

Higher levels of trait emotional awareness are associated with more efficient global information integration throughout the brain: a graph-theoretic analysis of resting state functional connectivity

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Abstract

Previous studies have suggested that trait differences in emotional awareness (tEA) are clinically relevant, and associated with differences in neural structure/function. While multiple leading theories suggest that conscious awareness requires widespread information integration across the brain, no study has yet tested the hypothesis that higher tEA corresponds to more efficient brain-wide information exchange. Twenty-six healthy volunteers (13 females) underwent a resting state functional magnetic resonance imaging scan, and completed the Levels of Emotional Awareness Scale (LEAS; a measure of tEA) and the Wechsler Abbreviated Scale of Intelligence (WASI-II; a measure of general intelligence quotient [IQ]). Using a whole-brain (functionally defined) region of interest (ROI) atlas, we computed several graph theory metrics to assess the efficiency of brain-wide information exchange. After statistically controlling for differences in age, gender and IQ, we first observed a significant relationship between higher LEAS scores and greater average degree (i.e. overall whole-brain network density). When controlling for average degree, we found that higher LEAS scores were also associated with shorter average path lengths across the collective network of all included ROIs. These results jointly suggest that individuals with higher tEA display more efficient global information exchange throughout the brain. This is consistent with the idea that conscious awareness requires global accessibility of represented information.

Key words: emotional awareness; Levels of Emotional Awareness Scale (LEAS); graph theory; conscious access

Introduction

The construct of trait emotional awareness (tEA) refers to an individual's stable ability to conceptualize the affective responses of self and others in a fine-grained and differentiated manner (Lane *et al.*, 2015; Smith *et al.*, 2017b). For example, those with low tEA would tend to conceptualize affective responses in somatic (e.g. 'feeling sick to my stomach') or coarse-grained (e.g. 'feeling bad')

terms, and they would have trouble recognizing that others may feel differently than they do; in contrast, those with high tEA would tend to understand such responses in fine-grained conceptual (e.g. 'feeling a blend of sadness and anger') terms, and could more easily differentiate the emotions of self and others.

An individual's tEA level, as measured by the Levels of Emotional Awareness Scale (LEAS) (Lane and Schwartz, 1987;

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Lane et al., 1990), is widely recognized as an important factor in both physical and mental health. Across multiple studies, higher LEAS scores have been correlated with several adaptive traits/abilities (e.g. greater emotion recognition ability, impulse control, openness to experience, empathy, and stability of felt well-being; Lane et al., 1990, 1996, 2000; Ciarrochi et al., 2003; Barchard and Hakstian, 2004; Bréjard et al. 2012; Wright et al., 2017). On the other hand, low LEAS scores (relative to healthy individuals) have been observed within multiple clinical populations (e.g. eating disorders, post-traumatic stress disorder, schizophrenia, borderline personality disorder, essential hypertension, and somatoform disorders, among others; Levine et al., 1997; Berthoz et al., 2000; Bydlowski et al., 2005; Donges et al., 2005; Lackner, 2005; Subic-Wrana et al., 2005, 2007; Frewen et al., 2008; Baslet et al., 2009; Consoli et al., 2010; Beutel et al., 2013).

The underlying brain basis of tEA has also been investigated in a number of studies. For example, higher LEAS scores have been associated with greater activity in the dorsolateral prefrontal cortex (DLPFC), anterior temporal cortex, and the dorsal (dACC) and rostral (rACC) anterior cingulate cortex in a range of task-based contexts (Lane et al., 1998; Frewen et al., 2008; McRae et al., 2008; Tavares et al., 2011; Smith et al., 2017c). More recently, structural and functional imaging studies have further examined the large-scale network correlates of tEA (for reviews of large-scale networks, see Yeo et al., 2011; Barrett and Satpute, 2013), finding correspondences between higher LEAS scores and greater cortical thickness within the limbic network (LN; which includes orbitofrontal and anterior temporal cortex regions) (Smith et al., 2018), as well as stronger functional connectivity within regions of the salience network (SN; which includes dACC) and within regions of the default mode network (DMN; which includes rACC) (Smith et al., 2017a). Together, this work has led to the proposal of a “three-process model” (Smith et al., 2017b), which suggests that higher tEA may reflect (i) more context-sensitive affective response generation processes within the LN, (ii) more efficient interoception and emotion conceptualization processes within the SN and DMN (respectively), and (iii) greater attention to, and maintenance of, emotion-related representations within working memory (supported by DLPFC and other regions of the ‘executive control network’ or ECN).

While the studies described above have examined the association between tEA and the structure/function of specific regions/networks, at present no study has yet examined whether tEA is associated with broader differences in the overall efficiency of large-scale information integration throughout the brain. This is an important theoretical question, given that leading empirically supported models of the neural basis of conscious awareness posit that conscious access to represented information (including represented information about emotions) requires a brain-wide integration process in which the information represented in one brain system is “globally broadcast” and made available to all other relevant brain systems (Gaillard et al., 2009; Dehaene, 2014; Dehaene et al., 2014; Smith, 2016, 2017). These models have also been specifically applied to gaining conscious access to (i.e. awareness of) the various aspects of emotional experience (Lane et al., 2015; Smith and Lane, 2015, 2016; Panksepp et al., 2017; Smith et al., 2017d). Therefore, greater conscious awareness of emotion in those with higher tEA could perhaps be explained by more efficient patterns of functional connectivity that facilitate long-range information integration.

Whole-brain graph theory analyses (Bullmore and Sporns, 2009) represent one unexplored approach to studying such

network properties in relation to tEA and leading theories of the neural basis of conscious awareness. This approach to studying tEA could also inform a growing literature using graph theory metrics to examine a broader range of individual differences in cognitive-affective and social trait variables. For example, recent graph-theoretic analyses investigating personality variables have found that greater openness to experience is associated with greater network efficiency within the DMN (Beaty et al., 2016), and greater trait anxiety is associated with reduced efficiency in regions of the SN (Markett et al., 2016). Measures of reduced whole-network efficiency have also been linked to patient populations with theory-of-mind and related social-cognitive deficits (Serra et al., 2016; Keown et al., 2017). However, while graph theory approaches have begun to be applied to some aspects of socio-emotional processes (Huang et al., 2018), recent reviews of the social neuroscience literature have highlighted the need for greater application of these approaches to further refine neural theories of social, emotional, and related cognitive differences between individuals (Li et al., 2014), with tEA representing one such individual difference.

Based on the work reviewed above, we hypothesized that individuals with higher tEA would display indices of more efficient brain-wide information integration. In this study, we used whole-brain graph-theoretic analyses to test this hypothesis, with the specific prediction that higher tEA would be associated with graph theory indices of more efficient global information exchange (for a review of graph theory metrics, see Bullmore and Sporns, 2009); these indices included higher “network density” (or “average degree”; indicating more direct functional connections overall), as well as greater “global efficiency” and shorter “average path length” (both indicating more efficient message passing from any region to any other region on average). If this hypothesis were confirmed, it would provide empirical support for the notion that awareness of emotion is facilitated by the same kinds of whole-brain signal integration processes implicated in conscious awareness more generally (Dehaene, 2014). We also examined the possibility that higher tEA might correspond to indices of greater local processing efficiency and clustering, which could indicate enhanced domain-specific processing of relevant affective signals (e.g. more adaptive integration of somatovisceral sensations). We reasoned that such findings could also add more broadly to trends in the recent work reviewed above linking greater network processing efficiency to the personality and socio-cognitive variables with conceptual links to tEA.

Materials and methods

Participants

We recruited 26 adults (13 females; mean age = 23.1 ± 4.0) from the general population of Tucson, AZ to participate in the present study, via Internet advertisements and flyers. Participants did not have any history of neurological or psychiatric disorders (assessed using a phone screen questionnaire based on criteria within the Diagnostic and Statistical Manual for Mental Disorders, fourth edition; DSM-IV-TR), they were not taking any psychoactive medications, they did not report any other chronic diseases, they were all right-handed, and they all had English as a primary language (assessed via self-report). Prior to enrollment, all participants provided written informed consent. Participants received nominal financial compensation for their time. The Institutional Review Board of the University of

Arizona reviewed and approved the research protocol of the present study).

Procedure

During a single-day visit to the lab, and after completing the informed consent process, each participant was taken to the magnetic resonance imaging (MRI) scanner at the University of Arizona where they underwent a resting state functional MRI scan (see Neuroimaging methods section). After completing the resting state scan, participants were brought back to the lab, seated at a laptop computer, and asked to complete an on-line version of the LEAS (www.eleasest.net) that uses a validated automatic scoring program (Barchard et al., 2010).

LEAS. The LEAS presents participants with descriptions of 20 social situations (two to four sentences per description), where each situation includes 2 people. The described situations are designed to elicit four types of emotion (anger, sadness, happiness, and fear) at five levels of complexity. One situation description is presented on each electronically presented page, followed by two questions: “How would you feel?” and “How would the other person feel?” Separate response boxes are provided for typing in the answers to each question. When typing their responses into these boxes, participants are instructed to use as much or as little space as needed to answer. The only rule given is that they must use the word “feel” in their responses.

Trait emotional awareness level scores are assigned to each written response based on word choice. The lowest scores (Level 0) are given to words that do not refer to feelings. Level 1 scores are assigned to words that refer to physiological sensations (e.g. ‘tired’), whereas Level 2 scores are given to words referring to feeling-related actions (e.g. ‘hugging’) or simple valence discriminations (e.g. ‘bad’, ‘good’) that have inherent avoidance- or approach-related content. Level 3 scores are given to words referring to single emotion concepts (e.g. ‘happy’, ‘angry’). Level 4 scores are assigned to a response when at least two words from Level 3 are used (i.e. conveying greater emotional differentiation than either word alone). For each item, the self- and other-related responses are scored separately (i.e. with a value of 0–4). A “total” score is also given for each of the 20 LEAS items, which reflects the higher of the self- and other-related scores, unless a score of 4 is given for both. In this case, a total score of 5 is given for the item, as long as the self- and other-related responses are sufficiently differentiable (for more detail, see Lane et al., 1990). The final LEAS score is calculated by summing the scores assigned to each of the 20 items (i.e. LEAS SELF score = the sum of the scores for the 20 “How would you feel?” responses; LEAS OTHER score = the sum of the scores for the 20 “How would the other person feel?” responses, and LEAS TOTAL score = the sum of the 20 “total” item scores).

General intelligence. We estimated the intelligence quotient (IQ) of each participant using the two-subtest form (FSIQ-2) of the Wechsler Abbreviated Scale of Intelligence–Second Edition (WASI-II; Pearson Assessment, Inc., San Antonio, TX, USA; Wechsler, 2011). These scores were used to control for potential differences in general intelligence when examining graph-theoretic correlates of LEAS scores. This was based on the fact that LEAS scores have been positively related to general intelligence in previous studies (e.g. Barrett et al., 2000). We were also interested in assessing the unique contribution of tEA to functional network properties (i.e. over and above what might be

explained by greater cognitive performance ability more generally).

Neuroimaging methods

We used a 3T Siemens Skyra MRI scanner (Siemens, Erlangen, Germany) with a 32-channel head coil to collect neuroimaging data. T1-weighted structural images (3D MPRAGE) were acquired (TR/TE/flip angle = 2.1 s/2.33 ms/12°) covering 176 sagittal slices (256 × 256) with a slice thickness of 1 mm (voxel size = 1 × 1 × 1). Functional T2*-weighted scans were acquired over 32 transverse slices (2.5 mm thickness; matrix: 88 × 84; field of view = 240 mm). An interleaved sequence was used to collect each volume (TR/TE/flip angle = 2 s/25 ms/90°). The T2* sequence voxel size was 2.5 × 2.5 × 3.5 mm (i.e. with a 40% slice gap, allowing collection of 300 volumes within a 10-min acquisition time).

Resting-state preprocessing

We used the publicly available CONN functional connectivity toolbox (version 16.a; <https://www.nitrc.org/projects/conn>), in conjunction with SPM12 (Wellcome Department of Cognitive Neurology, London, UK; <http://www.fil.ion.ucl.ac.uk/spm>), to perform all preprocessing steps (using CONN’s default preprocessing pipeline), as well as subsequent statistical analyses, on all collected MRI scans. In this preprocessing pipeline, raw functional images are slice-time corrected, realigned (motion corrected), unwarped, and coregistered to each subject’s MPRAGE image in accordance with standard algorithms. Images are then normalized to Montreal Neurological Institute coordinate space, spatially smoothed (8 mm full-width at half maximum) and resliced to 2 × 2 × 2 mm voxels. We also used the Artifact Detection Tool (ART; http://www.nitrc.org/projects/artifact_detect/) to regress out scans as nuisance covariates in the first-level analysis exceeding 3 s.d. in mean global intensity and scan-to-scan motion that exceeded 0.5 mm. These were added in addition to covariates for the six rotation/translation movement parameters.

Graph theory analyses

Graph theory analyses were performed using the default functional connectivity processing pipeline in the CONN toolbox (for details, see Whitfield-Gabrieli and Nieto-Castanon, 2012). Using this processing pipeline, physiological and other sources of noise were estimated with the aCompCor method (Behzadi et al., 2007; Whitfield-Gabrieli et al., 2009; Chai et al., 2012); they were then removed along with the movement- and artifact-related covariates mentioned above. The residual BOLD time-series was then band-pass filtered (0.008–0.09 Hz). Every participant’s structural image was segmented into gray matter, white matter, and cerebral spinal fluid using SPM12. White matter and cerebral spinal fluid noise effects were removed through regression. The regions of interest (ROIs) in the present study were derived from a freely available ROI atlas defined by correlated activation patterns (http://findlab.stanford.edu/functional_ROIs.html). The 90 ROIs within this atlas span several networks: the anterior and posterior SNs, dorsal and ventral DMNs, left and right ECNs, auditory network, basal ganglia network, higher visual network, language network, sensorimotor network, primary visual network, visuospatial network and precuneus network (for details, see Shirer et al., 2012). However, rather than focus on any of these networks in isolation, we treated all ROIs as “nodes” within a whole-brain network.

We extracted the residual BOLD time course for each ROI for each participant to produce single-participant Pearson's correlation maps for the time courses of all pairs of ROIs. At the second level, controlling for age, gender and IQ, we used the CONN toolbox's automated graph theory analysis algorithms (for a detailed description, see <https://sites.google.com/view/conn/resources/manuals>) to examine the relationship between LEAS TOTAL scores and several graph theory metrics: (i) *Average path length*, defined as the mean shortest path length among all possible pairs of nodes, represents the efficiency of information transfer between ROIs (for this measure, CONN only computes the average path length across connected nodes; i.e. the analysis excludes ROIs with no connections to the graph, as the average path length from this node to any other node would be infinite). (ii) The *global efficiency* of the network, defined as the mean inverse shortest path length for all possible pairs of nodes, represents a complementary measure of the efficiency of information transfer among all ROIs. (iii) *Local efficiency*, which can be thought of as the global efficiency of the sub-network consisting only of a node's neighbors (regions to which a given ROI has direct functional connections; excluding the ROI itself); at the whole-network level, local efficiency reflects the average sub-network efficiency across all ROIs, and indicates the network's ability to effectively compensate for the localized failure of a single node. (iv) The *clustering coefficient*, which reflects the degree to which nodes tend to cluster together (i.e. the regions to which an ROI is directly connected also have direct connections among themselves); on the whole-network level, the clustering coefficient can be thought of as the average level of clustering (as defined above) across all ROIs—representing the average efficiency of information transfer within local ROI clusters. (v) The *degree of connectivity* is the number of edges linked to a node, representing the number of direct functional connections between an ROI and other ROIs. Average degree, also called 'network density', is a measure of the interconnectedness of the network as a whole.

Each of these metrics can be seen as complementary measures of how efficiently the information represented within a given node could be passed to (i.e. made available to) any other node in the network (for a review of these graph theory metrics, see Bullmore and Sporns, 2009). We predicted that individuals with higher tEA would display greater efficiency of information transfer throughout the brain, such that, for the whole-brain network, higher LEAS TOTAL scores would be associated with shorter average path length, higher global and local efficiency, a greater clustering coefficient, and higher network density. For these analyses, we initially set a binary ROI-to-ROI correlation threshold of $r=0.3$ to define the presence/absence of edges/connections between all possible pairs of nodes. However, as there is little consensus in the field about proper a priori threshold selection in graph theoretic neural network analyses, we repeated the analyses with thresholds of $r=0.2$ and $r=0.4$ as well (see Supplementary Results).

After confirming our a priori hypotheses regarding whole-network-level relationships between LEAS TOTAL scores and the above-mentioned graph theory metrics, we also explored ROI-specific graph-theoretic results using a false discovery rate (FDR)-corrected P -value threshold of $P \leq 0.05$ (all reported P -values are two-tailed).

Finally, we then re-performed the analyses of several of the graph theory metrics above, while controlling for individual differences in network density (average degree). This was done in order to clarify between two possible interpretations of our results, which arise because of the relationship between

network density and these other measures. Namely, increases in network density can either leave these other metrics unchanged or increase their measurement of network efficiency. Therefore, these analyses were performed to ascertain whether the increases in measured efficiency we observed using these other metrics were due primarily to a greater number of edges/connections in general during the resting state, or due to differences in network characteristics that were independent of density differences.

Results

Behavioral results

LEAS scores for the group as a whole were as follows: TOTAL=74.0 (± 9.8), SELF=63.0 (± 8.7), OTHER=58.5 (± 10.7). Females had numerically higher LEAS TOTAL scores than males (means: females = 76.8 ± 10.6 ; males = 71.2 ± 8.4), but this difference was non-significant [$t(24)=1.5$, $P=0.147$]. The correlation between age and LEAS scores for the sample as a whole was negative and non-significant ($r=-0.315$, $P=0.12$).

WASI-II FSIQ-2 scores had a mean of 115.23 (± 11.7). LEAS TOTAL scores were significantly positively correlated with FSIQ-2 scores ($r=0.619$, $P=0.001$).¹

Whole-network graph theoretic results

Manual inspection within CONN confirmed that every network graph examined had one connected component. After statistically controlling for differences in age, gender, and IQ, we observed significant relationships (in the expected directions) between LEAS scores and (i) average path length [$t(21)=-3.48$, $P=0.002$; Figure 1], (ii) global efficiency [$t(21)=2.35$, $P=0.029$], (iii) local efficiency [$t(21)=2.66$, $P=0.014$], (iv) clustering coefficient [$t(21)=2.37$, $P=0.027$] and (v) network density/degree [$t(21)=2.52$, $P=0.020$; Figure 2] for the collective network of all included ROIs. All of these whole-network results were also significant at the alternative liberal ($r=0.2$) and conservative ($r=0.4$) thresholds, with the exception of average path length at $r=0.4$ (Supplementary Results and Table S1.1).

To provide a post-hoc estimate of the statistical power afforded by our sample size in these analyses, we used the strength of the observed relationship between LEAS scores and network density/degree (i.e. partial $R^2=0.23$; i.e. after controlling for age, gender, and IQ) as a representative result. With 26 participants, and an alpha threshold of 0.05, this analysis (performed using G*Power; Faul et al., 2007) revealed a power estimate of 0.76, indicating a 24% chance of false negatives.

ROI-specific graph theoretic results

After statistically controlling for differences in age, gender, and IQ, we subsequently observed significant relationships (using an FDR-corrected P -value threshold of $P \leq 0.05$) between LEAS scores and several graph theory metrics for specific ROIs. In this case, we observed that those with higher LEAS TOTAL scores also displayed shorter average path lengths for specific ROIs within the anterior and posterior SNs (four ROIs in each), auditory network (right thalamus), basal ganglia network (three

1 The LEAS scores and FSIQ-2 scores from this data set have previously been published in conjunction with both task-related and resting state imaging data (Smith et al., 2017a,c, 2018). However, their relation to the graph-theoretic metrics presented here is novel to the present manuscript.

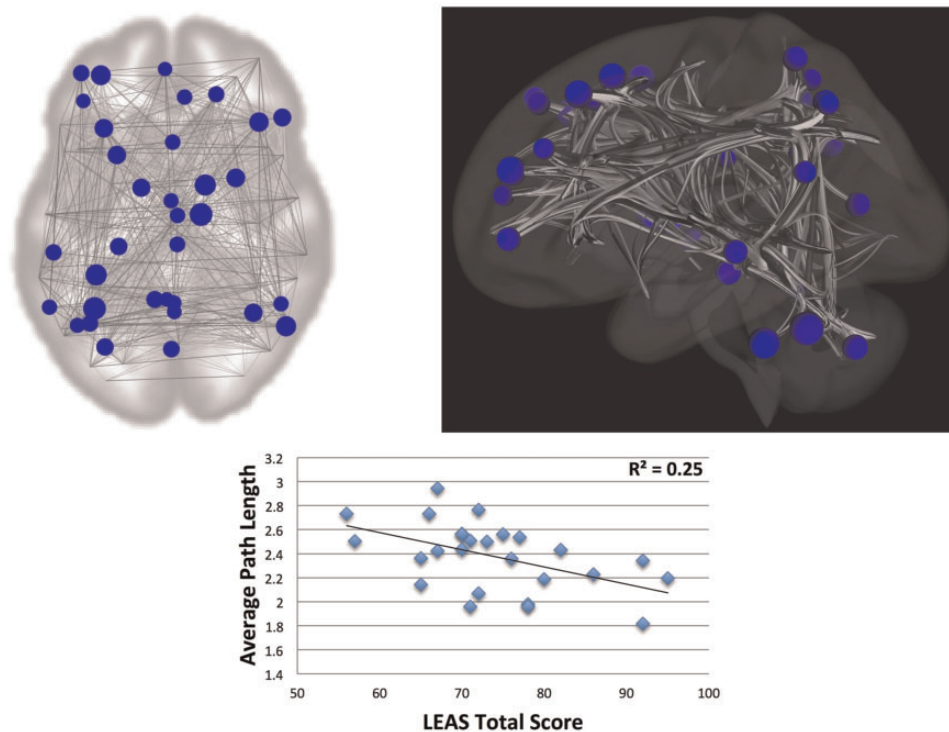


Fig. 1. Illustration of our initial analysis examining the relationship between LEAS Total scores and Average Path Length. The top panel provides two depictions of the resulting graph's edges and FDR-corrected significant nodes (listed in Table 1), in which larger blue nodes indicate stronger negative relationships (i.e. T-values; while statistically accounting for age, gender and IQ). The bottom panel displays a scatterplot illustrating the (zero-order) correlational relationship between LEAS Total scores and whole-network Average Path Length (i.e. prior to accounting for our covariates stated above, where accounting for these covariates increased the strength of the observed relationship).

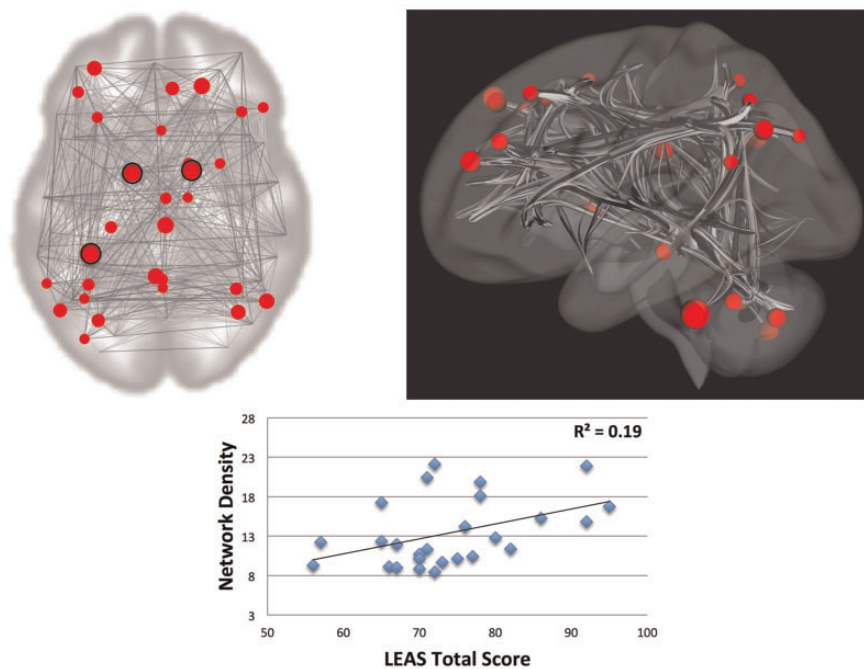


Fig. 2. Illustration of our initial analysis examining the relationship between LEAS Total scores and Degree. The top panel provides two depictions of the resulting graph's edges and significant nodes. Larger red nodes indicate stronger positive relationships (i.e. T-values; while statistically accounting for age, gender and IQ). To provide a clearer illustration of how the distribution of nodal relationships contributes to our whole-network results, we have displayed all nodes that showed a significant relationship with Degree at a liberal threshold of $P < 0.05$, uncorrected (these included nodes within the majority of functionally defined networks examined, except for the auditory network, sensorimotor network, and the primary and higher visual networks). T-values range from 2.10 to 4.29. The three large nodes with black outlines are those that survived FDR-correction (listed in Table 2). The bottom panel displays a scatterplot illustrating the (zero-order) correlational relationship between LEAS Total scores and whole-network Density (or average degree; i.e. prior to accounting for our covariates stated above, where accounting for these covariates increased the strength of the observed relationship).

ROIs), dorsal and ventral DMNs (seven and two ROIs, respectively), language network (two ROIs), precuneus network (two ROIs), primary visual network (calcarine sulcus), right and left ECNs (four and three ROIs, respectively), sensorimotor network (one ROI) and visuospatial network (one ROI) (displayed in Figure 1). We also observed that those with higher LEAS TOTAL scores displayed greater degree within two basal ganglia ROIs and one posterior SN ROI (i.e. the nodes outlined in black within Figure 2). For detailed ROI-specific results, see Tables 1 and 2. For ROI-specific results at the alternative liberal ($r=0.2$) and conservative ($r=0.4$) thresholds we examined, see [Supplementary Results and Tables S2–S4](#).

Analyses controlling for network density

After adding network density (average degree) as an additional covariate, and re-performing the other analyses described above, we observed that many of the other graph theory metrics no longer showed a significant relationship with LEAS TOTAL scores. Specifically, only average path length at the whole-network-level continued to display the significant negative relationship with LEAS TOTAL scores observed above [$t(20)=-2.34$, $P=0.03$; Figure 3]. Qualitatively similar to our initial whole-network results for average path length described above, this finding also held at a trend level [$t(20)=-1.88$, $P=0.075$] using the alternative liberal ($r=0.2$) threshold, but was not present at the conservative ($r=0.4$) threshold. No other significant whole-network or ROI-specific (i.e. after FDR-correction) relationships with LEAS TOTAL scores were observed in these analyses.

Discussion

Major findings

In this study, we hypothesized that higher levels of tEA (as indicated by higher LEAS TOTAL scores) would be associated with a range of complimentary graph theory metrics that reflect greater efficiency of whole-brain information exchange. As predicted, across a whole-brain network of 90 functionally defined ROIs (nodes) we initially observed that individuals with higher tEA also displayed shorter average path lengths, higher global and local efficiency, a higher clustering coefficient and higher network density. Importantly, age, gender, and IQ were each statistically controlled for, which affords greater confidence that these results cannot be attributed to any of these other factors (especially as IQ was positively associated with tEA in our sample). These findings also remained significant when alternatively tested using more liberal ($r=0.2$) and conservative ($r=0.4$) edge thresholds (i.e. with the exception of average path length, which was not significant at the $r=0.4$ threshold; see [Supplementary Results](#)). The qualitatively similar network-level results, and somewhat overlapping ROI-specific results, at each threshold, provide added confidence in the robustness of our findings (i.e. especially the hypothesized network-level results), and suggest that they are not simply due to the selection of a single arbitrary threshold.

After subsequently controlling for individual differences in network density (average degree), however, we found that only shorter average path length continued to show the initially observed association with higher tEA. This suggests that the other indices of more efficient information exchange that we observed with increasing tEA were primarily due to the fact that increasing levels of tEA appear to correspond to a generally increasing number of functional connections (edges) present

Table 1. Significant relationships observed between LEAS TOTAL scores and average path length (edge threshold: $r=0.3$)

Average path length		
ROIs by network	T	P-FDR
<i>Basal ganglia</i>		
R thalamus, R caudate, R putamen	-3.20	0.031
L thalamus, L caudate	-3.74	0.031
L inferior frontal gyrus	-3.17	0.031
<i>Dorsal default mode</i>		
L angular gyrus	-2.69	0.042
Medial prefrontal cortex, anterior cingulate cortex, orbitofrontal cortex	-2.54	0.048
Posterior cingulate cortex, precuneus	-2.67	0.043
R angular gyrus	-2.85	0.040
R hippocampus	-3.57	0.031
R superior frontal gyrus	-3.09	0.034
L thalamus, R thalamus	-2.74	0.042
<i>Ventral default mode</i>		
Precuneus	-3.27	0.031
L retrosplenial cortex, L posterior cingulate cortex	-2.59	0.048
<i>Left executive control</i>		
L middle frontal gyrus, L superior frontal gyrus	-2.68	0.042
L inferior frontal gyrus, L orbitofrontal gyrus	-3.29	0.031
L superior parietal gyrus, L inferior parietal gyrus, L precuneus, L angular gyrus	-2.90	0.040
<i>Right executive control</i>		
R middle frontal gyrus, R superior frontal gyrus	-3.07	0.034
R middle frontal gyrus	-3.42	0.031
R inferior parietal gyrus, R supramarginal gyrus, R angular gyrus	-2.69	0.042
R caudate	-2.71	0.042
<i>Anterior salience</i>		
L middle frontal gyrus	-2.73	0.042
L insula	-3.51	0.031
L lobule VI, L crus I	-4.00	0.029
R lobule VI, R crus I	-3.26	0.031
<i>Posterior salience</i>		
L thalamus	-3.75	0.031
R thalamus	-4.02	0.029
L lobule VI	-3.01	0.037
L posterior insula, L putamen	-2.57	0.048
<i>Auditory</i>		
R thalamus	-2.8	0.048
<i>Language</i>		
L inferior frontal gyrus	-2.70	0.042
L middle temporal gyrus, L superior temporal gyrus, L supramarginal gyrus, L angular gyrus	-2.87	0.040
<i>Precuneus</i>		
L angular gyrus	-2.94	0.039
Precuneus	-2.80	0.042
<i>Primary visual</i>		
Calcarine sulcus	-2.93	0.039
<i>Sensorimotor</i>		
L precentral gyrus, L postcentral gyrus	-2.57	0.048
<i>Visuospatial (dorsal attention)</i>		
R frontal operculum, R inferior frontal gyrus	-3.31	0.031

during the resting state. That is, they are less plausibly attributable to differences in network properties that are independent of overall differences in the number of total connections. Therefore, these findings suggest that the indices of more efficient whole-brain information exchange we observed

(with increasing tEA levels) primarily reflect independent contributions of decreasing average path lengths and increasing degree/network density.

In general, these results provide support for the application of leading empirical models of conscious awareness (Dehaene, 2014; Dehaene et al., 2014) to the domain of emotion (e.g. as in the three-process model described in the introduction; Smith et al., 2017b; also see Lane et al., 2015; Smith and Lane, 2015, 2016; Panksepp et al., 2017). This is because such models suggest that becoming consciously aware of emotion requires that relevant locally represented information (e.g. situational appraisals, interoceptive/somatic percepts, emotion concepts, etc.) is “globally broadcast” to a domain-general “global neuronal

workspace” of cortical network hubs throughout the brain’s association cortices (i.e. plausibly requiring direct functional connections from one region to many others; i.e. higher degree). This is thought to allow that information to be maintained in working memory and integrated into multi-step, goal-directed decision-making and action selection processes. Other proposals also similarly suggest that conscious experience requires the kind of complex information integration processes that would be supported by efficiently connected whole-brain networks (Oizumi et al., 2014; Tononi et al., 2016). Therefore, one would expect that greater awareness of emotion would correspond to whole-brain network architectures supporting more efficient global information exchange (e.g. with higher degree, facilitating the widespread broadcasting/integration processes postulated in the previously described theories). It is also worth highlighting that, because we used a functionally defined atlas of ROIs covering the whole brain (Shirer et al., 2012), this helps to ensure that the relationships we observed were between functionally homogenous regions (and likely improves within-ROI signal-to-noise ratios). This therefore adds to the plausibility of the functional interpretation we suggest here.

Table 2. Significant relationships observed between LEAS TOTAL scores and Degree (edge threshold: $r = 0.3$)

ROIs by network	Degree	
	T	P-FDR
<i>Basal ganglia</i>		
R thalamus, R caudate, R putamen	3.74	0.036
L thalamus, L caudate	4.17	0.020
<i>Posterior salience</i>		
L thalamus	4.29	0.020

Possible implications of findings for distinct metrics

We will now consider more specific implications that might follow from the specific measures we examined. At the network

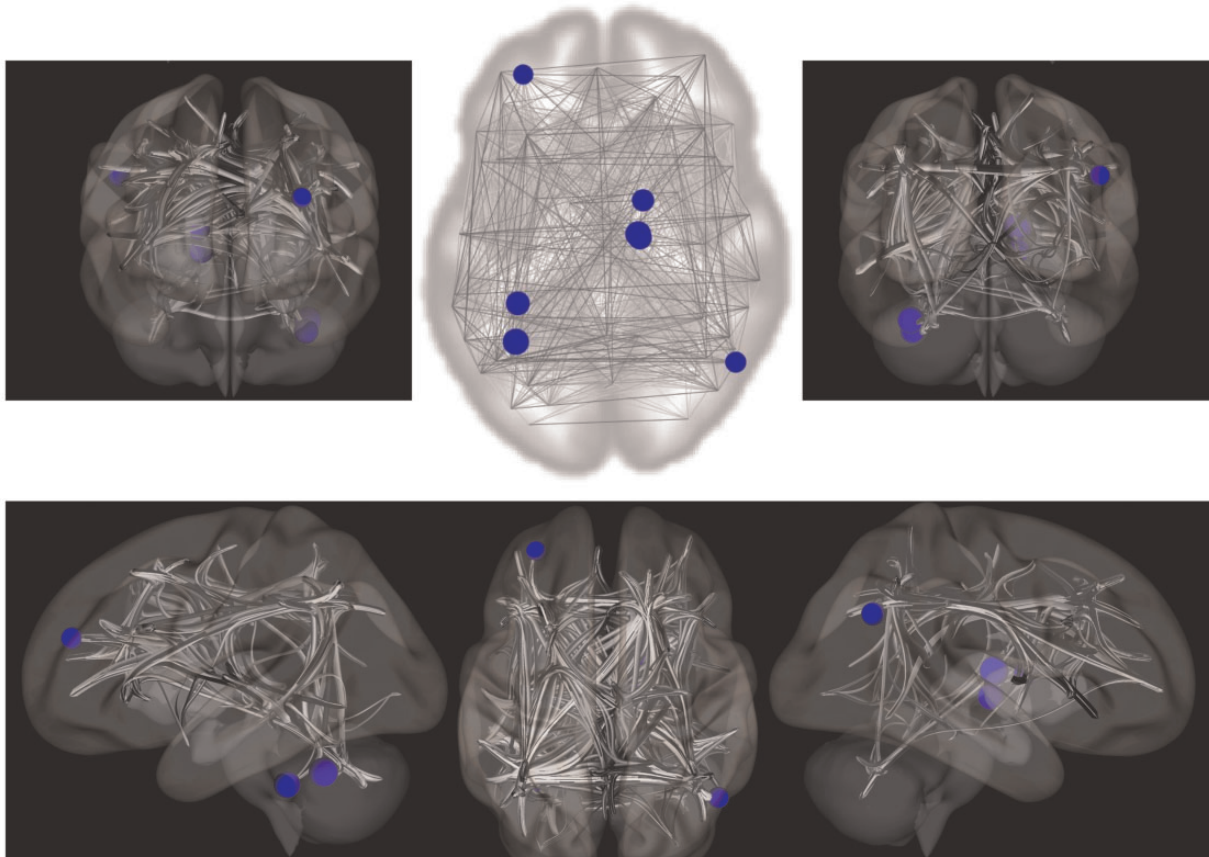


Fig. 3. Illustration of our subsequent results when examining the relationship between LEAS Total scores and Average Path Length, after further accounting for individual differences in Network Density. Only the whole-network relationship remained significant in this analysis. However, to provide a clearer illustration of how the distribution of nodal relationships contributes to the aforementioned whole-network results, we have displayed all nodes that showed a significant relationship with Average Path Length at a liberal threshold of $P < 0.05$, uncorrected (these included nodes within the dorsal DMN, basal ganglia network, auditory network, and both anterior and posterior SNs). Larger blue nodes indicate stronger negative T-values. T-values range from -2.14 to 2.80 .

level, average path length is a measure of how many intermediate nodes (on average) a signal would need to pass through in order for any node to convey information to any other node throughout the brain. Thus, the finding that higher tEA corresponds to shorter average path length suggests that locally represented information about emotion could be more easily/efficiently passed to other brain regions/networks. When subsequently exploring this metric for individual nodes, we also observed a large number of ROIs that contribute to several large-scale neural networks, which also showed the same relationship with tEA. This included: (i) Salience and Sensorimotor network regions (perhaps suggesting more efficient broadcasting/use of information about affective bodily states in those with higher tEA; Smith et al., 2009, 2017a; Yeo et al., 2011; Chong et al., 2017); (ii) Auditory and Language Network regions (perhaps suggesting more efficient broadcasting/use of verbal information in those with higher tEA; Fedorenko and Thompson-Schill, 2014); (iii) Primary Visual, Precuneus and DMN regions (perhaps suggesting more efficient broadcasting/use of emotion-related information in episodic/semantic memory in those with higher tEA, including their use in internal simulation processes such as those involved in imagining feelings in the LEAS's hypothetical scenarios; Barrett and Satpute, 2013; Eustache et al., 2016); (iv) Visuospatial (Dorsal Attention) and ECN regions (perhaps reflecting more efficient top-down control processes in those with higher tEA; Seeley et al., 2007; Corbetta et al., 2008; Yeo et al., 2011) and (v) Basal Ganglia Network regions (perhaps reflecting more efficient cognitive/behavioral reward-/habit-learning processes, and more efficient broadcasting of affective value information, in those with higher tEA; Hazy et al., 2007; Dolan and Dayan, 2013). However, none of these ROI-specific results remained significant after controlling for network density (i.e. although average path length at the whole-network level did); as such, these possible region-specific functional implications would most plausibly follow from their greater number of direct connections (as opposed to the specific character of those connections).

Previous studies have also found evidence that differences in tEA correspond to differences in resting state and task-related activation within similar DMN, ECN, and SN regions (Lane et al., 1998; Frewen et al., 2008; McRae et al., 2008; Smith et al., 2017c); however, this is the first study to find evidence of tEA-related differences in function within the other network regions listed above, and no previous study has examined the relationship between tEA and average path length (although only findings for some Default Mode, Salience, Visuospatial, and Basal Ganglia Network regions remained significant at the alternative $r=0.2$ threshold, and none were significant the $r=0.4$ threshold; see Supplementary Results). While future studies will be necessary to replicate these novel findings, this provides initial evidence that tEA may index very widespread differences in information processing throughout the brain.

At the network level, density (average degree) can be thought of as a measure of overall network complexity (i.e. the average number of connections per node). Therefore, the finding that higher tEA corresponds to greater average values for this metric further supports the idea that awareness of emotion is supported by more complex network architectures capable of supporting more thorough information integration. These relationships were also present for Basal Ganglia Network regions and for one subcortical SN region (i.e. a left thalamic region involved in interoceptive processing). This further supports the idea mentioned above that tEA may in part reflect the efficiency of processing/broadcasting information about affective body

states and reward/value information (these findings also remained significant at the alternative $r=0.2$ threshold, although not at the $r=0.4$ threshold; see Supplementary Results).

It is important to note that many of the same psychiatric disorders associated with lower tEA (reviewed in the introduction) have also been found to have aberrant values for graph theory metrics consistent with what we observed with lower tEA. For example, relative to healthy individuals, those with schizophrenia show significantly lower values for clustering coefficient and local efficiency (Kambeitz et al., 2016), as well as lower global efficiency and greater average path length (Zhu et al., 2016). Individuals with depression show similar reductions in clustering coefficient and global efficiency, as well as increases in average path length (Luo et al., 2015). Decreased global and local efficiency have also been found in cocaine addiction (as well as other types of substance-dependence; Wang et al., 2015). Given that these disorders are also characterized by lower tEA (reviewed in Lane et al., 2015), this opens up interesting questions for future research about the relationship between tEA, psychiatric symptoms, and functional network architectures. For example, it is possible (i) that lower tEA levels index particular network architectures that in turn promote vulnerabilities to psychiatric symptoms, (ii) that psychiatric disorders reflect aberrant network architectures, which in turn hinder performance during assessments of tEA or (iii) that there are bi-directional combinations of these influences over time. Longitudinal studies would be necessary to investigate such questions, and the results of the present study underscore the importance of carrying out such studies.

It is also worth highlighting that socio-cognitive and personality variables, with both empirical and conceptual links to tEA, have also been studied using graph theory—and these previous results dovetail well with our own. For example, greater openness to experience has been associated with both higher tEA (Lane et al., 1990; Smith et al., 2018) and with metrics of greater network efficiency within the DMN (Beatty et al., 2016). Thus, our present results suggest that greater network efficiency could perhaps relate to the shared variance in these two individual difference variables. As another example, individuals with autism display reduced whole-brain network efficiency, and are also characterized in part by reduced theory-of-mind abilities (Keown et al., 2017). Given that low tEA in part indexes low affective theory-of-mind abilities, our results further suggest that high network efficiency may be important for theory-of-mind abilities generally. It will be important for future work to employ graph theory analyses to further examine these relationships, as well as other similar social and affective information processing abilities.

Limitations, future directions and conclusions

One limitation of the present study was that our sample size was relatively small. Therefore, we may have failed to detect existing relationships between network properties and LEAS scores due to reduced power (e.g. power = 0.76 for the network density analysis). This possibility of false negatives is especially notable for our subsequent ROI-specific analyses, given the need to correct for a large number of multiple comparisons. Some related limitations were that our sample had a fairly restricted age range (i.e. early adulthood), and was in the above-average range for both IQ and LEAS scores. Each of these limitations calls the generalizability of our results into question. Therefore, future studies should attempt to replicate these findings in larger samples with greater power that include older adults as well as individuals with a wider range of IQ and LEAS scores. Yet another

limitation is the lack of total consistency in our ROI-specific results at different edge thresholds. Our suggested interpretations of ROI-specific findings should therefore be treated with caution prior to replication in future work. In general, given that some (but not all) of the ROI-specific results at the intermediate ($r=0.3$) threshold were also present at the liberal ($r=0.2$) threshold, and that almost none survived at the conservative ($r=0.4$) threshold, this suggests that tEA may be most relevant for predicting differences in the liberal-to-intermediate threshold range (i.e. in individuals with higher tEA, more ROI-to-ROI connections survive the jump in threshold from $r=0.2$ to 0.3 than in those with lower tEA, but most relevant connection differences are removed by the jump from the $r=0.3$ to 0.4 threshold). Finally, as our results are purely correlational, no causal/directional claims are warranted. Therefore, future studies, and perhaps especially longitudinal studies, will be necessary to ascertain whether individuals with higher tEA subsequently develop greater network complexity, or whether greater network complexity instead promotes the development of higher tEA. At present, it appears most plausible to expect that such interactions would be bidirectional and mutually reinforcing.

In summary, the findings of the present study extend previous work on the neural basis of stable individual differences in emotional awareness. While previous work has focused on patterns of activation/connectivity in specific brain regions/networks, this is the first study to examine how tEA is related to brain-wide information integration processes using graph theory metrics. Consistent with current neural models of conscious awareness in general (e.g. Dehaene, 2014; Smith, 2016, 2017), and conscious awareness of emotion in particular (e.g. Smith et al., 2017b), our findings support the idea that stable tendencies to become more aware of emotions may be facilitated by more complex and efficient information sharing dynamics throughout the brain. As differences in tEA are currently thought to play a role in moderating the development and treatment of multiple emotional and systemic medical conditions (reviewed in Lane et al., 2015), graph-theoretic analyses should be extended to such clinical populations in future work. This may represent a currently under-investigated avenue for discovering potential biomarkers useful to differential diagnosis and the prediction of treatment outcomes. Finally, our results add to a small but growing body of literature using graph theory to examine individual differences in personality and social, cognitive, and affective processing abilities, and they highlight the need for further work in this area. This could help elucidate both common and unique neural network properties that may underlie these important differences.

Supplementary data

Supplementary data are available at SCAN online.

Conflict of interest. None declared.

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