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ORIGINAL ARTICLE

A dimensional approach to jealousy reveals enhanced fronto-striatal, insula and limbic responses to angry faces

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Abstract

Jealousy is a complex social emotion combining the different primary emotions of anger, fear and sadness. Previous evidence has suggested the involvement of fronto-striatal dopaminergic circuitry in pathological jealousy, although little is known about overlaps with the neural representation of primary emotions involved in non-morbid jealousy and the utility of a dimensional neuroimaging approach. In the current study, 85 healthy subjects underwent fMRI during an emotional face recognition paradigm and resting state. A total of 150 faces (happy, angry, fearful, sad, neutral) were presented and subjects required to identify the expression and rate its intensity. Trait jealousy was assessed using the Multidimensional Jealousy Scale. Behavioral results showed that only intensity ratings of angry faces were positively associated with subjects' jealousy scores. During processing of angry versus neutral expression faces, subjects with elevated jealousy exhibited increased activation in the right thalamus, insula, fusiform gyrus and hippocampus, left dorsal striatum, superior parietal lobule and bilateral cerebellum and inferior frontal gyrus after controlling for trait aggression and sex. Functional connectivity between the inferior frontal gyrus and dorsal striatum was also increased. No associations with resting-state functional connectivity were found. Overall, the present study demonstrates an association between exaggerated jealousy and increased intensity ratings of angry faces as well as activity and functional connectivity of the dorsal striatal–inferior frontal circuitry. Thus, increased emotional responsivity to social threat and enhanced activity in limbic regions and dopaminergic fronto-striatal circuitry may be features of both non-morbid and pathological jealousy confirming the utility of a dimensional approach.

Keywords Anger · Jealousy · Dimensional approach · Face emotion · Fronto-striatal circuits · Limbic system

Introduction

Jealousy is an important and complex social emotion which can be displayed when an individual is threatened with losing something of personal value and involves affective, behavioral and cognitive components (Harris 2004; Pfeiffer and Wong 1989). Jealousy is characterized by distrust, fear of loss, anger and anxiety (Parrott and Smith 1993). Jealousy is considered as a combination of the primary emotions anger, fear and sadness (Ekman 1999; Hupka 1984). From an evolutionary perspective, jealousy in a relationship is an evolved adaptation (Buss and Haselton 2005) that can be beneficial for stabilizing it by providing a warning that a sexual partner is potentially desirable and attractive to others who may, therefore, compete for them. Extreme, pathological jealousy includes delusional symptoms and promotes aggression in terms of domestic violence, self-mutilation and even murder (Camicioli 2011) and can also occur in association with depression (Aronson and Pines 1980) and autism (Bauminger 2004).

Initial neuroimaging studies have examined the neural basis of jealousy and its pathological forms by monitoring neural reactivity when it is induced experimentally. In male monkeys, the amygdala, striatum and superior temporal sulcus (STS), the temporal pole in right hemisphere and

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bilateral insula are activated when the male monkeys were confronted with threats to their exclusive sexual access to a female mate (Rilling et al. 2004). In humans, pathological jealousy has been associated with altered dopaminergic fronto-striatal reward circuitry and in the ventral medial prefrontal cortex (vmPFC) and insula involved in mentalizing/self-related processing and interoception/salience processing, respectively (Marazziti et al. 2013). In line with this conclusion, the experience of jealousy in healthy humans is accompanied by increased activation in the basal ganglia (BG), and frontal, particularly ventromedial prefrontal (vmPFC), regions, with exaggerated jealousy also being associated with increased incidence of interpersonal aggression (Harmon-Jones et al. 2009; Sun et al. 2016). Furthermore, there is some evidence for sex differences in neural responses during the experience of jealousy with men demonstrating greater activation than women in brain regions involved in sexual/aggressive behaviors such as amygdala and hypothalamus while women showed greater activation in the posterior superior temporal sulcus (Takahashi et al. 2006). A study of the neural correlates associated with complex social emotions such as envy and gloating has also demonstrated an important role for the vmPFC (Shamay-Tsoory et al. 2007), suggesting that this region is involved more widely in emotions related to jealousy.

Jealousy usually occurs in social interactive contexts, especially relationship triangles, and subtle alterations in the processing of social signals may, therefore, represent the neural mechanism that promotes its expression. Additionally, it is possible that jealousy may be associated with more general neural processing differences which can be determined even in the absence of external stimulation during resting-state conditions. Previous studies in the field have not controlled for potential overlaps with the neural representation of the individual emotions which comprise jealousy, anger, fear and sadness, and as such we do not know whether there is a neural circuitry which uniquely encodes either pre-morbid or pathological jealousy. An additional important issue that no previous studies have attempted to distinguish jealousy from aggression, with both being strongly correlated and evoked by a perception of threat (Sun et al. 2016). In recent years, there has been increasing interest in applying dimensional approaches to help characterize psychiatric disorders derived from the proposed Research Domain Criteria (RDoC) framework (Cuthbert 2014; Insel et al. 2010). Dimensional frameworks propose that pathology-relevant traits are normally distributed in the population and that psychiatric populations represent the extreme end of the distribution (see Ruzich et al. 2015). Translated into the research context, dimensional frameworks allow control for serious confounding factors that commonly hamper the interpretation of findings in patient populations, including co-morbid disorders as well as unspecific confounders such as socioeconomic background. Dimensional approaches have, therefore, been increasingly combined with neuroimaging to determine pathology-relevant neurofunctional markers in healthy and psychiatric populations (Hägele et al. 2015, 2016; Li et al. 2019; Luo et al. 2018). In line with these previous approaches, we thus employed a dimensional neuroimaging approach in a large sample ($n = 85$) of healthy subjects to determine neurofunctional markers of trait jealousy. To explore whether altered reactivity toward social signals promotes jealousy as distinct from aggression, we have investigated associations between individual variations in trait jealousy and trait aggression and differential responses to social stimuli which convey threat versus neutral or positive social signals. Additionally, associations between trait jealousy as opposed to aggression on neural processing have been investigated in the absence of external stimuli by analyzing correlations with resting-state functional connectivity.

Against this background, the current study has employed a dimensional neuroimaging approach to investigate associations between trait jealousy and neural activity and functional connectivity using functional magnetic resonance imaging (fMRI) both during the resting state and in response to social emotional signal (face emotion processing) conditions in a cohort of 85 healthy young adults. Trait aggression and sex were controlled for during the analyses to account for potential contributions of these factors as confounders. Since jealousy often develops during social contexts, and in interaction with emotional responses of others, we hypothesized that this complex emotion would be specifically associated with neural reactivity toward social emotional signals (affective facial stimuli) rather than the intrinsic interaction of the underlying brain networks during the task-free state. We further hypothesized that trait jealousy would be particularly associated with a heightened behavioral and neural response to social threat signals (i.e., primarily angry and fearful faces).

Materials and methods

Participants

92 healthy adult Han Chinese subjects (male = 47; age range = 18–27 years, mean age ± SD = 21.68 ± 2.22 years) were enrolled in the present study. 38 subjects (male = 22) were in a current stable relationship and 54 were currently single (male = 25). All volunteers reported no history of medical, neurological or psychiatric disorders, and no history of head injury or frequent drug, cigarette or alcohol use and were free of MRI contraindications. All subjects provided written informed consent. The study had full ethical approval by the local ethics committee at the University of Electronic Science and Technology of China

and experiments were carried out in accordance with the latest revision of the Declaration of Helsinki.

Measurements

To exclude potential confounding effects from clinically relevant levels of depression and anxiety, all subjects completed Chinese versions of validated clinical screening scales before the experiment, including the Beck Depression Inventory-II (BDI-II, 21 items rated on a 4-point Likert-scale) (Beck et al. 1996; Wang et al. 2011) and State-Trait Anxiety Inventory (STAI, 40 items rated on a 4-point Likert scale) (Li and Qian 1995; Spielberger 1983). Individuals with clinically relevant scores on these two scales were excluded (BDI-II > 28; SAI > 69 or TAI > 69). Individual levels of trait jealousy were assessed using the Multidimensional Jealousy Scale (MJS) (Pfeiffer and Wong 1989). The MJS consisted of 24 items, each rated on a 7-point Likert scale, with low scores indicating low levels of jealousy whereas higher scores reflect tendencies for pathological increased levels of jealousy. To control for potential confounding effects of trait aggression, all subjects were additionally administered a Chinese version of the Buss–Perry Aggression Questionnaire (AQ) (Buss and Perry 1992; Li et al. 2011). The AQ consisted of 30 items, each with a 5-point Likert scale rating format with higher scores indicating higher trait aggression.

Experimental procedures and stimuli

A total of 150 faces including 5 different emotional expressions happy, angry, fearful, sad, and neutral (each from 30 different actors, 15 males) were selected from the Chinese Facial Affective Picture System (Gong et al. 2011) and the Taiwanese Facial Expression Image Database (TFEID) (Chen and Yen 2007). All faces were standardized into grayscale pictures and covered with an oval mask to remove hair and other individual features using Photoshop CS6.0 (see Fig. 1). Before the fMRI session, subjects completed 20 training trials after receiving detailed instructions. Subjects were told to lie still during scanning and foam pads were used to minimize head movement and reduce the impact of scanner noise. The MRI acquisition started with an 8 min 30 s resting-state fMRI acquisition where subjects were instructed to keep their eyes closed and to think of nothing in particular without falling asleep. Subsequently, subjects performed an event-related fMRI face emotion recognition paradigm comprising a total of 150 trials that were equally distributed across 3 runs (50 trials each run, duration 570 s per run). Face emotion and gender were balanced across the three runs. Each trial started with passive viewing of the facial stimulus followed by emotion recognition and intensity ratings (total duration, 7000 ms). In the first 1500 ms, a face was displayed for passive viewing. Next, subjects had to indicate the emotion from choices below the face (1 = neutral, 2 = sad, 3 = happy, 4 = angry, and 5 = fearful) for 2500 ms. Ratings of emotional intensity were then required

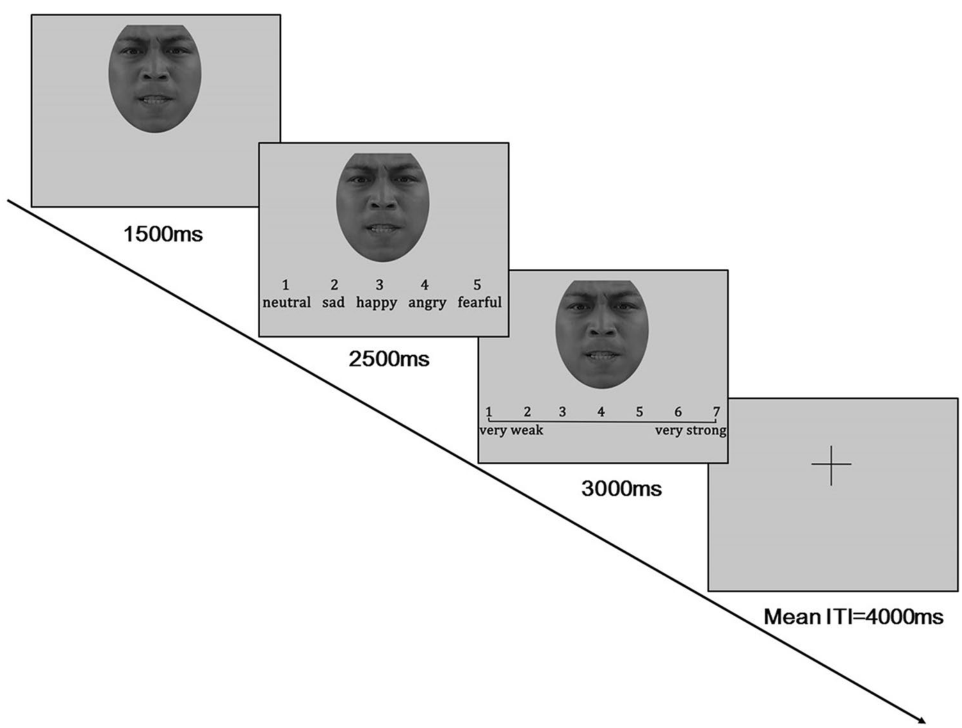

Fig. 1 Example trial of the event-related emotional face fMRI paradigm

using a 7-point rating scale (1 = very weak to 7 = very strong) presented for 3000 ms. A jittered fixation cross was displayed between the trials for 3600–4400 ms (mean ITI = 4000 ms) and served as an implicit baseline for the analysis (see Fig. 1). The Face Recognition Task paradigm was presented via E-prime 2.0 (Psychology Software Tools, USA, http://www.pstnet.com/eprime.cfm).

Image acquisitions

MRI data were obtained using a 3 Tesla GE Discovery MR750 system (General Electric, Milwaukee, WI, USA). During the task-based fMRI acquisition, a time series of volumes was acquired using a T2*-weighted gradient echo-planar imaging pulse sequence (repetition time (TR), 2000 ms; echo time (TE), 30 ms; numbers of slices, 39; thickness, 3.4 mm; spacing, 0.6 mm; field of view (FOV), 240×240 mm^2; flip angle, 90°; matrix size, 64×64). Identical sequence parameters were used for the acquisition of the preceding 8 min 30 s resting-state fMRI acquisition. Each run of the Face Recognition Task consisted of 285 volumes and each of the resting-state scans consisted of 255 volumes. High-resolution whole-brain T1-weighted images were additionally acquired to improve normalization of the functional images (spoiled gradient echo pulse sequence; repetition time (TR), 6 ms; echo time (TE), 1.964 ms; number of slices, 156; thickness, 1 mm; FOV = 256×256 mm^2; flip angle = 9°; matrix = 256×256).

Behavioral data analyses, quality control and assessment of collinearity

In an initial step, a reliability analysis was conducted to evaluate the psychometric quality of the MJS and AQ and both demonstrated excellent internal consistencies (Cronbach's α coefficients: MJS, $\alpha = 0.848$; AQ, $\alpha = 0.921$). Independent sample tests further revealed no sex differences for trait jealousy ($t_{83} = 0.635$, $p = 0.527$) or aggression ($t_{83} = 0.712$, $p = 0.478$) and also no effect of current relationship status (MJS – $t_{83} = -1.165$, $p = 0.247$; AQ – $t_{83} = 0.349$, $p = 0.728$).

Next, the normal distribution of MJS and AQ scores, as well as the emotional intensity ratings given during the task and recognition accuracy for all emotional face categories, was assessed using Shapiro–Wilk tests. Results showed that the AQ, emotional intensity ratings of neutral faces and recognition accuracy for all emotional expression faces displayed a non-normal distribution ($p < 0.05$). Associations between normal distributed indices were examined using Pearson correlation and where normal distribution was violated corresponding non-parametric tests (Spearman) were employed. Subsequently, associations between the two scales were explored and associations between MJS scores and the behavioral indices of the emotion recognition task (accuracy) were examined (Spearman). Correlation analyses between MJS scores and intensity ratings of angry, happy, fearful and sad faces used Pearson and whereas for neutral expressions Spearman was used. All behavioral analyses were conducted using SPSS 18 (Armonk, NY: IBM Corp).

Given that collinear regressors in fMRI models might lead to unreliable estimations (Andrade et al. 1999; Mumford et al. 2015), the variance inflation factor (VIF) (see Chau et al. 2017; Ohashi et al. 2017) was additionally examined to investigate collinearity between the regressors. A VIF > 5 is typically considered to indicate problematic collinearity (Mumford et al. 2015; O'Brien 2007) and in the present study (factors amongst sex, AQ scores, intensity ratings of angry (or fearful) faces, relationship status and MJS scores; factors amongst sex, AQ scores and MJS scores, respectively) were all < 1.158, arguing against problematic collinearity.

A total of 6 subjects (male = 4) were excluded due to excessive head movement during the resting-state acquisition (head motions > 2.5 mm) and 1 subject with a clinically significant depression and high trait anxiety (female, BDI = 41, TAI = 72), leaving a total of 85 subjects (male = 43, age range = 18–27 years, mean age ± SD = 21.64 ± 2.18 years) for all further analyses. A total of 4 subjects exhibited head motions > 2.5 mm within a run of the face recognition task (two for Run 1, one for Run 3, and one for Runs 2 and 3), and these specific runs were, therefore, excluded from further analyses in these subjects.

fMRI analyses

Data preprocessing

Preprocessing of the fMRI data from the emotion recognition task was performed using SPM12 (Statistical Parametric Mapping, http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB. After discarding the first five volumes of each functional time series to achieve magnet-steady images, the remaining images were initially realigned to the first image. To facilitate accurate normalization of the functional images, the T1 structural image of each subject was segmented into gray matter (GM), white matter (WM) and cerebrospinal fluid (CSF) using skull-stripped bias corrected brain images created using ImCalc. The mean functional image of each subject was co-registered to the structural image and subsequently co-registration was applied to all functional images. The functional images were next normalized to MNI space by applying the normalization parameters that were obtained from the structural images. The resolution of the normalized functional images was $3 \times 3 \times 3$ mm (voxel size). Normalized data were spatially smoothed with a Gaussian kernel of $8 \times 8 \times 8$ mm.

On the first level, condition-specific regressors for the passive viewing phase of the happy, angry, fearful, sad, and neutral faces were modeled as main conditions of interest. Regressors for the emotion recognition and intensity ratings as well as for the six movement parameters were additionally included. For the group level analyses, 1st-level emotion-specific contrasts for each facial emotion compared with neutral faces were created (angry > neutral, happy > neutral, fear > neutral, sad > neutral).

Resting-state fMRI time series were preprocessed using Data Processing Assistant for Resting-state fMRI (DPARSF) (Yan and Zang 2010). The first five volumes were excluded to achieve magnet-steady images and allow the subjects to adapt to the scanning noise. After slice timing correction, the time series were realigned to the first volume to correct for head motion. Data were discarded if the head movement exceeded 2.5 mm of translation or 2.5 degrees of rotation in any direction. The fMRI images were filtered with a temporal band-path of 0.01–0.1 Hz, normalized using DARTEL and resampled to a 3 × 3 × 3 mm voxel size. Finally, the functional images were smoothed using a Gaussian kernel of 8 mm full-width at half of the maximum value (FWHM). Six motion parameters, white matter, cerebrospinal fluid and global mean signals were regressed out.

fMRI Analysis

Associations between the levels of trait jealousy and emotion-specific neural activity were examined using a whole-brain multiple regression analysis as implemented in SPM12. The whole-brain regression served to identify brain regions where activation showed a linear association with MJS scores for the contrasts angry > neutral, happy > neutral, fear > neutral and sad > neutral, respectively. All regression models included sex and AQ scores as covariates.

To further explore associations between MJS scores and task-related neural activity on the network level, a functional connectivity analysis was employed using a seed-to-whole-brain approach. A generalized form of context-dependent psychophysiological interactions (gPPI) (McLaren et al. 2012) was implemented to model psychophysiological interactions on the individual level. Seed regions were determined on the basis of the significant results from the BOLD level regression analyses. Seed regions were constructed by defining 6 mm radius spheres centered at peak coordinates of significant clusters from the BOLD level analysis using MarsBaR (Brett et al. 2002). Next, associations between MJS scores and the emotion-specific connectivity of these regions were examined using SPM multiple regression models with the contrasts showing significant results from the BOLD level regression analyses. Again, sex and AQ scores were included as covariates.

To explore associations between individual variations in jealousy and resting-state functional connectivity, we computed two resting-state analyses. Analysis 1 employed a seed-to-whole-brain approach to explore whether resting-state functional connectivity at the whole-brain level was associated with MJS scores. Seed regions of interest (ROIs) were defined as a sphere with a 6 mm radius centered on the peak voxel of significant associations in whole-brain BOLD level analysis. Analysis 2 aimed at directly examining the pathways that showed associations during task-based functional connectivity by employing a seed-to-ROI approach specifically examining the respective pairs of seed-target regions (seed region and significant target-region from the gPPI analysis). Partial correlation on the extracted connectivity indices was subsequently implemented in SPSS18 to calculate the association between resting-state functional connectivity strength and MJS scores with sex and AQ scores as covariates.

Thresholding and mapping

For all whole-brain BOLD level and functional connectivity analyses, a consistent thresholding was applied with $p < 0.05$ cluster-level FWE correction (according to recent recommendations to control false positives in cluster level-based correction methods an initial cluster-forming threshold of $p < 0.001$ was applied to data resampled at 3 × 3 × 3 mm, Slotnick 2017). Brain regions were identified using the automated anatomic labeling (AAL) atlas (Tzourio-Mazoyer et al. 2002) as implemented in the WFU Pick Atlas (School of Medicine, Winston-Salem, North Carolina).

Results

Face recognition accuracy and emotional intensity ratings

Recognition accuracy for all emotional face categories was high (happy, M ± SD = 98.00% ± 3.40%; angry, 91.30% ± 8.56%; fearful, 88.37% ± 10.01%; sad, 93.80% ± 6.32%; neutral, 91.07% ± 11.49%) demonstrating that the subjects both attentively processed the facial stimuli and correctly identified them. Emotional intensity ratings (7-point scale) given by subjects were also higher for all emotional expression faces compared to neutral ones (happy, M ± SD = 5.04 ± 0.89; angry, 5.22 ± 0.78; fearful, 5.23 ± 0.70; sad, 4.86 ± 0.82; neutral, 3.04 ± 1.76). A repeated-measures ANOVA on accuracy scores with sex (male, female) as a between subject factor and emotional expression (happy, angry, fearful, sad, and neutral) as a within subject factor revealed no main effect of sex ($F(1,83) = 0.732$, $p = 0.395$, $\eta_p^2 = 0.009$) or sex × emotion interaction ($F(4,332) = 0.624$, $p = 0.611$, $\eta_p^2 = 0.007$). A similar ANOVA for intensity rating scores also showed no main effect of sex ($F(1,83) = 0.067$, $p = 0.796$, $\eta_p^2 = 0.001$) or sex × face emotion interaction ($F(4,332) = 0.537$, $p = 0.511$, $\eta_p^2 = 0.006$). Thus, there were no sex differences in face recognition accuracy or intensity ratings.

Correlation analyses showed that MJS scores were positively associated with AQ scores (*Spearman rho* = 0.270, $p = 0.012$), and with intensity ratings of angry (*Pearson's* $r = 0.220$, $p = 0.043$) and marginally for sad faces (*Pearson's* $r = 0.212$, $p = 0.052$). No significant associations were found between MJS scores and other emotional intensity ratings (all $ps > 0.121$). No significant associations were found between MJS scores and recognition accuracy for all emotional face categories (all $ps > 0.05$). There were no correlations between intensity ratings of emotions and AQ scores (all $ps > 0.135$).

Task and resting-state fMRI analysis

Controlling for subject sex and AQ scores as covariates, MJS scores were significantly positively associated with the activity of right thalamus, insula, hippocampus, fusiform gyrus, left dorsal striatum (putamen and caudate) and superior parietal lobule and bilateral cerebellum and inferior frontal gyrus during processing angry relative to neutral faces, and positively associated with superior parietal lobule activation in response to fearful relative to neutral faces (Table 1 and Fig. 2). No significant associations were observed between MJS and other face emotion conditions.

Associations between jealousy and the functional connectivity of these regions revealed an association between higher trait jealousy and increased functional connectivity between the right inferior frontal gyrus and left caudate ($k = 99$, $p = 0.034$, $t_{81} = 5.68$, x/y/z: −3/17/5) (Fig. 3) for angry versus neutral faces, with sex and AQ scores being controlled for. No significant associations between MJS

Table 1 Regions which showed positive correlation with MJS, using multiple regression on whole-brain level with gender and AQ as covariates

Region	Side	P_{FWE}	*k*	MNI coordinates			*t*
				x	*y*	*z*	
Angry faces > neutral faces							
Positive correlation							
Triangular inferior frontal gyrus	R	0.015	135	51	29	26	4.85
Opercular inferior frontal gyrus	R			51	14	32	3.46
Opercular inferior frontal gyrus	R			48	14	14	3.43
Hippocampus	R	0.000	303	33	−19	−10	4.73
Insula	R			36	5	−10	4.28
Thalamus	R			21	−13	−1	4.20
Superior parietal lobule	L	0.027	114	−15	−61	56	4.66
Inferior occipital gyrus	R	0.001	242	45	−73	−10	4.59
Cerebellum	R			39	−64	−31	4.55
Fusiform	R			36	−43	−19	4.40
Putamen	L	0.000	296	−30	−7	5	4.53
Thalamus/putamen	L			−24	−19	11	4.33
Putamen/caudate	L			−21	−1	14	4.17
Orbital inferior frontal gyrus	L	0.001	227	−45	20	−13	4.52
Superior temporal lobe	L			−54	2	−10	4.23
Triangular inferior frontal gyrus	L			−48	17	8	4.08
Cerebellum	L	0.021	122	−12	−58	−19	3.93
Cerebellum	L			−6	−70	−31	3.29
Fearful faces > neutral faces							
Positive correlation							
Superior parietal lobule	L	0.037	100	−15	−61	56	3.87
Middle occipital gyrus	L			−24	−67	38	3.67
Superior parietal lobule	L			−21	−67	47	3.60

All with $p < 0.05$ cluster-level FWE correction with an initial cluster-forming threshold $p < 0.001$. Coordinates of peak voxels (*x/y/z*) are given in Montreal Neurological Institute (MNI) space

L left, *R* right, *MJS* Multidimensional Jealousy Scale, *AQ* Buss–Perry Aggression Questionnaire

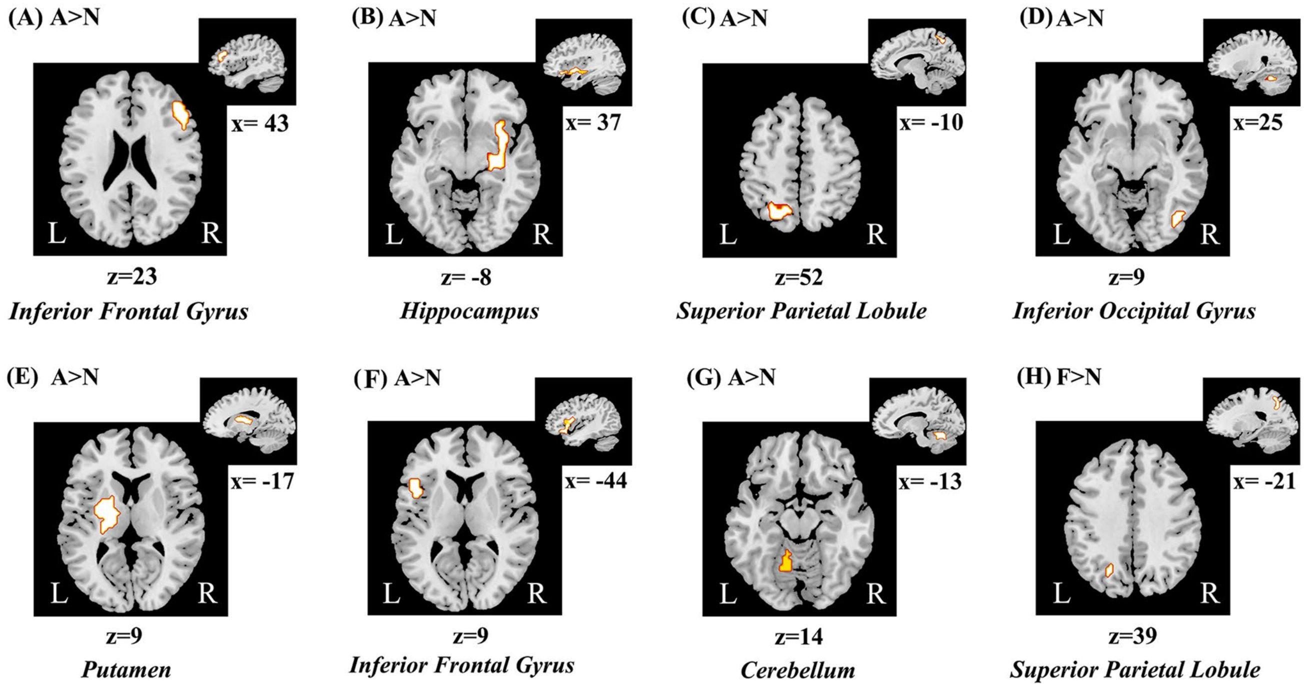

Fig. 2 Whole-brain analysis. (**a**–**g**) Regions showing increased activation with higher jealousy traits (as assessed by the MJS) during processing angry facial expressions relative to neutral faces. **h** Regions showing increased activation with higher trait jealousy (as assessed by the MJS) during processing of fearful relative to neutral faces. Both sex and AQ were included as covariates. Findings are displayed at $p < 0.05$ cluster-level FWE correction with a cluster-forming threshold $p < 0.001$. Coordinates of peak voxels (x/y/z) are given in Montreal Neurological Institute (MNI) space. *A > N* contrasts angry > neutral, *F > N* contrasts fearful > neutral, *L* left, *R* right, *MJS* Multidimensional Jealousy Scale, *AQ* Buss–Perry Aggression Questionnaire

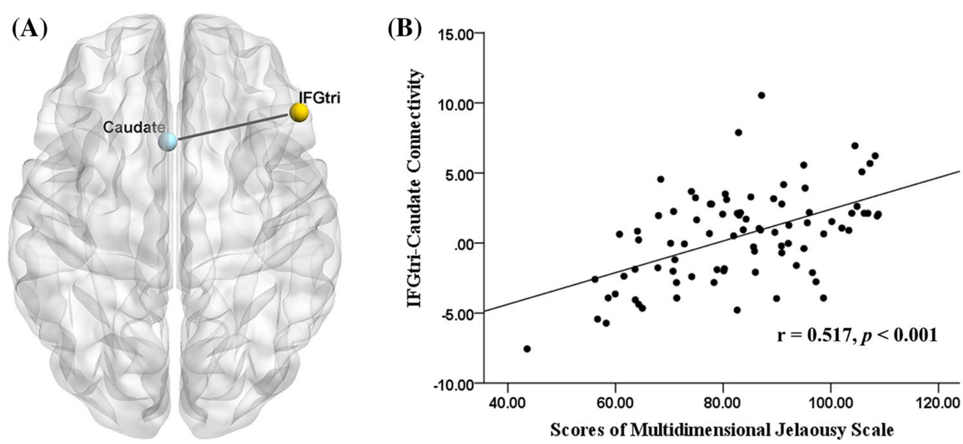

Fig. 3 Associations on the task-based network level. **a** Right triangular inferior frontal gyrus–IFGtri (6 mm sphere centered at $MNI_{xyz} = [51, 29, 26]$) as a seed region. Right IFGtri–left caudate (peak MNIxyz = [−3, 17, 5], $t_{81} = 5.68$, $p_{\text{cluster-FWE}} = 0.034$, $k = 99$) functional connectivity was positively correlated with trait jealousy (MJS) during processing of angry relative to neutral faces. **b** Scatter plot visualization of the association between trait jealousy and right IFGtri–left caudate coupling using extracted parameter estimates. *MNI* Montreal Neurological Institute space

scores and functional connectivity were observed during processing of fearful versus neutral faces.

To control for potential effects of co-variations of the intensity ratings as well as the relationship status of subjects with trait jealousy, we re-ran the analyses for the significant BOLD level associations including intensity ratings of angry and fearful faces and relationship status as nuisance covariates with sex and AQ scores. The main results of whole-brain analysis and gPPI analysis remained stable for associations with neural responses toward angry faces after additionally controlling for intensity ratings and relationship status, although not for regions showing correlations with fearful relative to neutral faces (see supplementary Table S1 and Figs S1 and S2).

There were no significant associations between MJS scores and functional connectivity in the seed-to-whole-brain analyses of resting-state functional connectivity, with sex and AQ scores controlled for. Similarly, there was no significant association between MJS scores and functional connectivity in the seed-to-ROI analysis.

Discussion

The present study aimed at investigating whether non-pathological levels of jealousy specifically relate to subtle alterations in neural reactivity toward social signals and/or more general alterations in intrinsic neural communication. To this end, a dimensional neuroimaging trait approach was employed to determine associations between individual variations in trait jealousy and neural reactivity in response to different emotional facial expressions as well as intrinsic processing in the absence of external stimulation during resting-state conditions. Our results revealed that trait jealousy was specifically associated with increased ratings of the intensity of angry faces and increased neural responses toward angry relative to neutral faces in the right thalamus, hippocampus, insula, fusiform gyrus, bilateral cerebellum, IFG and the left dorsal striatum (putamen and caudate) and superior parietal lobule as well as increased functional connectivity between the right IFG and left caudate. The specificity of the neural associations with variations in trait jealousy was established by controlling for trait aggression and sex as well as increased perception of the intensity for angry faces and relationship status in subjects with higher trait jealousy. Moreover, no associations which survived control for specificity were found in response to other facial emotions or in the absence of external stimuli during the resting state. Together, the present findings demonstrate that jealousy is a dimensional disorder with trait jealousy in healthy individuals being associated with increased sensitivity to social threat and that, similar to pathological jealousy (Marazziti et al. 2013), it is particularly linked with increased activation and functional connectivity in fronto-striatal circuitry as well as increased activation in limbic and visual processing regions.

Our whole-brain analysis of the emotional face task showed that subjects with higher trait jealousy only exhibited stronger neural responses in the thalamus, insula, hippocampus, inferior frontal gyrus, putamen, caudate, fusiform gyrus, visual cortex, superior parietal lobule and cerebellum during processing of angry versus neutral faces. A similar pattern of activation in response to angry faces has been found in previous fMRI studies (see Fusar-Poli et al. 2009), suggesting that the pattern of neural regions responding to angry faces is not influenced by levels of trait jealousy per se but by the magnitude of their responses. Significant jealousy-related neural responses to fearful versus neutral faces were also found in superior parietal lobe and visual cortex although these were not maintained when intensity ratings and relationship status were included as covariates, suggesting that differences were influenced by the intensity experienced and relationship status rather than related to trait jealousy per se. Indeed, the superior parietal lobe and middle occipital gyrus are both considered as primary sensory regions for visual processing and the middle occipital gyrus is important for perception of stimulus intensity (Cunningham et al. 2004; N'Diaye et al. 2009; Sprengelmeyer and Jentzsch 2006).

Higher trait jealousy was also associated with stronger activation in the bilateral inferior frontal gyrus. Case studies have reported that lesions in the right frontal gyrus (Luauté et al. 2008) and right orbito-frontal gyrus (Narumoto et al. 2006) are associated with delusional jealousy. A structural MRI study involving 105 patients also found greater gray matter loss predominantly in the dorsolateral frontal lobes in patients with Othello syndrome compared to matched control patients, indicating that dysfunction of the frontal lobes may be a neuroanatomical correlate for this pathology (Graff-Radford et al. 2012). Based on these clinical studies and the involvement of frontal regions in face emotion processing (Adolphs et al. 1996; Fusar-Poli et al. 2009; Nakamura et al. 1999), stronger activation of bilateral inferior frontal gyrus might indicate a role in enhanced responsivity to threatening faces in healthy individuals with higher trait jealousy. Additionally, jealousy has been proposed to be an "approach emotion" (Lazarus 1992) since it is associated with an increased motivation to approach the person toward whom jealousy is expressed, and the left inferior frontal lobe is involved in approach motivation (Gable and Poole 2014). Thus, the association between inferior frontal gyrus activation in response to angry faces and trait jealousy might also reflect a greater approach motivation. Indeed, a previous EEG study on healthy adults reported that evoked jealousy correlated with greater relative left frontal cortex responses to a "sexually" desired partner (Harmon-Jones et al. 2009).

The dorsal striatum comprising the putamen and caudate also showed enhanced activation during the processing of angry versus neutral faces in individuals with higher jealousy scores as well as increased functional connectivity with the inferior frontal gyrus. Increased activity in the dorsal striatum has consistently been reported in pathological jealousy (Marazziti et al. 2013). While dorsal striatum activation is associated with the receipt of rewards

(Delgado 2007), it also occurs during the processing of negative valence stimuli (Carretié et al. 2009), including viewing those who have rejected individuals romantically (Fisher et al. 2010). Thus, greater activation of the dorsal striatum and its functional connectivity with the inferior frontal gyrus may reflect an enhanced responsivity to negative emotional stimuli, particularly those associated with social threat. Furthermore, the coupling of basal ganglia and prefrontal cortex plays an important role in habit formation (Yin and Knowlton 2006) and thus dorsal striatal and related prefrontal connections may be involved in the progressive transformation of jealousy into a habitual behavior (Marazziti et al. 2013).

Fronto-striatal circuitry exhibits a primarily dopaminergic innervation (Björklund and Dunnett 2007) and dopamine is a key modulator of emotional processes (Sevy et al. 2006). Delusional jealousy is often observed in Parkinson's disease (PD) patients and several neuroimaging studies have reported that the development of delusional jealousy in PD is significantly associated with dopamine agonist therapy (Poletti et al. 2012), which interferes with reward processing by facilitating dopaminergic bursts and hampering dopaminergic dips (Frank et al. 2004). Indeed, previous studies in a number of psychiatric and neurological disorders have generally emphasized the role of dopaminergic fronto-striatal circuits in jealousy (Marazziti et al. 2013). Additionally, increased frontal–striatal activity occurs in obsessive compulsive disorder (Pauls et al. 2014) and obsessional jealousy overlaps with several symptoms observed in disorders with a strong compulsion component.

Higher trait jealousy was also associated with increased insula activity while processing angry compared to neutral faces and increased insula activation has previously been reported in pathological jealousy (Marazziti et al. 2013). The insula has an important role in the perception and experience of emotion (Kawashima et al. 1999; Phillips et al. 2004; Wicker et al. 2003) and may act as a relay between fronto-parietal regions and limbic regions controlling emotion processing (Carr et al. 2003). Additionally, as a core region in the salience network, the insula is specifically sensitive to salient environmental events and facilitates bottom-up access to the brain's attentional resource (Menon and Uddin 2010). Thus, the insula may contribute to greater jealousy by enhancing the salience of environmental stimuli signaling a potential social threat such as angry faces.

Activation of thalamic and hippocampal limbic regions during processing of angry versus neutral faces was also associated with elevated trait jealousy, and case reports have implicated both in delusional jealousy (see Marazziti et al. 2013). The thalamus controls arousal (Anders et al. 2004; Colibazzi et al. 2010; Etkin et al. 2011; Huguenard and McCormick 2007), as well as providing a functional link between the frontal cortex and hippocampus (Vertes et al. 2007), and plays an important role in processing visual, auditory and somatosensory information (McCormick and Bal 1994). Thus, greater activation of these limbic regions in individuals with higher jealousy traits during processing of angry faces may reflect such threatening faces being more emotionally arousing.

The association observed between cerebellar activation in response to angry faces and trait jealousy may also reflect this region's increasingly recognized role in processing affective stimuli, particularly negative valence ones (Strata 2015). Indeed, damage to the cerebellum is associated with inability to process negative emotions (Lupo et al. 2015). A case study has also reported delusional behavior in a patient with cerebellar damage (Mitsuhata and Tsukagoshi 1992).

The absence of any significant associations at the whole-brain level between resting-state functional connectivity and trait jealousy is perhaps surprising given that some other traits do show changes across healthy and clinical populations (Angelides et al. 2017; Baur et al. 2013; Hahn et al. 2011; Zang et al. 2007). A recent study also reported resting-state associations with envy (Xiang et al. 2016), although this was a ReHo analysis rather than functional connectivity per se. Interestingly, this latter study also identified the IFG as showing increased activity in association with dispositional envy and so there may be overlap in frontal regions associated with both jealousy and envy. Overall, the lack of associations with resting-state indices in the present study may indicate that jealousy represents an emotional state which evolves in interaction with social stimuli rather than from an altered intrinsic processing of the brain per se.

There are several limitations in the present study. Firstly, associations were only made between questionnaire scores for trait jealousy and neural activity in a face emotion task and it would clearly be of interest to investigate if this same circuitry and responses to angry faces are evoked during the actual experience of evoked jealousy. Secondly, while we controlled for a potential contribution of trait aggression on the observed associations with trait jealousy by including it as a covariate, we cannot completely rule out that there may have been some influence of this. Thirdly, the subjects in the current study were mainly young (age range = 18–27 years) and so we cannot rule out the possibility that there might be some age-dependent influence on findings. Finally, there is some evidence that relationship status can have some effects on jealousy responses (Guadagno and Sagarin 2010; Orosz et al. 2015) and in the current study we did not have sufficient subject numbers to assess possible differences due to relationship status. However, including relationship status as a covariate did not influence the stability of our behavioral or neural findings.

Conclusion

Overall, the current study used a dimensional approach to investigate the neural basis of jealousy. Findings provide the first evidence for an association between jealousy and neural responses to angry expression faces and ratings of their intensity in healthy subjects and controlling for trait aggression and sex. Importantly, jealousy-associated activation was found in dopaminergic frontal–striatal circuitry associated with pathological jealousy as well as the insula, thalamus, hippocampus and cerebellum which have also been linked with emotional processing and pathological jealousy. These findings suggest that altered neural responsivity to angry faces may be a useful indicator of possible risk for pathological jealousy. Furthermore, by establishing jealousy as a dimensional disorder this potentially allows further studies to be conducted in healthy populations investigating dopaminergic contributions to jealousy to aid development of novel therapeutic approaches.

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Author contributions statement X.Z., B.B, and K.K designed the study and wrote the paper. X.Z. and L.L. prepared all the materials and programed the procedures. X.Z., L.L., J.L., L.X., and Z.G. acquired the data. X.Z., L.L, F.Z., B.B., and K.K. analyzed the data. X.Z., B.B and K.K interpreted the data and drafted the paper. All authors contributed to and have approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest We have nothing to disclose in terms of disclosure of potential conflicts of interest.

Research involving human and/or animal participants The study had full ethical approval by the local ethics committee at the University of Electronic Science and Technology of China and experiments were carried out in accordance with the latest revision of the Declaration of Helsinki.

Informed consent Informed consent was obtained in writing from all individual participants included in the study.

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