Positive and Negative Affective Processing Exhibit Dissociable Functional Hubs During the Viewing of Affective Pictures

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Abstract: Recent resting-state functional magnetic resonance imaging (fMRI) studies using graph theory metrics have revealed that the functional network of the human brain possesses small-world characteristics and comprises several functional hub regions. However, it is unclear how the affective functional network is organized in the brain during the processing of affective information. In this study, the fMRI data were collected from 25 healthy college students as they viewed a total of 81 positive, neutral, and negative pictures. The results indicated that affective functional networks exhibit weaker small-worldness properties with higher local efficiency, implying that local connections increase during viewing affective pictures. Moreover, positive and negative emotional processing exhibit dissociable functional hubs, emerging mainly in task-positive regions. These functional hubs, which are the centers of information processing, have nodal betweenness centrality values that are at least 1.5 times larger than the average betweenness centrality of the network. Positive affect scores correlated with the betweenness values of the right orbital frontal cortex (OFC) and the right putamen in the positive emotional network; negative affect scores correlated with the betweenness values of the left OFC and the left amygdala in the negative emotional network. The local efficiencies in the left superior and inferior parietal lobe correlated with subsequent arousal ratings of positive and negative pictures, respectively. These observations provide important evidence for the organizational principles of the human brain functional connectome during the processing of affective information. *Hum Brain Mapp* 36:415–426, 2015. © 2014 Wiley Periodicals, Inc.

Key words: affective pictures; connectome; fMRI; graph theory; small-world

INTRODUCTION

The processing of affective information is crucial for an individual's social adaptation and mental health [Dima et al., 2011], and its dysfunction within a cortico-limbic neural system may precipitate affective disorders [Mak et al., 2009]. However, the question of how affective processing is organized in the brain is unsolved [Rohr et al., 2013]. Specifically, how positive and negative emotional processing relates to network organization has yet to be determined. Recently, an increasing number of functional connectivity studies have revealed that the processing of positive and negative emotions

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depends on different neural circuits [Hamann, 2012; Kim and Hamann, 2007].

Positive emotional processing mostly involves the frontostriatal circuit, which is important for rewards and approaching motivation [Buckholz and Meyer-Lindenberg, 2012]. Particularly, the orbital frontal cortex (OFC) and the ventral striatum, including the putamen, have reciprocal anatomical links, and they have been shown to be sensitive to positive emotional stimuli in numerous studies of emotions [Rolls and Grabenhorst, 2008; Wickens et al., 2007]. Resting-state research has indicated that individual positive affect (PA) scores correlate with the functional connectivity between the putamen and superior temporal cortex and between the caudate and medial OFC, precuneus, and posterior cingulate cortex [Rohr et al., 2013]. Changes in striatal coupling with the ventromedial prefrontal and cingulate cortex have been observed in mental disorders (e.g., anhedonia) [Kehagia et al., 2010].

In contrast, the amygdala and medial prefrontal cortex (mPFC) (ventromedial and medial orbital aspects) comprise a corticolimbic circuit that is consistently engaged during the task of evoking negative emotional arousal or regulating negative emotional responses [Zald, 2003]. Animal anatomical studies have determined the heaviest projections from the amygdala to the mPFC and OFC in the macaque [Roberts et al., 2007]. Retrieval of encoding negative emotional context increases the effective connectivity between the amygdala and hippocampus, parallel with enhanced OFC activity [Smith et al., 2006]. Moreover, negative emotional stimuli tend to enhance the connectivity between the left middle/inferior frontal gyri (Brodmann's area 47) and amygdala [Curcić-Blake et al., 2012]. Dysfunction in the frontoamygdala circuit predicts high levels of negative affect (NA) traits and is evident in mood and anxiety disorders [Cremers et al., 2010].

However, results from functional connectivity research have not revealed the characteristics of the affective functional network as a whole, the connectome of the brain [Bullmore and Sporns, 2009]. Graph theory metrics is an advanced research tool that is used to quantify the properties of all connections between a set of brain regions or nodes. By using the concept of efficiency measuring of how efficiently information is exchanged over the network [Latora and Marchiori, 2001], graph theory analyses of the human brain from diffusion tensor imaging (DTI) have shown that the brain network follows a small-world topography, with high global and local efficiency [Yan et al., 2011]. The structural network of the human brain is optimally organized to support both globally and locally efficient information processing [Bullmore and Sporns, 2009; Sporns et al., 2004]. Moreover, these authors have also revealed several cortical hubs that have a high degree of nodal betweenness centrality, which measures important influences over information flow between other nodes in the network. These hubs were predominantly located in the heteromodal association regions, including the middle

frontal and inferior temporal gyri as well as the para/limbic regions of the hippocampus, parahippocampal gyrus, and amygdala [Achard and Bullmore, 2007; Buckner et al., 2009].

The functional connectome describes a graph that represents functional interactions in the brain and is dynamic, as it underpins a multitude of brain states that involve cognition and emotion [Zuo et al., 2012]. If measured during rest, the graph maps the intrinsic functional architecture of the brain. In task-driven experiments, it represents integration systems between specialized brain areas [Varoquaux and Craddock, 2013]. Resting-state studies have revealed several functional hubs that constitute the default-mode network (DMN) [Jin et al., 2013]. Performing a *n*-back task increases the ratio between functional connectivity and regional cerebral blood flow (rCBF) in task-positive hub regions, especially within the task-related executive control network; engaging greater cognitive effort in task performance was associated with a more efficient network topology [Liang et al., 2013]. Moreover, functional networks have weaker connections between modules and, consequently, lower global efficiency [Rubinov and Sporns, 2010]. However, it remains largely unknown which nodes are critical for affective information flow, which hubs of affective functional networks are better structured for local versus global processes, or whether the graph-theoretic characteristics of these hubs correlate with the Positive and Negative Affect Scale (PANAS) scores.

To address these issues, the present study collected functional magnetic resonance imaging (fMRI) data from 25 healthy college students while they viewed 81 images from the Chinese Affective Picture System (CAPS) [Bai et al., 2005] and rated the arousal of these images afterward viewing. After the experiment, each participant completed a self-reported PANAS form. For each participant, we first extracted the time series of the volumes of interest (VOIs) separately from the positive vs. neutral and negative vs. neutral picture contrasts on the basis of a first-level analysis. Next, we constructed the weighted functional networks for positive and negative emotions through thresholding the correlation coefficient matrices. Then, we calculated several network parameters (e.g., small-worldness) and characterized the functional hubs by estimating graph-theoretic-based measures. Finally, we performed correlational analyses between the PANAS scores and several hub properties.

METHODS

Participants

Twenty-five right-handed undergraduates (14 females: 18.42 ± 0.71 years, range 18.2–23.5 years; 11 males: 18.86 ± 0.69 years, range 18.4–23.8 years) were recruited from East China Normal University. All of the participants

had normal or corrected-to-normal visual acuity. None of the participants had a prior history of neurological or psychiatric disorders nor had they experienced anxiety or depression within the last three months. Data from two participants (one male and one female) were excluded because of poor-quality data recordings. All of the participants provided written informed consent and were paid ~\$15 for their participation. The relevant institutional ethical committee approved this research.

The Positive and Negative Affect Scale

The affective tendencies of the participants were assessed with the PANAS, a self-report form designed by Watson et al. [1988] and revised to a Chinese version by Qiu et al. [2008]. Briefly, PA reflects the extent to which a person feels enthusiastic, active, and alert. High PA is a state of high energy, full concentration, and pleasurable engagement, whereas low PA is characterized by sadness and lethargy [Watson et al., 1988]. In contrast, NA is a general dimension of subjective distress and unpleasurable engagement that subsumes a variety of aversive mood states, with low NA being a state of calm [Watson et al., 1988]. Therefore, PANAS PA and NA do not represent opposite ends of the pleasantness–unpleasantness spectrum, as the PA and NA of other affective scales do. Rather, they are designed to be orthogonal and independent of each other. The scale consists of 18 items, which are self-rated on a 5-point scale, ranging from 1 = very slightly or not at all to 5 = extremely. Cronbach's α was 0.87 for PA and 0.85 for NA. In this study, the participants were asked to consider the items in general or within the last three months to provide scores of affective disposition.

Stimulus Materials

Participants viewed 81 pictures from the CAPS [Bai et al., 2005], which is a collection of standardized photographic material that was obtained from the International Affective Picture System [Lang et al., 1999]. Of these images, 27 depicted positive events (e.g., an attractive infant, a smiling face, or two people hugging), 27 depicted neutral events (e.g., vegetation, a household object, or a building), and 27 depicted negative events (e.g., a wreckage, snake, or burnt face). These visual stimuli were projected on a transparent screen inside the scanner tunnel and could be viewed by the participant through a mirror system mounted on the top of the MRI head coil. E-prime 1.1 software (Psychology Software Tools, Pittsburgh, PA) was used to control the timing of all stimuli. The participants' responses were registered by an MRI-compatible device with five buttons on a keypad for each hand.

Experimental Procedure

During fMRI scanning, a fixation mark (+) was first presented for 2 s, and then, a picture was presented for 6 s. Next, the picture disappeared and the Chinese word

“assessment” appeared at the center of the screen, which cued the participants to rate the arousal intensity of the picture by pressing a button using a Likert scale ranging from 1 (extremely weak) to 9 (extremely strong). After the participants completed the rating within 2 s, the screen became blank for a random period of time (between 2 and 10 s). The experimental task initiated with a 12 s dummy scan and consisted of 81 randomized trials in a single acquisition. A 15 s resting baseline was inserted between every 27 trials. The participants were familiarized with the task off-line half an hour before the scan. After the scan, the participants completed the self-report PANAS form outside the scanner.

Image Acquisition

MRI images were acquired using a 3-T Trio Tim Magnetic Resonance Imaging scanner (Siemens Company) with a head coil gradient set at East China Normal University. Whole-brain data were acquired with echo-planar T2*-weighted imaging (EPI) that was sensitive to blood oxygen level-dependent (BOLD) signal contrast (32 axial slices, repetition time (TR) = 2,000 ms, echo time (TE) = 30 ms, flip angle = 90°, slice thickness = 5 mm, field of view (FOV) = 240 mm × 240 mm, matrix size = 64 × 64, voxel size = 3.75 mm × 3.75 mm × 5 mm). The first two volumes were discarded to allow for equilibration effects. T1-weighted anatomical images were acquired at a resolution of 1 mm × 1 mm × 1 mm (TR = 1,900 ms, TE = 3.43 ms, flip angle = 7°).

Image Processing

Data were analyzed using SPM8 software (www.fil.ion.ucl.ac.uk/spm). The EPI images were interpolated in time to correct for slice time differences and were realigned to the first scan by rigid body transformations to correct for head movements. To minimize movement artifacts, individuals with an estimated maximum displacement in any direction larger than 1 mm or a head rotation larger than 1° were discarded from the study. Data from two participants (one male and one female) were excluded under this criterion. The T1-weighted images were coregistered to the mean EPI image. The coregistered data were subsequently normalized onto the standard template in MNI space (Montreal Neurological Institution), resampled to 3 mm isotropic voxels, and smoothed with a Gaussian kernel of full-width-half-maximum (FWHM) 8 mm.

The first-level analysis was performed using a general linear model (GLM). Vectors of onset representing positive, neutral, and negative pictures, with a 6-s picture duration and a 2-s arousal rating period, were convolved with a canonical hemodynamic response function. The mean time courses from the deep white matter and ventricles were regressed out from the fitted time series [Van Dijk et al., 2010]. Removal of the global signal can cause a shift in the distribution of the correlation coefficients and make interpretation of the sign of the correlation ambiguous [Murphy et al., 2009]. Therefore,

Figure 1.

Neuroanatomical location of network nodes. Brain regions with significant activation in the contrast of positive and negative vs. neutral pictures [$P < 0.05$ using the AlphaSim corrected (combined height threshold of $P < 0.005$ and a minimum cluster size of 10 voxels)]. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

the global signal was not regressed in the present study. Six movement parameters were also entered as nuisance covariates. Low-frequency signal drift was removed using a high-pass temporal filter with a cutoff of 128 s, and an autoregressive model (AR1) was applied to adjust for autocorrelations. For each participant, positive vs. neutral and negative vs. neutral picture contrasts were produced and were then entered into a second-level random-effect group analysis (see Supporting Information Results).

Construction of the Weighted Region-based Network

To define the network nodes, we first performed another GLM that only included the contrast of positive and negative vs. neutral pictures on the second-level analysis [Tettamanti et al., 2012]. The significance value was set at $P < 0.05$ using the AlphaSim corrected (combined height threshold of $P < 0.005$ and a minimum cluster size of 10 voxels). Based on the group maxima, we selected 56 VOIs that were implicated in emotional processing in previous studies (Fig. 1) by the PickAtlas toolbox [Maldjian et al., 2003]. For each participant, the center of the VOI was then defined as the subject-specific maxima (positive and nega-

tive vs. neutral picture contrast, $P < 0.001$, uncorrected) in the given region that was within 16 mm of the group maxima and still belonged to the same anatomical region (visual inspection). Next, 6 mm spheres were drawn around the center, defined above, for the positive or negative vs. neutral picture contrasts ($P < 0.05$, uncorrected), and then, the time courses for each participant were computed using the first eigenvariate from the VOI.

We considered these VOIs as network nodes and created weighted region-based networks for the positive or negative vs. neutral picture contrasts. The partial correlation coefficient between the two regions was computed as the weight of the edge after filtering out the contributions of all of the other variables included in the dataset. Weak and non-significant links may represent spurious connections [Rubinov and Sporns, 2010] and were therefore discarded by applying a proportional weight threshold (23%) [Tijms et al., 2012]. As a result, only positive correlation coefficients were preserved. All self-connections were also removed from the present study.

Graph Metric

Although graph theoretic network analysis offers a broad selection of measures, in this study, we mainly

TABLE I. Graph metrics of positive and negative emotional functional networks

Graph metrics	Positive-neutral network		Negative-neutral network	
	Mean	SD	Mean	SD
γ	1.46	0.13	1.53	0.11
λ	1.05	0.014	1.12	0.012
σ	1.39	0.097	1.37	0.10
Global efficiency	0.32	0.012	0.34	0.015
Local efficiency	0.46	0.064	0.47	0.065
Clustering coefficient	0.41	0.044	0.39	0.042
Degree	6.53	1.28	6.37	1.18
Betweenness centrality	27.85	3.55	30.26	3.62
Modularity	0.32	0.061	0.34	0.064
Assortativity	-0.12	0.009	-0.03	0.007

γ , the ratio of the network's cluster coefficient and that of its randomized version; λ , the ratio of the average minimum path length of the network and that of its randomized version; σ , the small-world coefficient (γ/λ).

focused on a few network characteristics, including small-worldness, global efficiency, local efficiency, clustering coefficient, degree, betweenness centrality, modularity, and assortativity. Hub characteristics mainly included nodal global efficiency, nodal local efficiency, nodal clustering coefficient, nodal shortest path length, nodal degree, nodal normalized betweenness, module, and nodal vulnerability. Supporting Information Methods provided the definitions and mathematical equations of these measures in detail. We calculated these graph metrics using the Gretna software (www.nitrc.org/frs/download.php/5534/gretna.zip).

Visualization

Data were visualized on the brain surface using the smoothed ICBM152 surface and plotted using the Brainnet Viewer Toolbox [Xia et al., 2013]. The ICBM152 volume image represents the average of 152 healthy T1 brain images. This template corresponds (but only approximately) to a brain neurosurgical atlas, the Talairach and Tournoux atlas [Talairach and Tournoux, 1988]. Brainnet Viewer, a graph-theoretical network visualization toolbox, draws the brain surface, nodes, and edges in sequence and displays brain networks in multiple views. This software is freely available on the NITRC website (www.nitrc.org/projects/bnv/).

Statistical Analysis

For behavioral data, a one-way repeated measure ANOVA with three valence levels was first performed for arousal ratings, and then, Pearson correlation analyses were performed between arousal ratings for positive, neg-

ative, and neutral pictures and PANAS scores. For graph-theoretical measures, we first computed their weighted averages to correct for the number of hubs and considered that different networks have different numbers of hubs and then compared these measures using a paired *t*-test with a Bonferroni correction for the number of tests on the global and hub level. Finally, Pearson correlations were performed between hub characteristics and either PANAS scores or arousal ratings. Threshold levels of significance for Pearson's correlation coefficients were adjusted for multiple comparisons by the Bonferroni correction, and the new $P < 0.005$ was reported [Curtin and Schulz, 1998].

RESULTS

Behavioral Data

A one-way repeated measure ANOVA with three valence levels (positive, neutral, and negative) yielded a significant main effect of valence on arousal rating ($P < 0.001$). *Post hoc* tests indicated that negative and positive pictures were rated with higher arousal compared with neutral pictures ($P < 0.01$; $M \pm SD$: Positive = 5.87 ± 0.44 ; Neutral = 4.58 ± 0.41 ; Negative = 5.91 ± 0.47). However, there was no significant difference between negative and positive pictures ($P = 0.58$).

Pearson correlation analysis revealed no significant correlation between individual PA and NA scores ($r = 0.09$, $P > 0.05$; PA = 2.96 ± 0.56 , NA = 3.21 ± 0.49), which was expected based on their construction as independent dimensions. Furthermore, PA scores correlated marginally with the arousal of positive pictures ($r = 0.35$, $P = 0.064$); NA scores correlated marginally with the arousal of negative pictures ($r = 0.37$, $P = 0.061$).

Network Analysis

Functional network characteristics

Table I shows network characteristic values of positive or negative vs. neutral picture contrast networks. To assess whether the functional networks were small world, we calculated the weighted clustering coefficient (C_p) and the weighted characteristic path length (L_p) for both the functional networks and 100 corresponding random networks with the same number of nodes, edges, mean degrees, and degree distribution. Compared to random graphs, the functional networks had almost identical path lengths ($\lambda = 1.05$, 1.12 for positive or negative vs. neutral picture contrasts, respectively) but was more locally clustered ($\gamma = 1.46$, 1.53 for positive or negative vs. neutral picture contrasts, respectively), resulting in small-world scales ($\sigma = 1.39$, 1.37 for positive or negative vs. neutral picture contrasts, respectively).

However, the global efficiency was lower than the local efficiency (one-side paired *t*-test: $t_{22} = 5.73$, 5.28 , $P < 0.001$

TABLE II. The characteristics of functional hubs in the positive emotional network

	bi	M	$LocEi$	Gei	Cpi	Lpi	Ki	vi	X	Y	Z
OFC_R	15.24	1	0.35	0.48	0.17	2.05	24.61	2.91	50	24	-11
OFC_L	11.42	2	0.35	0.48	0.17	2.06	20.38	2.43	-51	23	-11
SPL_L	5.65	5	0.54	0.44	0.25	2.27	16.71	1.43	-29	-54	55
S1_R	3.68	5	0.43	0.41	0.33	2.46	14.23	0.87	42	-28	58
Put_R	3.61	1	0.37	0.28	0.29	3.55	3.45	2.58	30	-13	7
STG_R	1.95	1	0.40	0.38	0.26	2.61	12.86	1.79	62	-19	-2
MCC_R	1.92	5	0.45	0.32	0.38	3.04	7.28	0.70	-9	2	43
SOG_R	1.84	2	0.42	0.29	0.35	3.37	5.62	0.08	21	-87	16
MFG_R	1.78	3	0.47	0.32	0.41	3.08	7.81	0.34	6	56	16
SMA_R	1.59	5	0.43	0.35	0.36	2.87	9.72	0.71	3	8	62

bi , the nodal normalized betweenness; M , module; $LocEi$, nodal local efficiency; Gei , nodal global efficiency; Cpi , nodal clustering coefficient; Lpi , nodal shortest path length; Ki , nodal degree; vi , nodal vulnerability; X , Y , and Z , the MNI coordinates. OFC_R, right orbit frontal cortex; OFC_L, left orbit frontal cortex; SPL_L, left superior parietal lobe; S1_R, right primary sensorimotor cortex; Put_R, right putamen; STG_R, right superior temporal gyrus; MCC_R, right middle cingulate cortex; SOG_R, right superior occipital gyrus; MFG_R, right medial frontal gyrus; SMA_R, right supplemental motor area.

for positive or negative vs. neutral picture contrasts, respectively). Moreover, the functional networks had low negative assortativity coefficients, indicating that these networks have widely distributed and vulnerable high-degree hubs. Overall, these functional networks are highly segregated but poor integrated networks and therefore have weaker small-world attributes.

Hub characteristics

Nodal betweenness centrality measures the influence of a node on information flow between additional nodes in the network. Generally, nodes with high betweenness may serve as way stations for network traffic or as centers of information integration [Hagmann et al., 2008]. According to a previous study [Yan et al., 2011], we identified the following hubs because of their large values in nodal betweenness centrality (e.g., the betweenness value of a node is 1.5 times greater than the average betweenness of the network).

Positive-neutral picture contrast

Table II shows the node-specific graph metrics of the positive vs. neutral picture network. Ten regions were identified as functional hubs with a normalized betweenness higher than 1.5 [Yan et al., 2011]. These hubs included the bilateral OFC, right medial frontal gyrus (MFG), left superior parietal lobe (SPL), right superior temporal gyrus (STG), right primary sensorimotor cortex (S1), right supplemental motor area (SMA), right superior occipital gyrus (SOG), right middle cingulate cortex (MCC), and right putamen (Fig. 2). These functional hubs belonged to five different modules. Specifically, the right OFC and the right putamen had greater vulnerability values compared with other hubs (all $t_{22} > 3.94$, all $P < 0.01$). The right SPL had a

larger local efficiency than other hubs (all $t_{22} > 2.08$, all $P < 0.05$).

Negative-neutral picture contrast

Table III shows the node-specific graph metrics of a negative vs. neutral picture contrast network. Twelve regions with a normalized betweenness higher than 1.5 were identified as functional hubs, including the bilateral OFC, left inferior parietal lobe (IPL), right middle temporal gyrus (MTG), left precuneus, left S1, right middle occipital gyrus (MOG), right fusiform, right MCC, bilateral hippocampus, and left amygdala (Fig. 3). These hubs belonged to five different modules. Specifically, the left OFC and the left amygdala had larger vulnerability values compared with other hubs (all $t_{22} > 4.07$, all $P < 0.01$). The left IPL had a larger local efficiency value than other hubs (all $t_{22} > 2.18$, all $P < 0.05$).

Relationship between hub characteristics and behavioral measures

Pearson's correlation analyses indicated that PA scores correlated positively with the betweenness values in the right OFC ($r = 0.71$, $P < 0.001$, corrected; Fig. 4a) and the right putamen ($r = 0.62$, $P < 0.005$, corrected; Fig. 4b) in the positive vs. neutral picture contrast; however, we did not observe significant correlations between PA scores and the betweenness values in the hubs of the negative vs. neutral network (all $P > 0.05$, uncorrected). NA scores correlated positively with the betweenness values in the left OFC ($r = 0.68$, $P < 0.001$, corrected; Fig. 4c) and the left amygdala ($r = 0.63$, $P < 0.001$, corrected; Fig. 4d) in the negative vs. neutral picture contrast; however, we did not observe significant correlations between NA scores and the

Figure 2.

The functional network of positive vs. neutral picture contrast. Ten functional hubs (red color) with a normalized betweenness higher than 1.5 were identified, including the left and right orbit frontal cortex (OFC.L/OFC.R), left superior parietal lobe (SPL.L), right primary sensorimotor cortex (S1.R), right putamen (Putamen.R), right superior temporal gyrus (STG.R), right middle

cingulate cortex (MCC.R), right superior occipital gyrus (SOG.R), right medial frontal gyrus (MFG.R), and right supplemental motor area (SMA.R). The size of the nodes represents the magnitude of normalized nodal betweenness centrality. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE III. The characteristics of functional hubs in the negative emotional network

	<i>bi</i>	<i>M</i>	<i>LocEi</i>	<i>Gei</i>	<i>Cpi</i>	<i>Lpi</i>	<i>Ki</i>	<i>vi</i>	<i>X</i>	<i>Y</i>	<i>Z</i>
OFC_L	10.42	1	0.43	0.46	0.27	2.17	17.82	4.98	-50	31	-11
PCN_L	7.21	3	0.38	0.28	0.31	3.58	3.35	4.25	-6	-52	37
OFC_R	5.20	1	0.43	0.46	0.27	2.16	18.68	2.71	51	20	-14
MOG_R	4.79	4	0.47	0.43	0.35	2.35	15.11	1.53	29	-76	25
Hipp_L	3.64	5	0.45	0.32	0.34	3.13	4.80	0.78	-25	15	-11
S1_L	2.75	2	0.48	0.38	0.36	2.58	12.31	1.54	51	-1	46
MTG_R	2.68	1	0.46	0.40	0.33	2.43	13.53	1.81	60	-7	-11
MCC_R	1.61	1	0.48	0.31	0.45	3.13	6.29	3.42	6	11	37
Fus_R	1.56	4	0.52	0.34	0.52	2.92	7.72	3.51	37	-64	-17
Amy_L	1.56	5	0.38	0.29	0.30	3.41	3.94	4.58	-24	-4	-11
Hipp_R	1.56	5	0.24	0.22	0.22	4.39	1.88	1.23	18	-7	-11
IPL_L	1.52	2	0.57	0.34	0.43	2.95	7.62	0.69	-30	-46	55

bi, the nodal normalized betweenness; *M*, module; *LocEi*, nodal local efficiency; *Gei*, nodal global efficiency; *Cpi*, nodal clustering coefficient; *Lpi*, nodal shortest path length; *Ki*, nodal degree; *vi*, nodal vulnerability; *X*, *Y*, and *Z*, the MNI coordinates. OFC_L, left orbit frontal cortex; PCN_L, left precuneus; OFC_R, right orbit frontal cortex; MOG_R, right middle occipital gyrus; Hipp_L, left hippocampus; S1_L, left primary sensorimotor cortex; MTG_R, right middle temporal gyrus; MCC_R, right middle cingulate cortex; Fus_R, right fusiform; Amy_L, left amygdala; Hipp_R, right hippocampus; IPL_L, left inferior parietal lobe.

Figure 3.

The functional network of negative vs. neutral picture contrast. Twelve functional hubs (red color) with a normalized betweenness higher than 1.5 were identified, including the bilateral OFC (OFC.L/OFC.R), left inferior parietal lobe (IPL.L), right middle temporal gyrus (MTG.R), left precuneus (Precun.L), left SI (SI.L), right middle occipital gyrus (MOG.R), right fusiform

(Fus.R), right middle cingulate cortex (MCC.R), bilateral hippocampus (Hipp.L/Hipp.R), and left amygdala (Amyg.L). The size of the nodes represents the magnitude of normalized nodal betweenness centrality. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

betweenness values in the hubs of the positive vs. neutral picture network (all $P > 0.05$, uncorrected).

Moreover, the local efficiency in the left SPL in the positive vs. neutral picture network correlated positively with the arousal difference between positive and neutral pictures ($r = 0.45$, $P < 0.05$, uncorrected; Fig. 5a) but not with the arousal difference between negative and neutral pictures ($P > 0.05$, uncorrected). The local efficiency in the left IPL from the negative vs. neutral picture network correlated positively with the arousal difference between negative and neutral pictures ($r = 0.52$, $P < 0.05$, uncorrected; Fig. 5b) but not with the arousal difference between positive and neutral pictures ($P > 0.05$, uncorrected).

DISCUSSION

In this study, we used the graph theoretic approach to examine whether small-worldness is evident in the affective functional network and which functional hubs are crucial for positive and negative emotional networks. We

found that affective processing exhibited a small-world network with lower global efficiency as the participants viewed affective pictures from the CAPS. Positive and negative emotional networks had different functional hubs that exhibited dissociable correlational patterns with the PANAS scores. Finally, local efficiencies in the left SPL and the left IPL correlated with the subsequent arousal ratings of affective pictures. These results suggest that the affective functional networks dynamically reorganize with emotional processing demands.

Affective Functional Networks Show Weaker Small-worldness

A growing number of the structural and resting-state functional studies have determined that the human cerebral cortex demonstrates small-worldness properties [Achard et al., 2006; Liang et al., 2013; Tijms et al., 2012; Yan et al., 2011]. Consistent with these results, the small-worldness is also present in weighted functional networks in our study. The consistency partially supports the

Figure 4.

The relationships between the PANAS scores and nodal normalized betweenness values. The correlation between the PANAS scores and the normalized betweenness in the right orbit frontal cortex (OFC) (a) or in the right putamen (b) of the positive function network; the correlation between the PANAS scores

and the normalized betweenness in the left OFC (c) or in the left amygdala (d) of the negative affective function network. PA, positive affect; NA, negative affect. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

fundamental principle of the brain organization that the functional network reflects the underlying anatomical architecture with small-worldness properties [Achard et al., 2006].

However, the affective functional networks showed higher local efficiency (but lower global efficiency). This unbalance might be attributed to the task effect. First, the resting-state measures only reflect intrinsically organized

Figure 5.

The correlation (a) between the arousal difference from positive minus neutral pictures and the local efficiency in the left SPL of the positive functional network or (b) between the arousal difference from negative minus neutral pictures and the local efficiency in the left IPL of the negative functional network. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

patterns of spontaneous signal fluctuation; therefore, the resting-state network shows the balance of high global and local efficiency [Power et al., 2010]. In contrast, task-based measures assess the BOLD signal change caused by an experimental manipulation. During the viewing of affective pictures, the functional network was dynamically reorganized according to the specific cognitive demands of the task, and extra metabolism was needed to support the reorganized functional architecture [Liang et al., 2013]. To optimize information processing efficiency, task performance increased local functional connectivity, which resulted in higher local efficiencies but lower global efficiencies [Sepulcre et al., 2010]. Additionally, the affective functional networks had negative assortativity coefficients, indicating that the affective functional networks become highly segregated but poorly integrated [Rubinov and Sporns, 2010]. Taken together, these results suggest that affective functional networks exhibit weaker small-worldness properties.

Positive and Negative Emotional Processing Exhibit Dissociable Functional Hubs

In our study, functional hubs emerged mainly in task-positive regions, especially with the executive control network, although there was partial overlap with the DMN (e.g., MFG, precuneus, and hippocampus) [Northoff et al., 2010]. In contrast, functional hubs occur only in the DMN in resting-state studies [Jin et al., 2013; Liang et al., 2013]. Moreover, positive and negative emotional functional networks had distinct functional hubs that are broadly distributed over the network.

In the positive emotional network, functional hubs included the bilateral OFC, right MFG, left SPL, right STG, right S1, right SMA, right SOG, right MCC, and right putamen. Particularly, both the right OFC and the right putamen had greater vulnerability values compared with other hubs. Their removal would result in the secondary disconnection of other nodes, and the functional network efficiency would drop more rapidly compared with other hubs [Latora and Marchiori, 2003]. Consistent with this result, their disruption is closely associated with anhedonia (which is present in both schizophrenia and mood disorders) [Kehagia et al., 2010]. Moreover, the betweenness values of the right OFC and the right putamen correlated positively with PA scores. These results are consistent with previous results that demonstrated that both the right OFC and the right putamen are involved in processing positive emotions [Rolls and Grabenhorst, 2008; Wickens et al., 2007].

In the negative emotional network, functional hubs included the bilateral OFC, left IPL, right MTG, left precuneus, right MOG, right fusiform, right MCC, bilateral hippocampus, and left amygdala. Particularly, the left OFC and the left amygdala had greater vulnerability values than other hubs. This might be because the amygdala is

situated in the salience network and interconnect densely with the OFC [Roberts et al., 2007; van den Heuvel and Sporns, 2011]. Additionally, NA scores correlated positively with the betweenness in the left OFC and the left amygdala. These observations are consistent with the finding that their dysfunctions are associated with the symptoms of NA in mood and anxiety disorders [Cremers et al., 2010; Drabant et al., 2006].

The Local Efficiency in the Left Parietal Cortex Correlates With Arousal Rating

During the fMRI scan, the participants were instructed to rate picture arousal after viewing each picture so that they were probably thinking the rating while viewing the picture as well as during 2-s rating period. Therefore, our GLM models included the 6-s picture viewing and the 2-s arousal rating period. Because all picture conditions included the same 2-s rating period, doing so do not change the nature of positive, neutral, and negative picture processing but keeps the baseline true. Pearson correlation analyses revealed that the local efficiencies in the left SPL and the left IPL during picture processing exhibited correlations with the arousal differences between positive or negative and neutral pictures. This might be because the SPL and IPL are part of the executive control network that is associated with individual differences in task performance [Liang et al., 2013]. Moreover, the left SPL and left IPL demonstrated greater local efficiencies compared with other hubs. Previous results revealed that task performance increases local functional coupling in hub regions engaged in the task [Sepulcre et al., 2010]. Consistent with this, the left SPL and the left IPL increase the local connections with the rest of the brain. The increase in local efficiency might be parallel with increased rCBF that is biased to maintain these connections [Paulson et al., 2010]. Therefore, affective processing increases local efficiency in the parietal cortex, which correlates with the subsequent arousal ratings of affective pictures.

The limitations of this study need to be mentioned. First, we only measured weighted (and undirected) functional networks that do not allow causal inferences to be made. Future studies should use an effective connectivity matrix to construct directed (weighted or unweighted) functional networks to verify our results. Second, viewing affective pictures in our study is an easy and passive task. It is unclear how affective functional networks dynamically evolve when participants perform more active tasks. Future studies should consider using an active task (e.g., emotion regulation) to replicate the present results.

CONCLUSION

In summary, we used graph theory analysis to determine the characteristics of weighted functional networks during affective picture processing. Affective functional

networks become highly segregated and exhibit weaker small-worldness. Positive and negative emotional networks demonstrate dissociable functional hubs that present mainly in the executive-control network. Particularly, PA scores correlate with the betweenness values of the right OFC and the right putamen in the positive emotional network. In contrast, NA scores correlate with the betweenness values of the left OFC and the left amygdala in the negative emotional network. The local efficiencies in the left SPL and the left IPL separately correlate with the arousal ratings of positive and negative pictures. These observations increase our understanding of the task-state-based functional connectome of the human brain.

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