition and not the other, a topic we turn to next.

An important contribution of the current study is application of CPM to resting EEG to identify predictive networks related to motivational processes that are thought to underlie a wide range of behaviors. We identified four important directions for future research to advance understanding of networks identified using CPM with EEG. One direction for future research is to study the link between resting state network activity and ongoing processes at rest. The intrinsic dynamics of the brain at rest may reflect individual differences in ongoing regulatory processes also at work in other contexts. For example, a study by Diaz and colleagues (2013) asked participants to report on their thoughts during a resting state task, ranging from planning for the future to thinking about other people. Participants also reported on the quality of their thoughts (e.g., "I had busy thoughts"), their emotional valence during the task (e.g., "I felt happy"), and attention to their body (e.g., "I thought about my heartbeat"; Diaz et al., 2013). Importantly, participants' ongoing cognition during rest was shown to relate to trait-level indicators of mental well-being, anxiety, and depression. Asking participants about their ongoing cognition across conditions during the resting state task may shed light on the activity of BAS or BIS networks at rest and whether it relates to BIS and BAS activity in other contexts.

A second direction for future research is to test the generalizability of BAS and BIS networks. This could be achieved in several ways. For example, the activity of resting BAS and BIS networks could be extracted during a gambling task to test whether their activity predicts behavioral measures of sensitivity to rewards and losses. In the current study, we did not identify any resting networks that predicted Reward Responsiveness or the mean of all BAS items. It is possible that tasks that require reward processing would be more likely to engage networks relating to Reward Responsiveness and a BAS composite score. Another example is applying CPM to performance in several tasks designed to measure BAS

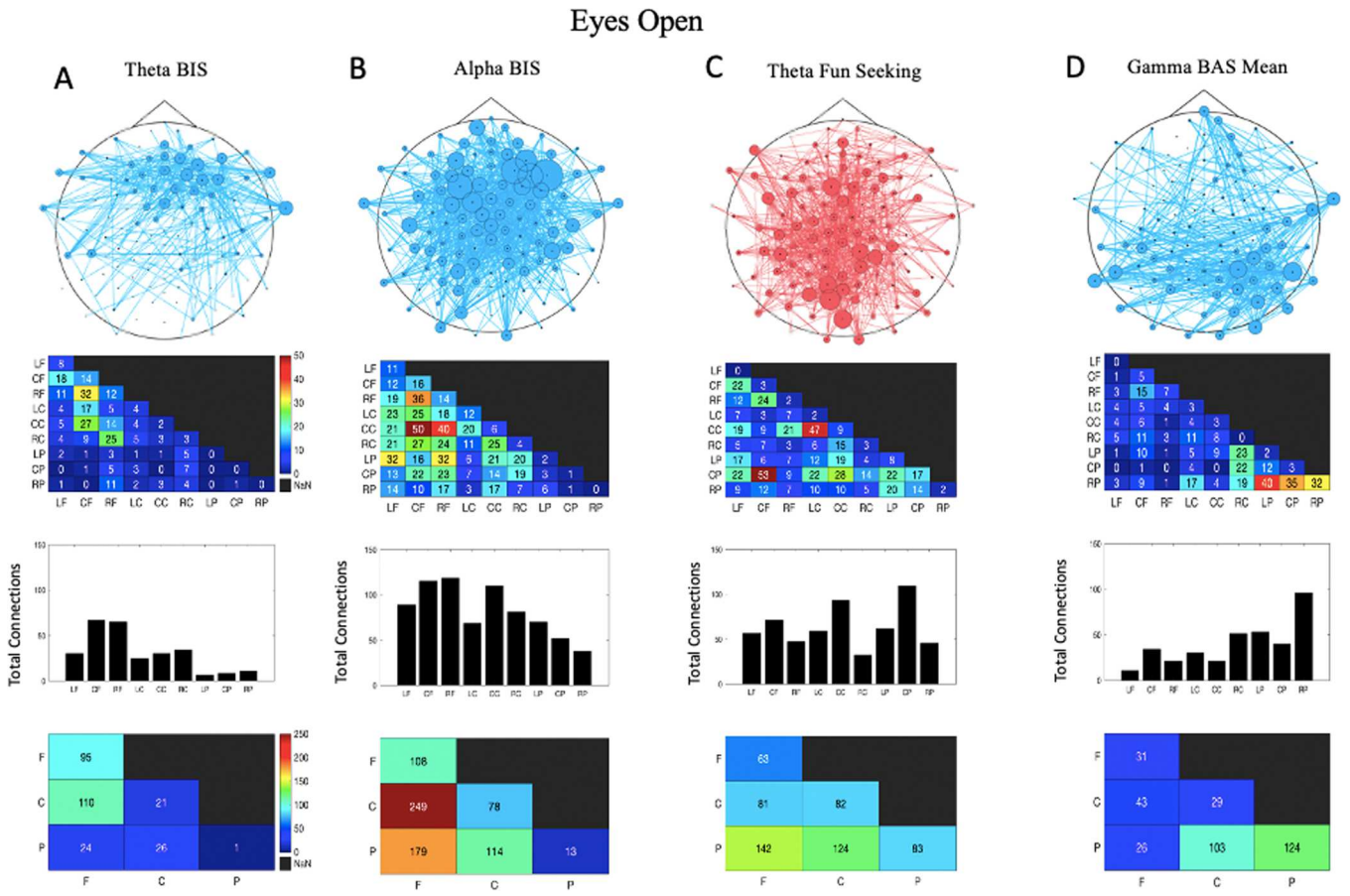

Fig. 6. Shows visualizations of predictive networks for the eyes open condition. The top row shows the topography for predictive networks that fit the behavioral data well. Networks shown depict connectivity shared by 95% of iterations for the leave-one-out cross-validation procedure. Negative networks are shown in blue and positive networks are shown in red. The second row shows a connectivity matrix depicting the number of connections (warmer colors, more connections) within and between regions over the scalp as shown in Fig. 2, including left frontal (LF), central frontal (CF), right frontal (RF), left central (LC), central central (CC), right central (RC), and left posterior (LP), central posterior (CP), right posterior (RP). The third row shows the total number of connections involving each region. The bottom row shows a connectivity matrix depicting the number of connections within coarsely divided regions into frontal (F), central (C), and posterior (P) regions.

and BIS activity and identify whether core regions emerge across a range of networks identified in a data-driven fashion. A third direction for future research is to study networks across developmental periods to determine their stability. For example, one question is whether the same resting BAS and BIS networks identified during early adulthood have predictive value during other periods of development. Braams et al. (2014) found BAS-related processes (e.g., risk-taking) exhibited an inverted u-shape trend from 8 to 27 years of age, which was also observed for neural activity in a brain region associated with reward processing (nucleus accumbens). Such age-related changes may be associated with change in the strength of the same BAS or BIS networks, or age-related change may be associated with distinct networks.

A fourth direction for future research is to test the clinical value of CPM applied to the EEG. CPM is especially useful to identify networks predictive of specific behaviors, and studies using fMRI have shown there is clinical value to identifying such predictive networks. For example, Yip et al. (2019) used CPM to identify networks that predicted abstinence of cocaine use in novel subjects during treatment for cocaine use disorder. Ju et al. (2020) identified networks that predicted how well novel subjects with depression responded to treatment. One implication of this clinical research is CPM may help tailor treatment options to specific individuals. EEG is widely used across the lifespan, and disruptions to functional networks might underlie disorders (Nunez et al., 2015). Indeed, abnormalities in functional connectivity in the EEG has been shown to relate to disorders, such as ADHD (Murias et al., 2007), and abnormalities in functional connectivity in the EEG are present prior to the emergence of neurodevelopmental disorders, such as Autism (Orekhova et al., 2014; Righi et al., 2014). CPM may be helpful in predicting responsiveness to treatment of developmental disorders or identifying networks predictive of the later emergence of neurodevelopmental disorders before they develop.

In conclusion, we applied CPM to resting EEG and identified BAS and BIS networks capable of predicting trait levels of BAS and BIS in novel subjects measured via self-report. The BAS and BIS are widely studied because their activity underlies regulatory processes across a range of contexts, and variation in their activity across individuals is associated with distinct behavioral profiles. Several areas of future research are needed to advance use of CPM with EEG, including identifying core interconnected regions across a range of contexts relying on BAS and BIS activity and testing the stability of such networks across development. CPM has been shown to have clinical value when applied to fMRI and may be especially useful for EEG because it is widely used across the lifespan and abnormalities in the EEG may be an important physiological marker of disorders.

Data availability

The authors are unable or have chosen not to specify which data has been used.

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