

Psychopathic traits are differentially associated with efficiency of neural communication

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Abstract

Recent advances in the application of graph theory made it possible to quantify the efficiency of communication within a neural network, going beyond traditional connectivity methods that only identify the degree to which neural regions are connected. Psychopathic traits, namely, interpersonal-affective and impulsive-antisocial traits, have been linked to widespread and distinct disruptions in neural connectivity. The efficiency of neural communication for individuals high on these psychopathic traits, though, is unknown. In the present study, resting-state EEG was used to generate a connectivity matrix (i.e., weighted phase lag index) for multiple frequency bands. These connectivity matrices were examined using minimum spanning tree analysis, a graph theory approach that allows for the examination of neural efficiency, and regressed on Self-Report Psychopathy-Short Form scores ($n = 158$, unselected community sample). Results indicated that individuals with higher interpersonal-affective traits had significantly less efficient communication within alpha1 (i.e., long-range neural communication) and gamma (i.e., short-range neural communication) frequency bands. Conversely, individuals with higher impulsive-antisocial traits had more efficient communication within these same frequency bands. Overall, elevated psychopathic traits were related to alterations in the basic efficiency of neural communication. Moreover, this unique application of graph analysis provides a new avenue for inquiry into the mechanisms underlying the chronic and severe behavior of individuals with psychopathic traits.

KEYWORDS

connectivity analysis, EEG, minimum spanning tree, psychophysiology, psychopathic traits

1 | INTRODUCTION

The capacity for socialization is one of the most fundamental and important qualities of human nature. Yet, throughout

history and across cultures, we find individuals whose biological temperament precludes normal socialization (Lykken, 1957). Psychopathic individuals exemplify this personality type, showing social, emotional, and behavioral deviances that violate socialization norms. These individuals are characterized by interpersonal-affective traits that interfere with their ability to form genuine relationships and display an adequate

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depth and breadth of emotion, as well as impulsive-antisocial traits that involve a general failure to inhibit inappropriate actions and a chronic antisocial lifestyle (Hare, 2003). Although their numbers in the general population are small (approximately 1%), the behavior of individuals high on psychopathic traits comes at a great cost to the individual and to society, resulting in a substantial economic and public health burden (Kiehl & Hoffman, 2011). A clear understanding of the mechanisms that underlie their abject failure to adhere to social norms remains somewhat elusive. Increasingly, though, there is evidence that the interpersonal deficits, emotional disturbances, and antisocial behavior characteristics of individuals high on psychopathic traits are rooted in widespread neural abnormalities (Carre, Hyde, Neumann, Viding, & Hariri, 2013; Cohn et al., 2015; Finger et al., 2012; Glenn, Raine, & Schug, 2009; Hoppenbrouwers et al., 2013, 2014; Koenigs, Kruepke, & Newman, 2010; Motzkin, Newman, Kiehl, & Koenigs, 2011; Pape et al., 2015; Philippi et al., 2015; Yang et al., 2012; Yoder, Lahey, & Decety, 2016).

One way of gaining further insight into these neural abnormalities in individuals high on psychopathic traits is the examination of neural connectivity. To date, two connectivity methodologies have been applied in psychopathy research: (a) traditional connectivity analyses that examine region-to-region relationships, and (b) thresholded graph analyses. First, traditional connectivity analyses examine the strength of neural communication between brain regions by either evaluating the degree to which discrete brain regions are functionally coupled (i.e., the degree to which neural activity in one region is correlated with activity in another region; Fox & Greicius, 2010) or by determining the thickness or integrity of white matter tracts connecting various brain regions (Hua et al., 2008). Across studies using these traditional connectivity methods, individuals high on psychopathic traits exhibit widespread disruptions in neural communication. For example, individuals high on psychopathic traits exhibit connectivity abnormalities between discrete brain regions (Finger et al., 2012; Hoppenbrouwers et al., 2013; Motzkin et al., 2011; Pape et al., 2015; Yoder et al., 2016), within and between major neural networks (Carre et al., 2013; Cohn et al., 2015; Glenn et al., 2009; Philippi et al., 2015), and between cortical hemispheres (Hoppenbrouwers et al., 2014; Raine et al., 2003). While psychopathic traits are consistently associated with aberrant neural connectivity, the directionality of these differences is not always consistent, particularly when examining the subcomponent traits of psychopathy (Carre et al., 2013; Pape et al., 2015; Philippi et al., 2015).

Philippi and colleagues (2015) find that the deficits in functional connectivity seen in individuals high on psychopathic traits are primarily driven by the interpersonal-affective psychopathic traits (i.e., factor 1 traits), not the impulsive-antisocial psychopathic traits (i.e., factor 2 traits).

In fact, when factor 1 and factor 2 traits are modeled separately, factor 1 traits are associated with blunted connectivity in the default mode, frontoparietal, and cinguloopercular networks, while factor 2 traits are associated with hyperconnectivity in those networks (Philippi et al., 2015). This differential, and opposite, pattern of results is consistent with dual-trait conceptualizations of psychopathy (Neumann, Johansson, & Hare, 2013; Patrick, 2007) and suggests that these subcomponent psychopathic traits are associated with distinct abnormalities in the neural networks subserving social cognition, initial allocation of attention, and cognitive control, respectively (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Jack et al., 2013; Spreng & Grady, 2010; Spreng, Mar, & Kim, 2009). Regardless of these directional inconsistencies, there is an overwhelming amount of evidence from traditional connectivity analyses that individuals high on psychopathic traits display distinct differences in neural connectivity (Carre et al., 2013; Cohn et al., 2015; Finger et al., 2012; Glenn et al., 2009; Hoppenbrouwers et al., 2013, 2014; Koenigs et al., 2010; Motzkin et al., 2011; Pape et al., 2015; Philippi et al., 2015; Yoder et al., 2016).

A second method for examining the aberrant connectivity exhibited in individuals high on psychopathic traits is the application of thresholded graph analyses to structural network organization data. Whereas traditional connectivity analyses essentially quantify whether or not regions communicate with one another, graph analyses are used to estimate how well and in what manner neural regions communicate with one another by quantifying various network characteristics, including metrics of network efficiency. To illustrate the distinction between traditional connectivity and network efficiency measures, consider the following example: Two small airlines (Airline I and II) offer flights between five airports (A, B, C, D, and E). Airline I offers flights between airports A-B, B-C, C-D, and D-E, meaning to get from airport A to airport E a passenger needs to travel through three additional airports. In contrast, Airline II offers all flights between airports through airport A, a “hub,” allowing a passenger to travel to any airport while only going through one additional airport (i.e., A) at most. Using traditional connectivity analyses, Airline I’s network and Airline II’s network are equally connected; passengers can travel from any of the airports to any other airport. However, using a graph theory approach, Airline I is less efficient than Airline II, requiring more time and energy for passengers to travel among the various airports. In the context of neural networks, traditional connectivity analyses estimate the amount of communication between brain regions while graph analyses can estimate the amount of time or energy required to transfer information from one part of the network (or node) to any other part of the network (Bullmore & Sporns, 2009; Minati, Grisoli, Seth, & Critchley, 2012; Reijneveld, Ponten, Berendse, & Stam, 2007; Smit, de Geus, Boersma, Boomsma, & Stam,

2016; Stam & Reijneveld, 2007; Stam et al., 2014; Tewarie, van Dellen, Hillebrand, & Stam, 2015). In thresholded graph analyses, specifically, the efficiency of neural communication is defined as the number of edges (i.e., connections between nodes defined by a specific arbitrary strength threshold) that information needs to travel through during neural communication. The more edges that information needs to pass through (i.e., the longer the average path length from one node to another node), the less efficient the network (Smit et al., 2016; Stam & Reijneveld, 2007; Stam et al., 2014; Tewarie et al., 2015). In general, less efficient networks tend to be associated with impairments in higher-order cognitive processes (e.g., decision making, social reasoning; Jakab et al., 2013; Minati et al., 2012). By contrast, networks with more direct edges between neural nodes are more efficient (requiring less time or energy to transfer information between nodes), particularly when those direct edges are connecting functionally related nodes (i.e., nodes that commonly communicate or coactivate). Moreover, more efficient neural communication tends to be associated with improved cognitive functioning (Langer et al., 2012; Minati et al., 2012; Neubauer & Fink, 2009; van Den Heuvel, Stam, Kahn, & Hulshoff Pol, 2009).

In research on psychopathic traits, only one study used this thresholded graph approach. Utilizing structural MRI data, Yang and colleagues (2012) find that individuals high on psychopathic traits display a less efficiently organized neural network within the frontal lobe. More specifically, when information is transferred from one node in the frontal lobe to any other frontal node, it travels through more edges in individuals high on psychopathic traits than in individuals low on these traits. This suggests that individuals high on psychopathic traits may display a delay or deficit in their ability to efficiently integrate information between frontal brain regions, potentially resulting in delayed or fractionated processing of information (Bullmore & Sporns, 2009; Yang et al., 2012).

While Yang and colleagues (2012) provide the first evidence of altered information flow in individuals high on psychopathic traits, recent advances in graph analysis led to criticism of the methods used in a thresholded graph approach. Results from thresholded graph analyses are unstable, often changing drastically in response to minor changes in the arbitrary threshold used to define the graph (Reijneveld et al., 2007; Smit et al., 2016; Stam & Reijneveld, 2007; Stam et al., 2014; Tewarie et al., 2015; Van Wijk, Stam, & Daffertshofer, 2010). Additionally, because edges in thresholded graphs are defined by an arbitrary threshold for connection strength, most thresholded graphs have a different total number of edges (e.g., if graph A has 7 connections with a connection strength over threshold X, but graph B has 18 connections with a connection strength over threshold X, then graph A will only have 7 edges, but graph B will have

18 edges), which is highly problematic for between-groups (i.e., between-graph) comparisons, like the ones reported by Yang and colleagues (2012). Comparing thresholded graphs with differing numbers of edges artificially inflates the likelihood of finding between-groups differences in network efficiency (Reijneveld et al., 2007; Smit et al., 2016; Stam & Reijneveld, 2007; Stam et al., 2014; Tewarie et al., 2015; Van Wijk et al., 2010). Moreover, beyond the specific limitations of thresholded graph analyses, Yang and colleagues (2012) used an indirect measure of structural connectivity (i.e., gray matter thickness). Notably, other research using traditional connectivity analyses in individuals high on psychopathic traits shows inconsistencies between abnormalities in structural and functional connectivity (Finger et al., 2012); thus, it remains unclear whether psychopathic traits also are associated with any abnormalities in neural network efficiency at a functional level. Despite these limitations, Yang et al. (2012) provides preliminary evidence that individuals high on psychopathic traits exhibit less efficiently organized neural networks in the frontal lobe.

Overall, there is strong evidence that individuals with psychopathic traits display widespread disruptions in neural connectivity (Carre et al., 2013; Cohn et al., 2015; Finger et al., 2012; Glenn et al., 2009; Hoppenbrouwers et al., 2013, 2014; Koenigs et al., 2010; Motzkin et al., 2011; Pape et al., 2015; Philippi et al., 2015; Yang et al., 2012; Yoder et al., 2016). Moreover, these disruptions may lead to inefficient neural communication, particularly within the frontal lobes (Yang et al., 2012). However, it is unlikely that any neural inefficiency is limited to the frontal lobes. From traditional connectivity findings, individuals high on psychopathic traits show abnormalities in a variety of different neural networks and circuits. Two of the networks most reliably identified include the frontostriatal circuitry (Motzkin et al., 2011; Sobhani, Baker, Martins, Tuvblad, & Aziz-Zadeh, 2015; Wolf et al., 2015) and the default mode network (Glenn et al., 2009; Motzkin et al., 2011; Philippi et al., 2015), which are essential for higher-order cognitive processes such as decision making (Brand, Labudda, & Markowitsch, 2006; Clark, Cools, & Robbins, 2004; Dalley, Mar, Economidou, & Robbins, 2008) and affective theory of mind (Jack et al., 2013; Sebastian, Fontaine et al., 2012; Spreng & Grady, 2010; Spreng et al., 2009), respectively. While inefficient communication within those networks might help explain the psychopathy-related impairments in those higher-order processes (e.g., decision making, Buckholz et al., 2010; Glenn et al., 2009; Koenigs et al., 2010; and affective theory of mind, Sebastian, McCrory et al., 2012; Shamay-Tsoory, Harari, Aharon-Peretz, & Levkovitz, 2010), the exact association between psychopathic traits and neural (in)efficiency remains unclear due to the limitations of the previous connectivity approaches used in psychopathy research.

Newer applications of graph theory using minimum spanning tree (MST) analysis address the critical limitations of thresholded graph analyses and other conventional graph analyses (Reijneveld et al., 2007; Smit et al., 2016; Stam & Reijneveld, 2007; Stam et al., 2014; Tewarie et al., 2015). Similar to thresholded graphs, MSTs are derived from connectivity data; however, they differ from thresholded graphs in that MSTs are loopless and have a fixed number of edges. While the loopless nature of MSTs limits their ability to evaluate certain network characteristics (e.g., clustering or modularity), the fixed number of edges confers a couple of advantages to MST analyses when evaluating network efficiency. First, it avoids the need to set an arbitrary threshold for an edge to be included in the network, allowing for more reliable and valid evaluations of network efficiency (Reijneveld et al., 2007; Smit et al., 2016; Stam & Reijneveld, 2007; Stam et al., 2014; Tewarie et al., 2015). Second, the fixed number of edges allows for unbiased comparisons of graphs between individuals or groups (e.g., comparisons between a psychopathy group and a control group; Fraga Gonzalez et al., 2016; Reijneveld et al., 2007; Smit et al., 2016; Stam & Reijneveld, 2007; Stam et al., 2014; Tewarie et al., 2015). Due to these advantages, this MST approach is often used to examine magnetoencephalogram (MEG) or EEG connectivity data in various clinical populations, (e.g., dyslexia, Fraga Gonzalez et al., 2016; multiple sclerosis, Tewarie et al., 2014). However, MST methods have not yet been applied to the examination of neural efficiency in psychopathic traits.

The present study uses MST analyses on resting-state EEG data to evaluate the relationship between psychopathic traits and the efficiency of neural communication. Given the research showing that the interpersonal-affective (factor 1) and impulsive-antisocial (factor 2) traits of psychopathy are associated with divergent, and even opposing, patterns of neural connectivity (Carre et al., 2013; Pape et al., 2015; Philippi et al., 2015; see also Patrick, 2007, for discussion of the dual-trait model of psychopathy), the present study focuses on these subcomponent traits of psychopathy. Additionally, the present study examines multiple resting-state EEG wavebands: alpha (8–12 Hz) and gamma (30–45 Hz). First, the alpha frequency bands are examined because low-frequency bands, such as alpha, are reliably implicated in long-range neural communication between spatially disparate brain regions (i.e., integration of information across disparate brain regions; Canolty et al., 2006; Doesburg, Vinette, Cheung, & Pang, 2012; Fell & Axmacher, 2011; Tewarie et al., 2014; von Stein & Sarnthein, 2000; Vourkas et al., 2014), which is vital for higher-order processes (Sepulcre et al., 2010); efficient alpha communication is linked with specific processes shown to be deficient in individuals high on psychopathic traits (e.g., decision making and affective theory of mind; Jakab et al., 2013; Minati et al., 2012); alpha activity is implicated in the functioning of the default mode network (Broyd et al., 2009; Chen, Feng, Zhao,

Yin, & Wang, 2008), which appears to be dysfunctional in individuals with psychopathic traits (Glenn et al., 2009; Motzkin et al., 2011; Philippi et al., 2015); and abnormal alpha activity is associated with aggressive and antisocial individuals (Kamarajan et al., 2006; Lindberg et al., 2005; Rybak, Crayton, Young, Herba, & Konopka, 2006). Second, the gamma frequency band is examined because it is implicated in short-range neural communication (von Stein & Sarnthein, 2000) vital to lower-order processes (Sepulcre et al., 2010), and recent evidence shows that individuals high on psychopathic traits display aberrant neural responses to more basic, lower-order sensory processes (Tillem et al., 2016). By considering both alpha and gamma frequency bands, it is possible to examine whether abnormalities related to psychopathic traits are specific to higher-order versus lower-order processes, or are a reflection of truly widespread abnormalities that span levels of processing.

Based on previous research showing that factor 1 traits are associated with hypoconnectivity, abnormal higher-order processes associated with alpha, and abnormal lower-order processes associated with gamma, it is expected that individuals high on factor 1 traits, but not factor 2 traits, will show less efficient neural communication within the alpha and gamma frequency bands. By contrast, based on previous research showing that factor 2 traits are associated with hyperconnectivity and opposite neural patterns as factor 1 traits, it is possible that these traits will be associated with efficiency patterns that are the opposite of factor 1 traits.

2 | METHOD

2.1 | Participants

Participants were 172 community members from the general population and student population at Erasmus University Rotterdam. The sample consisted of 108 male (62.79%) and 63 female (36.63%) adults aged 17 to 63 ($M = 22.58$, $SD = 7.47$) who were recruited through online social media, flyers, and an online research participation channel for students. Prior to data collection, a prescreen phone interview and in-person assessment materials were used to exclude individuals who were younger than 16 or over 65 and individuals who had a history of neurological or psychiatric issues that may impact their comprehension of the materials or completion of the self-report measures (e.g., uncorrectable auditory or visual deficits; head injury with loss of consciousness greater than 30 min; risk for psychiatric morbidity; and common mental health domains of depression, anxiety, somatic symptoms, and social withdrawal). All participants provided written informed consent. Research was conducted in compliance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and the standards established by the Institutional Review Board at

Erasmus University Rotterdam. Participants earned a candy bar or course credits (students) for their completion of the self-report measures and EEG recording.

2.2 | Psychopathic traits measure

2.2.1 | Self-Report Psychopathy-Short Form

(SRP-SF, Dutch version; Gordts, Uzieblo, Neumann, Van den Bussche, & Rossi, 2017). Psychopathic traits were assessed using the SRP-SF, which consists of 29 items derived from the full 64-item version of the Self-Report Psychopathy-III. Every item is measured on a 5-point Likert scale (1 = *disagree strongly* to 5 = *agree strongly*). The SRP-SF has a strong correlation with the Self-Report Psychopathy-III, which in turn correlated strongly with the Psychopathy Checklist-Revised (PCL-R; Neumann, Hare, & Pardini, 2015). The SRP-SF has a total minimum score of 29 and a maximum score of 145. The SRP-SF factors, factor 1 (interpersonal-affective) and factor 2 (impulsive-antisocial), are established strongly correlated measures of the subcomponent traits of psychopathy (in the present sample, $r = .713$, $p < .001$). Factors 1 and 2 have a minimum score of 14 and a maximum score of 70.

The reliability and validity of the SRP-SF and its factors are well established (Debowska, Boduszek, Kola, & Hyland, 2014; Gordts et al., 2017; Hare, 2003; Lilienfeld & Fowler, 2006; Mahmut, Menictas, Stevenson, & Homewood, 2011; Neumann & Pardini, 2014). In the present study, SRP-SF factor 1 and SRP-SF factor 2 scores had a Cronbach's α of .843 and .809, respectively. Regarding validity of the SRP-SF scores in the present study, we ran a confirmatory factor analysis with STATA using the weighted least squares means and recommended fit indices (Hu & Bentler, 1999). The two-factor solution achieved acceptable fit across multiple indices (chi-square/ $df = 896.25/376$, RMSEA = .07, $p_{close} < .001$, SRMR = .08, CFI = .86).

2.3 | EEG data acquisition

EEG was recorded during a resting state of either 8 ($n = 148$) or 6 min ($n = 24$) total, in which eyes open (EO) and eyes closed (EC) conditions alternated every 1 min. Brain activity was recorded with the EEG using a BioSemi ActiveTwo System amplifier (Amsterdam, The Netherlands) from the 32 standard (10–20 International system) scalp sites and two additional scalp sites (FCz, CPz) using active Ag/AgCl electrodes. Four additional electrodes were used to measure vertical electrooculogram (VEOG) and horizontal electrooculogram (HEOG) and were placed above and below the left eye (VEOG) and at the outer canthi of the eyes (HEOG). Two additional electrodes were placed on the left and right mastoids. All signals were digitized with a sampling rate of 512 Hz and 24-bit analog-to-digital conversion and were filtered offline.

2.4 | EEG data preprocessing

Prior to data processing, 10 participants were excluded from the analysis due to either technical issues during data acquisition (e.g., broken sensors, software crashes; $n = 9$) or missing questionnaire data ($n = 1$). For the remaining 162 participants, EEG data from 26 channels (F3, Fz, F4, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP1, CP2, P3, Pz, P4, O1, Oz, O2, Fp1, AF3, PO3, PO4, AF4, Fp2) were preprocessed offline using BrainVision Analyzer 2 software (Brain Products GmbH, Germany). The signals were rereferenced to the linked mastoids, and ocular artifacts were removed from the EEG using independent component analyses (Jung et al., 2000). Eye movements were recorded with electrodes placed above and below the left eye and at the outer canthi. For each condition, 120 ($n = 139$) or 90 ($n = 23$) epochs with a length of 2 s were created, which were then filtered using a 0.02–50 Hz (24 dB/oct) band-pass filter and checked for gradient artifacts (maximum voltage step of 50 $\mu\text{V}/\text{ms}$) and excessively low activity (below 0.5 μV in 100-ms intervals). The data were subsequently exported as text files for connectivity analysis in BrainWave (<https://home.kpn.nl/stam7883/brainwave.html>; version 9.152.4.1).

Following preprocessing, participants who had all their data rejected due to signal artifact ($n = 2$) or who had significantly fewer valid data than the rest of the sample (i.e., statistical outliers for amount of valid data following data rejection; $n = 2$) were excluded from further analysis, leaving the final sample at $n = 158$. We ran a logistic regression comparing SRP-SF scores in included versus excluded participants. The analysis showed that excluded participants did not significantly differ from included participants in SRP-SF factor 1 scores, $\chi^2(2) = 3.234$, $p = .198$; $\beta = -.027$, $p = .599$, or SRP-SF factor 2 scores, $\beta = -.043$, $p = .389$. For characteristics of the final sample, see Table 1.

2.5 | EEG connectivity analysis

Prior to generating the MST graphs, connectivity data for each node in the network needed to be obtained. Accordingly, the electrode space was rearranged and matched to the montage built into the BrainWave package, resulting in 18 usable electrodes.¹ Next, data were filtered into relevant frequency bands (i.e., alpha1, 8–10 Hz; alpha2, 10–12 Hz;² gamma, 30–45 Hz), and run through a weighted phase lag index (wPLI) connectivity analysis. This wPLI was calculated to evaluate functional connectivity between the 18

¹Useable electrodes included F3, Fz, F4, FC5, FC1, FC2, FC6, C3, Cz, C4, P3, Pz, P4, O1, Oz, O2, Fp1, Fp2.

²The alpha frequency band was broken down into alpha1 and alpha2 in accordance with recent methodological conventions in graph theory analysis (Fraga Gonzalez et al., 2016; Tewarie et al., 2014; van Diessen, Otte, Braun, Stam, & Jansen, 2014).

TABLE 1 Final sample characteristics

	<i>N</i>	Min	Max	Mean	<i>SD</i>
Age	158	17.00	63.00	22.66	7.72
Gender					
Male	103				
Female	55				
Number of valid epochs					
Eyes closed epochs	157	20	120	102.57	21.58
Eyes open epochs	158	25	120	102.37	22.39
Combined epochs	158	56	240	204.41	43.38
SRP-SF total score	158	29	98	53.83	14.16
SRP-SF factor 1	158	14	48	27.61	7.98
SRP-SF factor 2	158	15	52	26.22	7.31

electrodes, within each epoch, for each frequency band, for each condition, for each participant. Standard phase lag index analysis quantifies phase synchronization in two different time series by examining the asymmetry of the distributions of instantaneous phase differences. wPLI expands upon these analyses by also accounting for the magnitude of phase differences between the two time series (Hardmeier et al., 2014; Vinck, Oostenveld, Van Wingerden, Battaglia, & Pennartz, 2011). wPLI connectivity data were then reorganized into wPLI connectivity matrices for each epoch, for each frequency band, for each condition, for each participant to allow for the MST analysis. Then, connectivity matrices were averaged across epochs resulting in one average connectivity matrix, per frequency band, per condition, per participant. These average connectivity matrices were then inverted (i.e., matrices = $1 - \text{wPLI}$), in order to assign the smallest values to the shortest distances (i.e., the strongest connections) of one node to each other node in the network. This allowed the subsequent MST analysis to provide a robust estimation of a highly connected and efficient subnetwork.

2.6 | MST analysis

Using the average connectivity matrices and the Kruskal algorithm (Kruskal, 1956), MSTs were generated in MATLAB (using MATLAB's *graphminspanntree* function; <https://www.mathworks.com/help/releases/R2016a/bioinfo/ref/graphminspanntree.html>). This process generated one MST graph per frequency band, per condition, per participant. A MST is a subgraph in which all nodes are connected (either directly or indirectly) to all other nodes in the network, but which contains no loops. These specifications necessitate that all MST graphs with a specific number of nodes (N) have the same number of edges (E ; $E = N - 1$), allowing for unbiased between-graph comparisons (Reijneveld et al., 2007; Smit et al., 2016; Stam

& Reijneveld, 2007; Stam et al., 2014; Tewarie et al., 2015). The Kruskal algorithm constructs these MSTs by ordering all the possible edges in sequence from least costly (i.e., the strongest connection) to most costly (i.e., the weakest connection). Then, the algorithm goes down that list of possible edges adding each edge to the graph until the MST graph is complete (i.e., until $E = N - 1$). During this process, if the algorithm comes across an edge that would create a loop, it skips that edge and continues to the next edge on the list.

Following the construction of these MSTs, metrics about the configuration of each MST were extracted in MATLAB utilizing a combination of native MATLAB functions, the MIT graph toolbox (http://strategic.mit.edu/downloads.php?page=matlab_networks), and custom MATLAB scripts. Different MST configurations are associated with different levels of efficiency, ranging from a star configuration (the maximally efficient configuration) to a line configuration (the minimally efficient configuration; see Figure 1 for examples). A star configuration is a network in which all nodes, except one, are connected to a single central node, which acts as a hub for the network (e.g., Airline II in example above). This is a maximally efficient network configuration because information can flow from any node to any other node in the network, while only needing to travel through a maximum of two edges. In contrast, a line configuration is a MST in which every node is connected to exactly two other nodes, except for the two nodes at the ends of the graph, which are only connected to one other node (e.g., Airline I in example above). In this configuration, for information to flow from one node to any other node in the network would require that information travel through anywhere between one edge and all edges of the network (Reijneveld et al., 2007; Smit et al., 2016; Stam & Reijneveld, 2007; Stam et al., 2014; Tewarie et al., 2015).

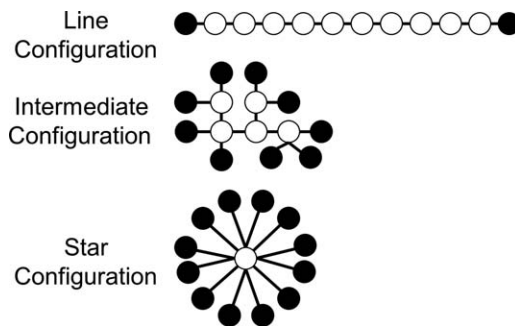


FIGURE 1 Examples of minimum spanning tree configurations. This figure depicts three examples of MST configurations, with black circles representing leaf nodes (i.e., nodes only connected to one other node), white circles representing hub nodes (i.e., nodes connected to two or more other nodes), and lines representing edges. The top MST depicts an example of a line configuration (the minimally efficient network configuration), the middle MST depicts an intermediate network configuration that would be of middling efficiency, and the bottom MST depicts an example of a star configuration (the maximally efficient network configuration)

TABLE 2 Minimum spanning tree (MST) measures defined

Nodes (N)	Total number of nodes in a MST
Edges (E)	Total number of edges in a MST ($E = N - 1$)
Degree	Ratio of the number of edges connected to a specific node (e) to the total number of possible edges connected to single node (degree = e/E)
Eccentricity (ECC)	Ratio of the longest distance between a specific node and any other node in the MST (ecc) to the longest possible distance between any two nodes in the MST ($ECC = ecc/E$)
Betweenness centrality (BC)	Ratio of the number of shortest paths passing through a specific node (C) to the total number of possible shortest paths passing through a specific node in the MST ($BC = C/E * [E - 1]$)
Kappa	A measure of the variance in the degree of nodes (e) throughout the MST
Diameter	Ratio of the longest, shortest path in the MST (D) to the longest possible distance between any two nodes in the MST (diameter = D/E)
Leaf fraction	The ratio of the number of leafs in the MST (L) to the possible number of leafs in the MST (leaf fraction = $L/N - 1$)

There is a variety of MST characteristics that can be used to quantify the degree to which any given MST's configuration is either starlike or linelike (i.e., efficiency of the configuration). For example, the leaf fraction of a MST can be used as a continuous metric of MST configuration efficiency. A leaf is a node that is only connected to one edge (i.e., a node that is only directly connected to one other node). Leaf fraction is defined as the ratio of nodes that are leafs to the maximum number of possible leafs in the graph (number of leafs/ $N - 1$). A MST with a star configuration will have the maximum number of possible leafs (leaf fraction = 1) as all nodes except one are only connected to a centralized hub. In contrast, a MST with a line configuration will have the minimum number of possible leafs (leaf fraction = $2/N - 1$) as this configuration only contains the two leafs that are required for a MST. MSTs in between these two extremes will display varying levels of leaf fraction, with higher leaf fractions indicating a more starlike (i.e., more efficient) network configuration and lower leaf fractions indicating a more linelike (i.e., less efficient) network configuration. In addition to leaf fraction, several other MST characteristics can be examined as quantifiable measures of the efficiency of a given MST configuration. These measures include maximum degree (degree_{max}), mean eccentricity (ECC_{mean}), maximum betweenness centrality (BC_{max}), kappa, and diameter (measures are summarized in Table 2; Reijneveld et al., 2007; Smit et al., 2016; Stam & Reijneveld, 2007; Stam et al., 2014; Tewarie et al., 2015).

2.7 | Data analysis

Analyses occurred in several stages (see Figure 2). First, the association among MST variables was examined by conducting an exploratory factor analysis (EFA) with varimax rotation on all measures of overall efficiency (i.e., degree_{max}, ECC_{mean} ,

BC_{max} , kappa, diameter, leaf fraction) using SPSS. The EFA analysis showed that all MST measures of network efficiency loaded onto a single factor, within each of the frequency bands, for both the EO (alpha1, eigenvalue = 5.39, total variance accounted for = 89.77%; alpha2, eigenvalue = 5.31, total variance accounted for = 88.58%; gamma, eigenvalue = 5.38, total variance accounted for = 89.68%) and EC data sets (alpha1, eigenvalue = 5.27, total variance accounted for = 87.79%; alpha2, eigenvalue = 5.30, total variance accounted for = 88.25%; gamma, eigenvalue = 5.30, total variance accounted for = 88.32%).

Second, to determine whether data from EO and EC could be combined, paired t -test contrasts were run within each frequency band to determine whether the efficiency factors significantly differed between the two data sets. The efficiency factors did not significantly differ between the EO and EC data sets within the alpha1 frequency band, $t(156) = -0.047$, $p = .963$, the alpha2 frequency band, $t(156) = 0.158$, $p = .874$, or the gamma frequency band, $t(156) = 0.195$, $p = .846$. Accordingly, data from EO and EC were averaged together. That is, each subject's connectivity matrices from both EC and EO data sets were averaged together to create one grand average adjacency matrix per frequency band, per participant. These grand average matrices were then rerun through the MST analysis described above.

Third, given the shared variance between MST metrics of network efficiency (Smit et al., 2016), examination of each individual MST metric would unnecessarily inflate the number of comparisons and risk for Type I error. Accordingly, we generated an overall measure of network efficiency by running the final MST characteristics through another EFA within each frequency band. These analyses showed that all of the MST measures of overall efficiency loaded onto a single overall efficiency factor (OEF) within each frequency

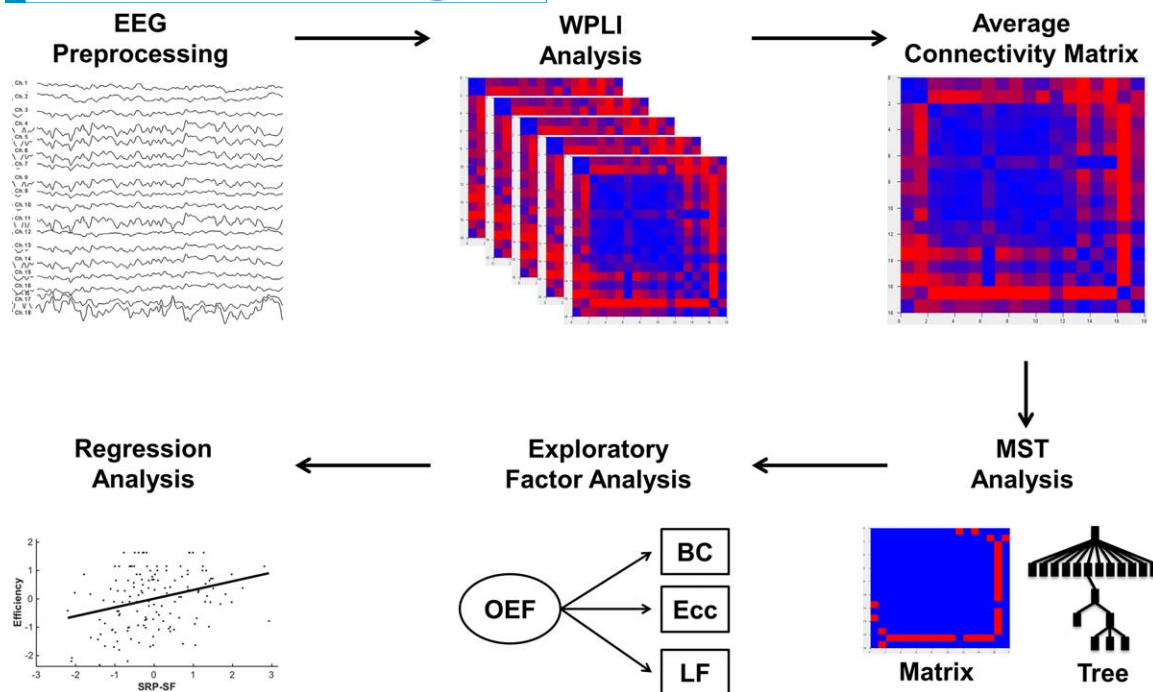


FIGURE 2 Schematic of data analysis. First, EEG data were preprocessed and epochs with signal artifact were rejected. Second, all artifact-free epochs were filtered for each frequency band and run through a weighted phase lag index (wPLI) connectivity analysis. Third, the connectivity data from the wPLI analysis were reorganized into connectivity matrices for each epoch, and then averaged together into a single averaged connectivity matrix. Fourth, minimum spanning tree (MST) graphs were generated for each participant's connectivity matrix using the Kruskal algorithm, and metrics of network efficiency were extracted from each MST. Fifth, these efficiency metrics were run through an exploratory factor analysis to generate an overall efficiency factor (OEF). Finally, the impact of psychopathic traits on neural efficiency was evaluated by regressing self-report psychopathy (SRP-SF) factor scores on the OEF

band (alpha1, eigenvalue = 5.32, total variance accounted for = 88.66%; alpha2, eigenvalue = 5.19, total variance accounted for = 86.51%; gamma, eigenvalue = 5.35, total variance accounted for = 89.11%).

Finally, separate linear regression models were run using SRP-SF factors (factor 1 and factor 2; z scored) as simultaneous predictors of OEF scores for each frequency band. In each model, gender (contrast-coded) also was included as a dichotomous moderating variable given previous research that the underlying etiology of psychopathic traits in men and women may differ (O'Leary, Loney, & Eckel, 2007; Rogstad & Rogers, 2008). Tests of significance were based on bootstrapping methods (2,000 samples, bootstrapped p values, $p < .05$).

3 | RESULTS

3.1 | Alpha1 frequency band

Higher SRP-SF factor 1 scores were associated with significantly lower alpha1 OEF, $F(5, 152) = 4.294$, $p = .001$; $\beta = -0.287$, $p = .039$, 95% CI = [-0.628, -0.054], indicating that individuals higher on factor 1 traits display less efficient neural communication within the alpha1 network (see Figure 3a). In contrast, higher SRP-SF factor 2 scores were associated with significantly higher OEF, $\beta = 0.317$, $p = .044$, 95% CI = [0.047, 0.646], suggesting greater

efficiency of neural communication within the alpha1 network (see Figure 4a). There was also a significant main effect of gender, where female participants displayed significantly higher OEF than male participants, $\beta = 0.296$, $p = .006$, 95% CI = [0.089, 0.506]. However, neither SRP-SF factor 1 scores ($p = .098$) nor SRP-SF factor 2 scores ($p = .129$) significantly interacted with gender.³

3.2 | Alpha2 frequency band

The model predicting alpha2 OEF was not significant, $F(5, 152) = 2.087$, $p = .070$.⁴

³Including alpha1 spectral power as a covariate in this model did not substantively alter any of the reported results.

⁴We also examined alpha band activity as a unitary (8–12 Hz) measure. Results were conceptually similar to those reported above for alpha1, but were not statistically significant (SRP-SF factor 1: $\beta = -.196$, $p = .097$; SRP-SF factor 2: $\beta = .187$, $p = .210$). A unitary measure of alpha band activity is essentially a combination of two different wavebands that are related to distinct underlying processes (Chen et al., 2008; Micheloyannis et al., 2006; Miraglia, Vecchio, Bramanti, & Rossini, 2016; Petsche, Kaplan, Von Stein, & Filz, 1997; Wu & Liu, 1995), are moderately correlated in the present study (Alpha1 Power \times Alpha2 Power: $r = .368$, $p < .001$; Alpha1 OEF \times Alpha2 OEF: $r = .687$, $p < .001$), and alpha2 was unrelated to SRP-SF traits in the present study. Therefore, though the direction of the effects was the same across the two sets of results, it may be unsurprising that the broader alpha measure yielded a null effect.

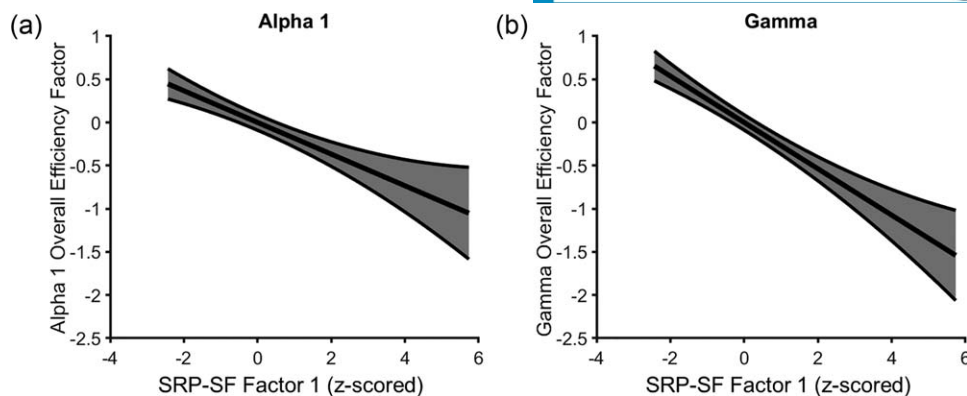


FIGURE 3 Individuals high on factor 1 traits showed inefficient neural communication. (a) Regression line depicting OEF scores for the alpha1 frequency band as a function of factor 1 traits, controlling for factor 2 scores, gender, and Gender \times Factor score interactions. (b) Regression line depicting OEF scores for the gamma frequency band as a function of factor 1 traits, controlling for factor 2 scores, gender, and Gender \times Factor score interactions. Error bands represent one standard error

3.3 | Gamma frequency band

SRP-SF factor 1 scores were significantly and negatively associated with gamma OEF, $F(5, 152) = 5.805$, $p < .001$; $\beta = -0.421$, $p < .001$, 95% CI = $[-0.695, -0.195]$, indicating that individuals higher on factor 1 traits showed less efficient neural communication within the gamma network (see Figure 3b). Conversely, SRP-SF factor 2 scores were significantly and positively associated with gamma OEF ($\beta = 0.507$, $p = .001$, 95% CI = $[0.228, 0.798]$), indicating that individuals high on factor 2 traits display more efficient neural communication within the gamma network (see Figure 4b). There also was a significant main effect of gender, $\beta = 0.270$, $p = .008$, 95% CI = $[0.060, 0.481]$, where female participants exhibited significantly higher OEF than male participants within the gamma network. However, neither the SRP-SF Factor 1 \times Gender interaction ($p = .113$) nor the SRP-SF Factor 2 \times Gender interaction ($p = .268$) significantly predicted OEF.⁵

4 | DISCUSSION

Psychopathic traits, whether interpersonal-affective or impulsive-antisocial, represent deviancies in social, emotional, and behavioral functioning. The correlates and processes associated with these traits appear to be distinct, and at times even opposite (Baskin-Sommers et al., 2015; Neumann et al., 2013; Patrick, 2007). The dissociation between factor 1 and factor 2 traits is clear when examining neural processes. Previous research shows that individuals high on psychopathic traits display differential disruptions in connectivity

between various neural regions (Carre et al., 2013; Pape et al., 2015; Philippi et al., 2015). However, the manner in which these disruptions in connectivity occur, and the effectiveness of the communication among regions, remains unclear. By applying a novel graph theory approach—MST analysis—to resting state EEG data, the present findings are the first to demonstrate that nonincarcerated individuals high on factor 1 psychopathic traits show significantly less efficient neural communication within the alpha1 and gamma frequency bands. Conversely, individuals high on factor 2 show increased efficiency of neural communication within those same frequency bands. Together, these findings indicate that psychopathic traits are differentially associated with abnormalities in the efficiency of neural communication in frequency bands vital for both higher-order (e.g., decision making, affective theory of mind) and lower-order cognitive processes (e.g., sensation, perception).

Individuals high on factor 1 traits showed more linelike network configurations (i.e., lower $degree_{max}$, BC_{max} , kappa, and leaf fraction, and higher ECC_{mean} and diameter), indicative of less efficient neural communication, in both the alpha1 and gamma networks. First, alpha1 is implicated in the long-range neural communication that subserves higher-order cognitive processes, such as decision making and affective theory of mind (Canolty et al., 2006; Doesburg et al., 2012; Fell & Axmacher, 2011; Minati et al., 2012; Sepulcre et al., 2010; von Stein & Sarnthein, 2000; Vourkas et al., 2014). The neural circuitry underlying these types of higher-order processes is highly distributed throughout the brain. For example, decision making evokes neural activity in a variety of disparate brain regions, including the ventromedial prefrontal cortex, dorsolateral prefrontal cortex, anterior cingulate cortex, anterior insula, and various other cortical regions (Ernst et al., 2002; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Shenhav & Greene, 2010). The distributed nature of these neural responses necessitates

⁵Including either gamma spectral power (30–45 Hz) or mean event-related spectral perturbation (ERSP) for high frequency gamma band activity (100–250 Hz) as covariates in this model did not substantially impact the SRP-SF factor 1 or SRP-SF factor 2 findings.

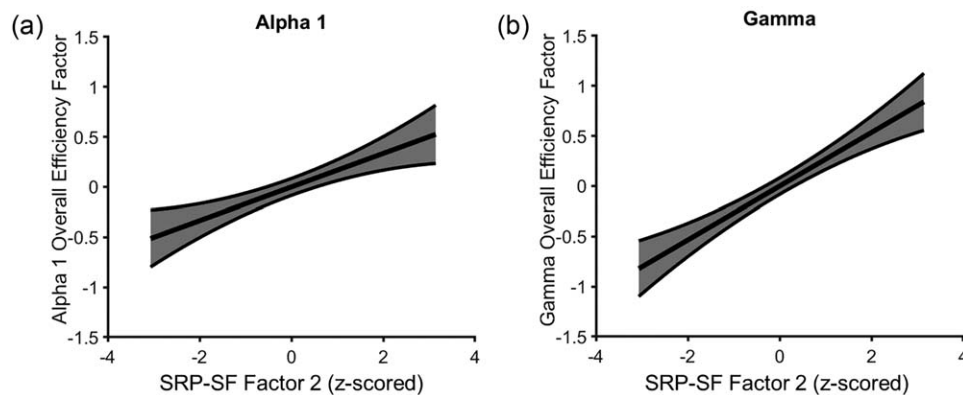


FIGURE 4 Individuals high on factor 2 traits showed hyperefficient neural communication. (a) Regression line depicting OEF scores for the alpha 1 frequency band as a function of factor 2 traits, controlling for factor 1 scores, gender, and Gender \times Factor score interactions. (b) Regression line depicting OEF scores for the gamma frequency band as a function of factor 2 traits, controlling for factor 1 scores, gender, and Gender \times Factor score interactions. Error bands represent one standard error

efficient long-range neural communication to ensure that all relevant information from these disparate brain regions can be integrated effectively (Sepulcre et al., 2010). Accordingly, the alpha 1 findings in the present study suggest that individuals high on factor 1 traits exhibit impairments in efficient long-range neural communication, which could result in impairment in higher-order processes, such as decision making (Babiloni et al., 2007; De Vico Fallani et al., 2010; Minati et al., 2012) and affective theory of mind (Jakab et al., 2013). Consequently, the present results suggest that the documented failures in decision making (e.g., value-based decision making, Buckholtz et al., 2010; Koenigs et al., 2010; moral decision making, Glenn et al., 2009), and affective theory of mind (Sebastian, McCrory et al., 2012; Shamay-Tsoory et al., 2010) in individuals high on factor 1 traits, may be due, at least in part, to inefficiencies in long-range neural communication.

Second, individuals high on factor 1 traits also showed inefficient communication in gamma. Gamma frequency activity is related to short-range neural communication, which is utilized for the integration of information from more localized regions of cortex (e.g., integration of information within primary visual cortex for basic visual processing; Sepulcre et al., 2010; von Stein & Sarnthein, 2000). This makes efficient gamma communication important for lower-order cognitive processes such as sensation, perception, and reflexive attention (Sepulcre et al., 2010). Prior research using traditional connectivity methods with psychopathic traits has not linked factor 1 traits with disruptions in this type of short-range communication. However, graph theory metrics are more sensitive to connectivity disruptions than traditional connectivity measures (Fraga Gonzalez et al., 2016). Furthermore, recent research has shown that factor 1 traits are associated with impairments in the integration of sensory information (Tillem et al., 2016) and perception of stimuli (Baskin-Sommers, Curtin, & Newman, 2013). The

current gamma findings for individuals high on factor 1 traits add to this growing body of literature, suggesting factor 1-related impairments in basic sensory processing, and that these impairments may be due to breakdowns in efficient short-range neural communication.

While these factor 1-related inefficiencies in neural communication may indicate a global deficit in integration of neural information, impacting a wide array of higher- and lower-order cognitive processes, it is also possible that these neural inefficiencies reflect more localized disruptions in communication within specific neural networks. Alpha 1 activity, for example, previously has been implicated with the default mode network (Broyd et al., 2009; Chen et al., 2008). Accordingly, the factor 1-related inefficiencies in neural communication within this frequency band may simply reflect factor 1-related disruptions in communication within the default mode network. Similarly, gamma-band activity previously has been linked with the frontoparietal network (Gregoriou, Gotts, Zhou, & Desimone, 2009a,b). Consequently, inefficient communication within the gamma frequency band may specifically reflect disruptions within this network, rather than a more general breakdown in short-range communication. While these more narrow interpretations are consistent with prior research linking psychopathic traits with disrupted connectivity within both the default mode (Glenn et al., 2009; Motzkin et al., 2011; Philippi et al., 2015) and frontoparietal networks (Philippi et al., 2015), they fail to explain the nature of the widespread connectivity abnormalities associated with individuals high on psychopathic traits (Carre et al., 2013; Cohn et al., 2015; Finger et al., 2012; Glenn et al., 2009; Hoppenbrouwers et al., 2013, 2014; Koenigs et al., 2010; Motzkin et al., 2011; Pape et al., 2015; Philippi et al., 2015; Yang et al., 2012; Yoder et al., 2016). Regardless of the specific interpretation, however, the current findings clearly demonstrate that individuals high on factor 1 traits exhibit less efficient integration of

information (either globally, or within specific networks), which, in turn, may lead to the information processing deficits characteristic of individuals high on factor 1 traits.

Unlike individuals with high factor 1 traits, individuals high on factor 2 traits displayed more efficient, starlike neural network configurations (i.e., higher degree_{\max} , BC_{\max} , kappa , and leaf fraction, and lower ECC_{mean} and diameter). At first glance, these findings suggest that factor 2 traits are associated with increased efficiency of information processing and integration, which should lead to enhanced cognitive processing. However, factor 2 traits typically are not associated with better cognitive processing (Baskin-Sommers et al., 2015; Dinn & Harris, 2000; Nigg et al., 2017). Consequently, there seems to be some inconsistencies between the neural and behavioral findings associated with factor 2 traits. On the one hand, more neural efficiency is consistent with the prior literature linking factor 2 traits with increased functional connectivity (Korponay et al., 2017; Philippi et al., 2015). On the other hand, it is possible that this efficiency is a sign of vulnerability, which would be more consistent with the neurocognitive profiles typically associated with factor 2 traits. While it is true that networks with a star configuration are maximally efficient, they are also maximally vulnerable. In a star-shaped network, all information is processed and transferred through a single node that acts as a hub for the network. If that hub node were to get overloaded (e.g., by increased processing demands) or damaged (e.g., by a stroke), then information transfer within that network would either slow dramatically or stop altogether. As such, an ideal neural network would actually balance efficiency and vulnerability (Reijneveld et al., 2007; Smit et al., 2016; Stam & Reijneveld, 2007; Stam et al., 2014; Tewarie et al., 2015). Accordingly, the hyperefficiency associated with individuals high on factor 2 traits may leave their neural networks highly vulnerable to being overloaded whenever processing demands increase (see also Baskin-Sommers et al., 2012; Brazil, Mathys, Popma, Hoppenbrouwers, & Cohn, 2017). This vulnerability, in turn, may explain why individuals high on factor 2 traits show more functional connectivity and efficiency, but also decreased processing speed and other executive functioning deficits. Future research is needed to evaluate the possibility of this type of vulnerability-efficiency trade-off in neural communication in individuals high on factor 2 traits.

While these findings provide strong evidence for abnormalities in the efficiency of neural communication in individuals high on psychopathic traits, they must be considered in light of two specific limitations. First, the current study was limited to an analysis of resting-state EEG data. No task-based neural data were collected and no measures of cognitive functioning were administered. Accordingly, the proposed link between psychopathy-related abnormalities in the efficiency of long- and short-range neural communication

(i.e., alpha and gamma networks) and psychopathy-related impairments in higher- (e.g., decision making) and lower-order (e.g., sensation and perception) cognitive processes is only speculative. Further research examining task-based neural activity would be needed to directly test whether neural efficiency either mediates or moderates any psychopathy-related impairments in cognitive functioning during task performance (Tavor et al., 2016). Second, this study utilized a community sample with a relatively low base rate of psychopathic traits. This potentially limits the generalizability of these findings to populations with higher rates of psychopathic traits. Future research will need to replicate these findings in samples more enriched for psychopathic traits (e.g., incarcerated samples) to ensure that these findings are generalizable.

In sum, the present study provides evidence that the subcomponent traits of psychopathy are differentially associated with dysfunction in the efficient integration of neural information. Individuals high on factor 1 traits show inefficient long- and short-range neural communication, whereas individuals high on factor 2 traits show hyperefficient long- and short-range neural communication. There are two clear implications of these findings. First, these findings identify previously unobserved abnormalities in neural integrity that likely impact the quality of information processing in individuals high on psychopathic traits, albeit in different ways for the two subcomponent traits. Second, these abnormalities in the efficiency of both long- and short-range neural communication suggest that neural network dysfunctions in individuals with psychopathic traits may extend beyond the network or circuit abnormalities previously found using traditional connectivity methods (e.g., default mode network, frontostriatal circuitry). In order to refine our understanding of the neurocognitive underpinnings of the subcomponent traits of psychopathy, further research is needed to clarify exactly what networks are and in what ways information processing is disrupted in these individuals.

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