Individual differences in common factors of emotional traits and executive functions predict functional connectivity of the amygdala

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ABSTRACT

Evidence suggests that individual differences in emotion control are associated with frontoparietal-limbic networks and linked to emotional traits and executive functions. In a first attempt to directly target the link between emotional traits and executive functions using resting-state fMRI analysis, 43 healthy adults completed a test battery including executive tasks and emotional trait self-assessments that were subjected to a principal component analysis. Of the three factors detected, two explained 40.4% of the variance and were further investigated. Both factors suggest a relation between emotional traits and executive functions. Specifically, the first factor consisted of measures related to inhibitory control and negative affect, and the second factor was related to reward and positive affect. To investigate whether this interplay between emotional traits and executive functions is reflected in neural connectivity, we used resting-state fMRI to explore the functional connectivity of the amygdala as a starting point, and progressed to other seed-based analyses based on the initial findings. We found that the first factor predicted the strength of connectivity between brain regions known to be involved in the cognitive control of emotion, including the amygdala and the dorsolateral prefrontal cortex, whereas the second factor predicted the strength of connectivity between brain regions known to be involved in reward and attention, including the amygdala, the caudate and the thalamus. These findings suggest that individual differences in the ability to inhibit negative affect are mediated by prefrontal–limbic pathways, while the ability to be positive and use rewarding information is mediated by a network that includes the amygdala and thalamostriatal regions.

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Introduction

The ability to respond adaptively to emotional events is crucial for socially competent behavior. Evidence indicates that individual differences in the ability to control emotional reactions are contingent upon emotional traits such as trait anxiety (Fox, 2002) and the tendency to use a certain emotion regulation strategy (Gross, 2001; Gross and John, 2003). The reaction to salient emotional information is further modulated by executive mechanisms, via frontoparietal-mediated projections to limbic and sensorimotor regions (see reviews in Ochsner et al., 2012; Okon-Singer et al., 2013; Pessoa, 2009). Several studies have demonstrated a relation between emotional traits and executive functions. For instance, introverts were found to be slower than extraverts in comparing the contents of working memory to an external target (Lieberman, 2000), and trait anxiety has been found to correlate with both pro- and reactive control (Forbes et al., 2014; Forster et al., 2013). In an attempt to provide a comprehensive examination of the relation between executive functions and personality traits, Unsworth et al. (2009) used various personality questionnaires and executive tasks. They demonstrated relations between specific personality types or traits and specific executive functions, such as a link between antisocial personality and avoidance ability and between the tendency toward behavioral inhibition and general fluid intelligence. Executive functioning and emotion processing are also jointly affected in several psychological conditions and psychiatric disorders. For example, bipolar disorder (BD) is characterized by periods of depression and periods of elevated mood (Anderson et al., 2012), as well as by an inability to modulate attention away from emotional stimuli (Mullin et al., 2012). Similarly, depressive symptoms often coexist with memory deficits (Xie et al., 2012) and are also associated with abnormal regulatory processes of negative emotions (Johnstone et al., 2007).

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Executive functions and emotional traits have also been observed to broadly rely on overlapping brain networks, suggesting neural communalities. For instance, both have been linked to prefrontal regions (Alvarez and Emory, 2006; Badre and Wagner, 2005; Chow, 2000; Forbes et al., 2014; Forster et al., 2013), to the amygdala (Aghajani et al., 2014; Gallagher and Holland, 1994; Ousdal et al., 2014) and to striatal regions (Depue and Collins, 1999; Luciana et al., 1992; Rammsayer, 1998). Aberrant connectivity between these regions has been observed in various psychiatric disorders. Much of the current literature suggests that lower connectivity between the amygdala and the prefrontal cortex indexes higher levels of anxiety in both healthy controls (Coombs et al., 2014; Kim et al., 2011; Loewenstern et al., 2014; Long et al., 2014) and patients (Dodhia et al., 2014; Keutmann et al., 2014). This lower connectivity was also observed in major depression (MDD) (Lui et al., 2011; Tang et al., 2013), BD (Anand et al., 2009; Chepenik et al., 2010) and obsessive–compulsive disorder (OCD) (Gottlich et al., 2014). Likewise, connectivity between prefrontal regions and striatal regions has been observed to either increase or decrease in several of the same disorders, for instance in OCD (Gottlich et al., 2014; Sakai et al., 2011) and MDD (Gabbay et al., 2013; Lui et al., 2011). Considering the joint affectedness of emotional traits and executive functions in psychiatric disorders, these studies suggest that emotional traits and executive functions may share underlying neural pathways involving the amygdala and prefrontal as well as striatal regions. Direct examination of this proposal using comprehensive assessment of executive functions and emotional traits is, however, still lacking.

In the present study, we investigated the link between executive functions and emotional traits in healthy participants by examining a comprehensive battery of self-assessments and tasks. Participants were thus characterized based on their variance both on emotional traits and on executive functions. This battery was subjected to a principal component analysis (PCA) to assess factors that underlie emotional traits and specific executive functions in our participants. Based on the indications of a relationship between emotional traits and executive functions, we hypothesized that common factors for emotional traits and executive functions would emerge. To elucidate the neural networks that reflect individual differences in these factors and based on the evidence outlined above that the amygdala's connectivity should be involved in networks that underlie both emotion and executive function, we then began interrogating resting-state functional connectivity using seeds in the amygdala, given its major importance in emotion-related behaviors and psychiatric illnesses. Additional seeds were then chosen for *exploratory* analyses based on the findings obtained within the amygdalar networks. We hypothesized that individual differences in these factors would be reflected in the strength of connectivity between the amygdala and regions previously associated with both executive functions and emotional traits, such as striatal and prefrontal regions. In contrast to existing literature, which typically assesses the impact of individual traits on emotional reaction and control or addresses emotional traits and executive functions separately, this approach investigates the neural processes that are shared by emotional traits and executive control mechanisms.

Methods

Participants

Forty-nine right-handed healthy adults without any history of neurological or psychiatric diseases volunteered to participate in the study in return for payment. The study was approved by the Ethics Committee of the University of Leipzig, and all participants gave informed consent prior to the experiment. Participants' data were evaluated for any current psychiatric problems by means of the Symptom Checklist-90-R (SCL-90-R, Franke, 2002), for deteriorated scores in executive function tasks, outliers in emotional trait scores and motion in resting-state fMRI scans. A total of six participants were excluded: three for excessive head motion (>1 mm), one for deteriorated executive function scores, one for both excessive head motion and deteriorated executive function scores and one due to a technical error during resting-state fMRI acquisition. The final sample consisted of 43 participants (23 females, 20 males; mean age = 25.84 ± 2.37 SD years, range = 20.56–30.2; mean education = 18.35 ± 2.69 SD years).

Assessment of emotional traits and executive functions

Materials

The behavioral battery encompassed a number of executive function tasks and emotional trait self-assessments. Executive function tasks were selected to span a range of indices of cognitive control, as described in the Data preparation section; emotional trait self-assessments were chosen based on their implications for increasing or decreasing the risk of psychiatric illnesses. The executive function tasks were German-language versions of the following: the Trail Making Test (TMT, Reitan, 1992; Tombaugh, 2004) was conducted to test for visual attention and task switching. Concentration and verbal learning interference effects were tested using the letter–number subtest from the Wechsler Adult Intelligence Scale (WAIS, Wechsler, 2006) and the California Verbal Learning Test (CVLT, Niemann et al., 2008), respectively. Conflict-solving as a combination of selective attention, cognitive flexibility and processing speed was tested with a version of the Stroop task (Farbe–Wort–Interferenztest, FWIT, Bäumler, 1985), and the digit–symbol subtest from the WAIS (Wechsler, 2006) was used to test visual perception/analysis and processing speed. The emotional trait self-assessments included the following: the trait version of the Spielberger State-Trait Anxiety Inventory (STAI, Spielberger et al., 1970; German translation, Laux et al., 1981) was used to assess trait anxiety. The trait version of the Positive Affect Negative Affect Schedule (PANAS, Watson et al., 1988; German translation, Krohne et al., 1996) was used to assess dispositions toward positive and negative affect; the Trier Inventory of Chronic Stress (TICS, Schulz and Schlotz, 1999) was used to assess chronic stress spread over the last 3 months; and finally the NEO Five-factor Inventory (NEO-FFI; Costa and McCrae, 1992; German translation; Borkenau and Ostendorf, 1993) was used to assess the emotional traits of neuroticism and extraversion.

Data acquisition

The behavioral session lasted approximately 1.5 h, depending on individual performance, for both executive function tasks and emotional trait questionnaires, with each taking approximately 45 min. The behavioral session was conducted in a separate testing room, with only the participant and the experimenter present. The executive function tasks started with the TMT. Then, participants took part in the first administration of the CVLT, after which the two subtests of the WAIS and the Stroop task FWIT were administered. This allowed a delay of approximately 20 min, after which the second part of the CVLT, testing long-term memory performance, could be administered. The executive function tasks were followed by the emotional trait and psychiatric self-assessments in the following order: PANAS, STAI, NEO-FFI, SCL-90-R, and TICS. The measures were not counterbalanced in order to provide a 20 min break between the two parts of the CVLT as well as to avoid carry-over effects of the two anxiety/stress questionnaires (i.e., STAI and TICS). Data were acquired at two sites for 23 and 20 participants, respectively.

Data preparation

From the executive function battery, the following indices of cognitive control were of particular interest for this study: the two WAIS subtests, scores for proactive and retroactive interference on the CVLT, as well as performance on the TMT and the Stroop task FWIT. For the latter two tasks, performance was defined as the affordance ratio, i.e. the difference in performance in the condition of interest and

the baseline condition divided by performance in the baseline condition, each measured in seconds needed to complete the tasks [condition(sec) − baseline(sec) / baseline(sec)]. This allowed us to determine the amount of additional processing time needed for the more complex condition of interest in relation to the baseline condition. In both tests, high scores indicated a relatively large amount of cognitive interference when the conditions of interest were performed. For the TMT, the baseline condition consisted of connecting numbered dots on a sheet of paper in ascending order, whereas the condition of interest consisted of connecting numbered or alphabetically labeled dots in an ascending fashion, alternating between numerical and alphabetical order, thus demanding the suppression of one cognitive task while the other was being processed. The baseline task in the FWIT consisted of reading the names of colors printed in colors that did not match the associated color words. In the condition of interest similar stimuli were presented, but participants were asked to name the color in which the words were printed, thus exploiting the classical Stroop effect (Stroop, 1935). Finally, Cronbach's α was computed to assert internal consistency for all emotional trait self-assessments, after which Levene's test was used to assess the equality of variances in scores, age and gender across the two sites, before employing a two-tailed t-test to ensure that they were not significantly different in any of these domains. Data were then tested for multivariate normality using Henze–Zirkler's test and Mardia's test, as recommended by Mecklin and Mundfrom (2005).

Principal component analysis

Indices of cognitive control and emotional trait variables were subjected to a principal component analysis (PCA). Following a parallel analysis to determine the number of factors (Horn, 1965), three factors were extracted. Both the Kaiser–Meyer–Olkin measure and Bartlett's test of sphericity indicated adequacy (>.5 and <0.001, respectively). While some of the variables in this analysis tend to correlate (e.g., neuroticism and stress), others tend to be close to orthogonal (e.g., neuroticism and extraversion), making it unclear as to whether factors should be expected to correlate or be independent. Therefore, resulting factors were first rotated using an oblique rotation method (Oblimin with Kaiser normalization), as recommended by Tabachnick and Fidell (2007). After the correlation matrix of this rotation suggested independence (correlations between the factors all r < .04), resulting factors were optimized using an orthogonal rotation method (Varimax with Kaiser normalization). Factor scores for each participant were calculated using the Bartlett method.

Resting-state functional connectivity

Data acquisition

Data were acquired on a Siemens Magnetom Trio Tim 3T and a Siemens Magnetom Verio 3T scanner using a 12-channel head coil. Resting-state functional images were acquired in 34 axial slices using a gradient-echo EPI sequence (200 and 400 volumes for the first 23 and subsequent 20 participants, respectively, TR = 2300 ms, TE = 30 ms, FA = 90, matrix size 64 × 64, voxel size 3 × 3 × 4 mm³ (1 mm gap)). Parameters were homogenous within scanners. Anatomical scans were acquired in a different session using a T1-weighted 3D MP-RAGE sequence (FOV 256 × 240 mm², spatial resolution 1 × 1 × 1.5 mm³).

Data preprocessing

All preprocessing was based on modified versions of the 1000 functional connectome scripts (Biswal et al., 2010) available at www.nitrc.org/projects/fcon_1000, using both AFNI (Cox, 1996) and FSL (Smith et al., 2004). Functional volumes were slice-time corrected, motion corrected and spatially smoothed using a 6 mm Gaussian kernel, as well as temporal band-pass filtered between 0.005 and 0.1 Hz. Linear and quadratic trends were removed, and the data were registered to 2 × 2 × 2 mm MNI152 standard space. Furthermore, the data were denoised by regressing out the six motion parameters, as well as white matter and cerebral spinal fluid. We did not regress out the global signal (Murphy et al., 2009; Saad et al., 2012).

Main data analysis

To investigate how the interplay of emotional traits and executive functions is reflected in the brain's functional connectivity at rest, we used 50% thresholded parcellation units from the Harvard–Oxford anatomical atlas as seeds and examined how connectivity across the entire brain covaried with the factors we had extracted. Based on our *hypothesis* that amygdalar connectivity should be involved in networks that underlie both emotional traits and executive functions, we examined how connectivity of the left and the right amygdala covaried with the factors. We then chose additional seeds for *exploratory* analyses based on the findings obtained within the amygdalar networks. The amygdala was chosen based on evidence that amygdala-prefrontal connectivity is aberrant in many psychiatric disorders in which executive functioning and emotion processing are jointly affected, and because of its major role in emotion-related behaviors such as fear responses (LeDoux, 2000). The average time course for each parcellation unit was extracted and used as a model for voxelwise correlation with every other voxel in the brain. Resultant whole-brain correlation maps were normalized using Fisher's r-to-z transform ($z = .5[\ln(1 + r) − \ln(1 − r)]$) for comparison across individuals.

Group-level statistical testing was conducted using a mixed-effects analysis as implemented in FSL's FEAT. Factor scores were de-meaned and entered into separate models alongside de-meaned scores for age, gender, and scanner site (covariates of no interest). Voxelwise thresholding was set at z-score > 2.3, and cluster correction was conducted using Gaussian random field theory with p < 0.05. This procedure was then repeated in exploratory analyses for another seven regions whose connectivity with the amygdala was significantly correlated to one of the factors. The p-value for all results was then Bonferroni-corrected for a total of eleven seeds (= the total number of all seeds that were examined in both models; p < 0.005).

Post hoc analysis

In order to assess whether the resting-state networks that correlated with the factors were driven by a specific executive function task or emotional trait questionnaire, we computed correlations between each individual variable within a factor and all connectivity patterns associated with that factor. These values were then entered into a one-way ANOVA.

Results

Participant scores on emotional trait self-assessments and executive function tasks

Participant scores are reported in Table 1 for the total sample of n = 43. A two-tailed t-test further ensured that the two sites in which the resting-state data acquired were not significantly different in any of these domains (all p < 0.08 n.s., see Inline Supplementary Table S1). Cronbach's α indicated high internal consistency for all emotional trait self-assessments. Multivariate normality was confirmed by Henze–Zirkler's test (p > 0.3), as well as Mardia's test (skewness p > 0.8, kurtosis p > 0.17).

Inline Supplementary Table S1 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.06.049.

Principal component analysis

After an Oblimin rotation suggested independence, three factors that explained a total of 52.8% of the variance were optimized using a Varimax rotation (Table 2).

Table 1
Participant scores on emotional trait self-assessments and executive function tasks (n = 43). Cronbach's α indicated high internal consistency for all emotional trait self-assessments. Multivariate normality was assessed using Henze–Zirkler's test (p > 0.3) as well as Mardia's test (skewness p > 0.8, kurtosis p > 0.17). SD = standard deviation.

	Mean	SD	Minimum	Maximum	Cronbach's α
STROOP (critical-color)/ color (sec)	0.53	0.16	0.25	0.91	–
TMT (B-A)/A (sec)	1.19	0.59	0.26	2.92	–
CVLT proactive interference	-0.68	1.18	-3.22	2.08	–
CVLT retroactive interference	0.22	0.53	-1.35	1.58	–
WAIS Letter–Number Score (# items correct)	13.81	2.3	8	20	–
WAIS Digit–Symbol Score (# items correct)	92.23	13.91	53	118	–
NEO-FFI Neuroticism	27.72	7.15	16	42	0.893
NEO-FFI Extraversion	42.58	5.78	31	54	0.925
STAI Trait Anxiety Scale	36.05	8.12	22	57	0.917
TICS Screening Scale for Chronic Stress	11.02	8.92	0	36	0.915
PANAS General Negative Affect	17.07	4.39	10	28	0.8
PANAS General Positive Affect	35.28	4.99	25	46	0.802

All three exhibited loadings of > .4 for both emotional trait and executive function scores. The first factor showed factor loadings between .4 and .9 on neuroticism, trait negative affect, chronic stress and proactive interference in the CVLT. This factor explained 22.5% of the variance and had an eigenvalue of 2.7. We refer to this factor as "Negative Affectivity and Task Interference" (NATI) (Fig. 1). The second factor showed factor loadings between .4 and .8 on extraversion, trait positive affect and the two WAIS subtests, as well as factor loadings between − .5 and − .7 for trait anxiety and the affordance ratio from the FWIT Stroop. This factor explained 17.9% of the variance and had an eigenvalue of 2.15. We refer to this factor as "Positive Affectivity and Conflict-Solving" (PACS) (Fig. 1).

The third factor showed factor loadings between .6 and .7 on trait negative affect and the TMT, as well as factor loadings between − .4 and − .5 on the two WAIS subtests. This factor explained only 12.5% of the variance and its eigenvalue was comparatively low (1.49). Therefore, its presentation and discussion will be limited, and the relevant figures and tables are supplementary. It should, however, be noted that

Table 2
Rotated principal component matrix of executive functions and emotional traits. Both executive function and emotional trait variables were subjected to a principal component analysis (PCA) using a Varimax rotation with Kaiser normalization. Three factors were extracted that accounted for 52.8% of the total variance. The first two, named NATI (1 below) and PACS (2 below), accounted for 22.5% and 17.9%, respectively, and were further used for the main resting-state analysis. Factor scores for each subject were calculated using the Bartlett Method (EF = executive function; ET = emotional trait).

|		Component factor loadings		
Variable	Category	1	2	3
STROOP (critical-color)/color (sec)	EF		− 0.549	
TMT (B-A)/A (sec)	EF			0.655
CVLT proactive interference	EF	0.603		
CVLT retroactive interference	EF			
WAIS Letter–Number Score (# items correct)	EF		0.492	− 0.491
WAIS Digit–Symbol Score (# items correct)	EF		0.512	− 0.473
NEO-FFI Neuroticism	ET	0.84		
NEO-FFI Extraversion	ET		0.758	
STAI Trait Anxiety Scale	ET		− 0.629	
TICS Screening Scale for Chronic Stress	ET	0.863		
PANAS General Negative Affect	ET	0.405		0.641
PANAS General Positive Affect	ET		0.641	
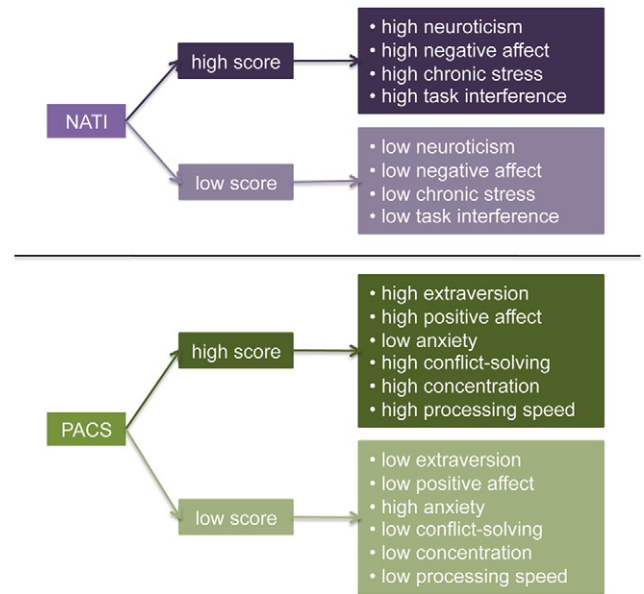
Fig. 1. Schematic illustration of the two major PCA components. Two major factors were detected in the PCA that combined executive function tasks and emotional trait self-assessment measures. The first factor included a combination of neuroticism, negative affect, chronic stress and high task interference. We called this factor Negative Affectivity and Task Interference (NATI) to represent the ability to inhibit negative information and negative affect. The second factor included a combination of extraversion, positive affect, low anxiety, high conflict-solving and high concentration and processing speed. We called this factor Positive Affectivity and Conflict-Solving (PACS) to represent the ability to maintain positive affect by solving conflicts efficiently.

this factor was more strongly characterized by EF loadings than NATI and PACS (see Inline Supplementary Fig. S1 for a schematic illustration of this factor).

Inline Supplementary Fig. S1 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.06.049.

Emotion–executive factors and resting-state connectivity

Factors were entered into a regression analysis with the resting-state fMRI data and correlated significantly with resting-state connectivity of the amygdala in the *hypothesis-based analysis*, as well as with resting-state connectivity of seeds that were derived from associated amygdalar connectivity patterns in the *exploratory analyses* (Tables 3 and 4, and Inline Supplementary Table S2).

Inline Supplementary Table S2 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.06.049.

In the *hypothesis-based analysis*, NATI negatively predicted the strength of connectivity between the left amygdala and right dorsolateral prefrontal cortex (dlPFC) and inferior frontal gyrus (IFG) (Fig. 2A), whereas it positively predicted connectivity between the left amygdala and the right insula (Fig. 2B). In the *exploratory analyses*, it also positively predicted connectivity of the right dlPFC with left dorsal anterior cingulate (dACC), supplementary motor area (SMA), precentral gyrus and superior parietal lobule (SPL), as well as with left putamen and insula (Fig. 2C).

In the *hypothesis-based analysis*, PACS positively predicted the strength of connectivity between the right amygdala and the bilateral thalamus, as well as between the right amygdala and the caudate (Fig. 3A). In the *exploratory analyses*, PACS also negatively predicted right thalamus connectivity with the left IFG and dlPFC (Fig. 3B). It further positively predicted connectivity between the right caudate and bilateral dACC, and between the right caudate and the precentral gyrus, as well as between the right caudate and the right cerebellar crus I and II and the right insula (Fig. 3C).

Table 3

Resting-state functional connectivity correlations with NATI. Fifty percent thresholded parcellation units from the Harvard–Oxford anatomical atlas covering the amygdalae were used in the *hypothesis-based analysis*. Average time courses were extracted for each parcellation unit and correlated with every other voxel in the brain. Resultant maps were entered into a regression model with the NATI factor scores and showed a relationship between amygdala-dlPFC/IFG and NATI, as well as amygdala-insula connectivity and NATI. In the *exploratory analysis*, this procedure was repeated for seeds covering the dlPFC, IFG, and insula, of which only the dlPFC yielded significant connections additionally correlated with NATI. Coordinates are in MNI space (dACC = dorsal anterior cingulate cortex; dlPFC = dorsolateral prefrontal cortex; IFG = inferior frontal gyrus; Lat = brain laterality SMA = supplementary motor area; and SPL = superior parietal lobule).

Correlation with NATI	Lat	Seed region	Lat	Connectivity cluster	Size (mm³)	p-Value	Peak Z	x	y	z
Negative	L	Amygdala	R	dlPFC, IFG	1072	0.00268	3.76	48	18	26
Positive			R	Insula	609	0.00151	3.78	42	6	−10
Positive	R	dlPFC	L	dACC, SMA, post-central gyrus, SPL	1165	0.000523	3.64	−38	−46	56
			L	Putamen, insula	853	0.00469	3.74	−32	0	2

Table 4

Resting-state functional connectivity correlations with PACS. Connectivity patterns covarying with the PACS factor scores were derived in the same way as connectivity patterns covarying with the NATI factor (see Table 3). Coordinates are in MNI space (dACC = dorsal anterior cingulate cortex; dlPFC = dorsolateral prefrontal cortex; IFG = inferior frontal gyrus; Lat = brain laterality).

| Correlation with PACS	Lat	Seed region	Lat	Connectivity cluster	Size (mm³)	p-Value	Peak Z	x	y	z
Positive	R	Amygdala	BIL	Thalamus, caudate	1052	0.000783	3.64	−18	−6	14
Negative	R	Thalamus	L	IFG, dlPFC	1815	0.000127	4.49	−26	6	52
Negative			L	Inferior parietal lobule	1013	0.00786	4.12	−34	−64	48
Negative	L	Thalamus		dPCC	1089	0.00521	3.83	−6	−50	14
Positive	R	Caudate	BIL	dACC, precentral gyrus	1499	0.00161	4.15	12	−18	74
			R	Insula	1306	0.0039	4.26	34	−12	−4
Negative			R	Cerebellar crus I + II	1315	0.00374	3.85	38	−70	−46
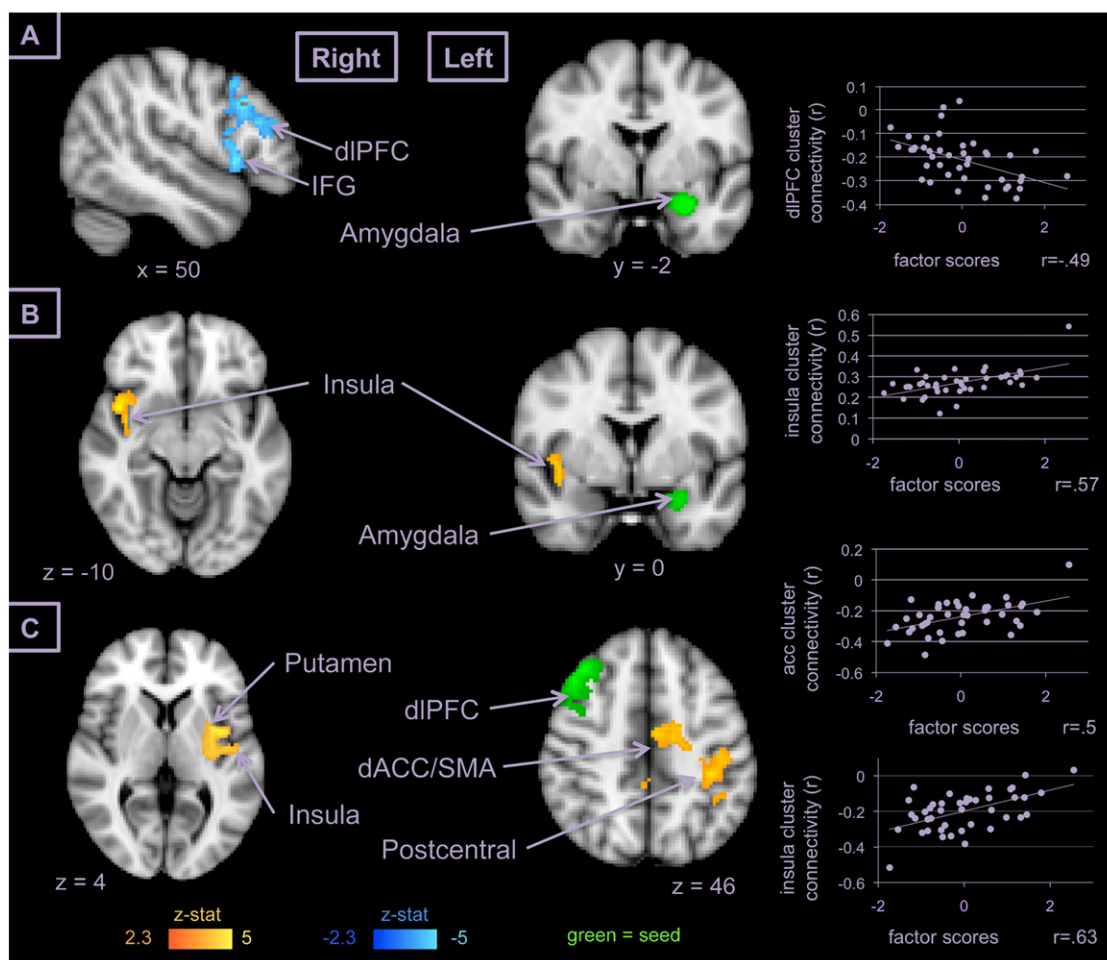
Fig. 2. Resting-state connectivity results with NATI. NATI factor scores showed a relationship between a seed covering the left amygdala according to the Harvard–Oxford atlas and its connectivity to dlPFC and IFG (A), and insula (B). Exploratory analyses were then conducted for seeds in the dlPFC, insula, and IFG, yielding significant connectivity between the dlPFC and two clusters in dACC/SMA, superior parietal lobule (not depicted), putamen and insula (C) (dACC = dorsal anterior cingulate cortex; dlPFC = dorsolateral prefrontal cortex; IFG = inferior frontal gyrus; SMA = supplementary motor area).
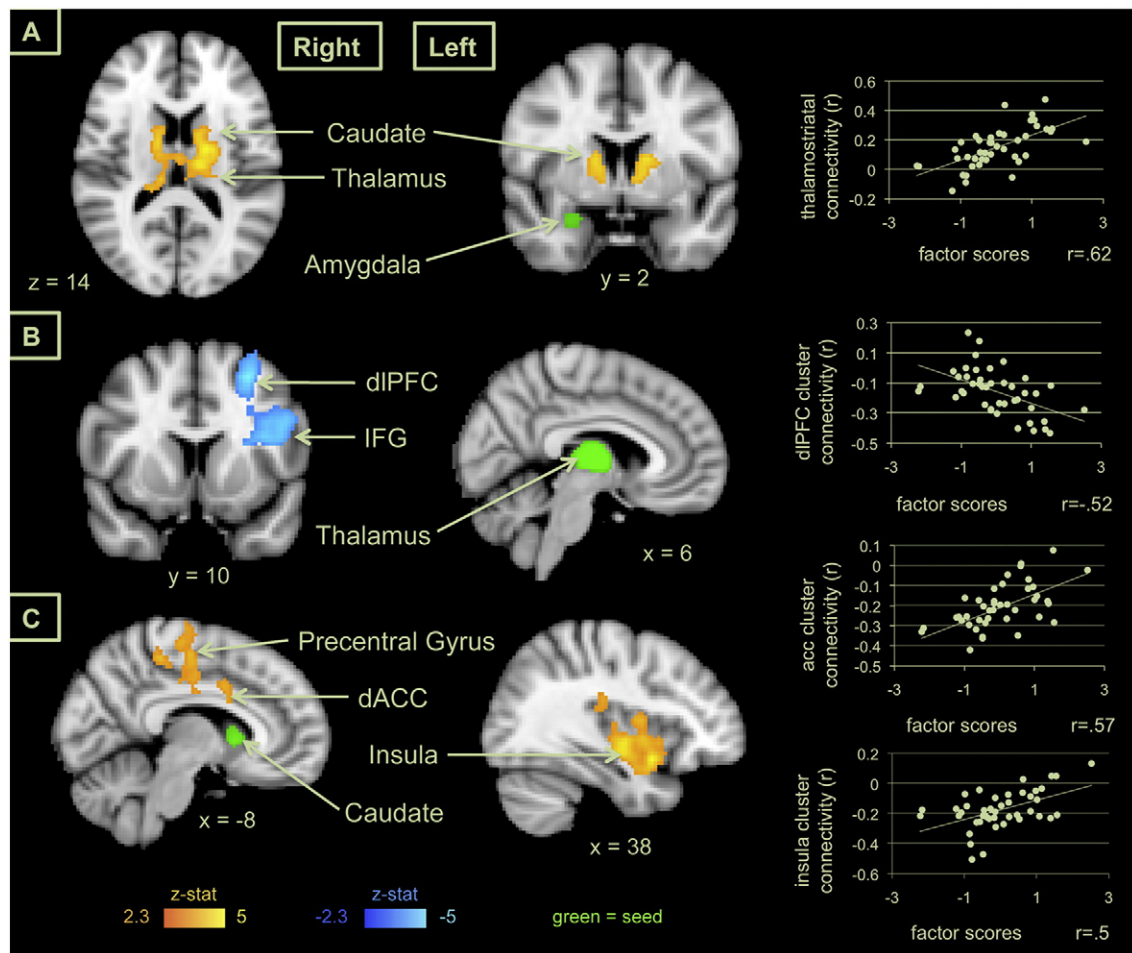
Fig. 3. Resting-state connectivity results with PACS. PACS factor scores showed a relationship between a seed covering the right amygdala according to the Harvard–Oxford atlas and its connectivity to bilateral thalamus and caudate (A). Exploratory analyses were then conducted for seeds covering thalamus (B) and caudate (C). These analyses uncovered significant correlations between PACS scores and thalamus-prefontal connectivity (B) as well as between PACS scores and connectivity of the caudate with precentral gyrus, dACC and insula (C) (dACC = dorsal anterior cingulate cortex; dlPFC = dorsolateral prefrontal cortex; IFG = inferior frontal gyrus).

Due to the comparatively low eigenvalue and small percentage of explained variance, the resting-state analysis for the third factor is supplementary and restricted to the amygdalar seeds. It predicted the strength of connectivity between the left amygdala and the right inferior parietal lobule (IPL), and between the left amygdala and the middle temporal gyrus (Inline Supplementary Fig. S2A), as well as right amygdala connectivity with the bilateral posterior cingulate cortex (PCC) (Inline Supplementary Fig. S2B). Results of the third factor will be discussed only briefly.

Inline Supplementary Fig. S2 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.06.049.

Post hoc analysis

None of the individual emotional trait and executive function variables that contributed to NATI or PACS correlated significantly more with the resting-state connectivity patterns than did any other variables (all p > 0.11; also see Inline Supplementary Tables S3 and S4). In contrast, NATI and PACS did correlate significantly more with the observed connections than the individual variables they were derived from (all p < 0.0001). We are therefore confident that our results are not carried by one or two variables only.

Inline Supplementary Tables S3 and S4 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.06.049.

Discussion

This study examined the neural networks underlying the relationship between emotional traits and executive functions. Emotional traits and executive functions have previously been linked (Unsworth et al., 2009), and attentional (Okon-Singer et al., 2007, 2013; Pessoa et al., 2002a,b, 2005) and cognitive regulation (John and Gross, 2004; Ochsner et al., 2002a,b, 2004; Urry et al., 2006, 2009) processes were shown to modulate the reaction to salient emotional information (Ochsner et al., 2012). These processes were further linked to individual differences in the ability to control emotional reactions, which is thought to be contingent upon emotional traits such as trait anxiety (Fox, 2002). Evidence suggests that individual differences in emotion control are associated with frontoparietal-limbic networks. However, a direct investigation of the neural networks underlying both traits related to emotional behavior and control behavior was lacking.

We therefore conducted a PCA on different measures of emotional traits and executive functions and entered the resulting factor scores into a regression with the resting-state fMRI data. The PCA revealed factors that showed loadings from both emotional traits and executive function tasks. The first factor, Negative Affectivity and Task Interference (NATI), pointed to a positive relation among neuroticism, negative affect, chronic stress and task interference, and may therefore reflect the ability to inhibit negative feelings or biases toward negative information. In line with this interpretation, individual differences in this factor

were reflected in the strength of connectivity in prefrontal-amygdala pathways previously implicated in cognitive control of negative emotions and behaviors. The second factor, Positive Affectivity and Conflict-Solving (PACS), revealed a positive relation among extraversion, positive affect, conflict-solving, high concentration and fast working memory/mental speed, which were negatively related to the levels of trait anxiety. This factor may reflect the ability to maintain positive affect via efficient conflict-solving. Indeed, this factor was related to connectivity within a network of regions previously implicated in emotion, attention and reward, including the amygdala, thalamus and caudate. From a more general perspective, these findings further suggest that individual differences in intrinsic functional architecture may shape the reaction toward emotional events via common factors for emotional traits and executive functions.

Factors of emotional traits and executive functions

Using a more direct methodology to examine the relation between emotional traits and executive abilities, our study supports the existence of common factors underlying these constructs. Specifically, we conducted a PCA on self-assessments and tasks, and found no evidence of distinct factors for emotional traits or executive functions. This is despite having shared method variance for self-assessment measures of emotional traits and shared method variance for tasks measuring executive functions. Rather, we found factors that included combinations of emotional traits and executive functions, indicating that both emotional traits and executive functions share common underlying latent factors.

Negative Affectivity and Task Interference (NATI)

The first factor identified in our PCA, NATI, represents high task interference on a verbal learning task and tendencies toward neuroticism, negative affect and chronic stress. We suggest that this factor represents the individual ability to inhibit distracting negative information and negative affect. Current models of emotion highlight the modulation of emotional reactions by inhibitory control. For example, the dual competition framework proposed by Pessoa (2009) suggests that affective value modulates visual processing via two interacting streams: (a) stimulus-driven projections from "evaluative" neural regions, including the amygdala; and (b) top-down projections from neural "control" sites located in prefrontal–parietal cortices, which modulate visual processing based on an item's behavioral relevance. Iordan et al. (2013) propose an interaction between bottom-up "warm" regions and top-down "cold" regions, and Pourtois et al. (2013) suggest that amygdala projections to sensory cortical areas may be modulated by the dorsolateral prefrontal cortex. The variables represented in NATI were related to frequent engagement in worry, rumination and negative "self-talk", which can be seen as introducing "noise" into regulatory mental processes and/or requiring ample cognitive resources which detract from (and thus lower) task performance (Flehmig et al, 2007; Nolen-Hoeksema, 1991; Nolen-Hoeksema and Morrow, 1991; Nolen-Hoeksema et al., 2007, 2008; Wisco and Nolen-Hoeksema, 2008). In line with this argument, Cohen et al. (2014a) demonstrated that training the executive control system leads to alleviated ruminative thinking and rumination-related sad thoughts. Moreover, they showed that rumination and reappraisal are both mediated by inhibitory processes (Cohen et al., 2014b). Furthermore, the use of maladaptive emotion regulation strategies (Yoon et al., 2013) has been identified as risk factors for depression.

The neural connectivity patterns associated with NATI are also in line with the view that this factor reflects a measure of an individual ability to inhibit negative feelings: NATI was mostly related to a network of regions related to the cognitive control of emotion. It negatively predicted connectivity between the amygdala and both the right dlPFC and the IFG, meaning that this connection was weaker for high NATI scores. This pattern is in line with studies that indicate a decrease in connectivity between the amygdala and the prefrontal cortex in MDD (Lui et al.,

2011; Tang et al., 2013), BD (Anand et al., 2009; Chepenik et al., 2010) and obsessive–compulsive disorder (OCD) (Gottlich et al., 2014). Amygdalar connectivity with the dlPFC, as we found in correlation with NATI, has been observed frequently, yet there are no direct projections between the amygdala and the dlPFC. Based on anatomical connections, it has been suggested that the dlPFC may impact the amygdala via a pathway from subgenual ACC to dACC in the interaction between emotion and cognition (Ray and Zald, 2012). NATI also positively predicted connectivity between the right dlPFC and the left dACC, and enhanced connectivity between dlPFC and ACC/mPFC was also found in BD (Favre et al., 2014). NATI further positively predicted connectivity between the right dlPFC and the left insula, as well as connectivity between left amygdala and right insula. The insula is known to have reciprocal anatomical connections with both the amygdala and the prefrontal cortex (Craig, 2002), and may thus constitute an additional pathway for emotion and cognition interactions. Moreover, connectivity between the amygdala and insula was also found to be enhanced during chronic stress (Golkar et al., 2014), and stressed participants also showed a decrease in their ability to down-regulate negative emotions (Golkar et al., 2014). Cerullo et al. (2012) also found enhanced connectivity between the amygdala and the insula in depressive-state BD patients.

In summary, we suggest that NATI represents an individual's ability to control and inhibit negative feelings and thoughts. In line with this view, NATI was shown to be related to the strength of connectivity in a neural network previously implicated in emotion control, which includes the amygdala, the right dlPFC and IFG, the dACC and the insula. We have previously suggested that individual differences in emotional situations and toward affective stimuli may be reflected in neural connectivity patterns (Okon-Singer et al., 2013). The current findings corroborate this view and suggest specific neural pathways that mediate the executive inhibition of negative feelings and thoughts.

Positive Affectivity and Conflict-Solving (PACS)

The second factor identified in our PCA, PACS, included a combination of extraversion, positive affect and low anxiety as well as high conflict-solving on a classic Stroop task and indices of high concentration and mental processing speed in two subtests of the WAIS. We suggest that this factor represents an individual's ability to maintain positive affect by solving conflicts in a reward-oriented fashion. High scores in PACS represent individuals who are more likely to be assertive and report greater levels of happiness (Pavot et al., 1990), who have heightened responsiveness to reward compared to punishment and who do not dwell on the negative aspects of life (Depue and Collins, 1999). It has previously been shown that the increased happiness in extraversion (compared with neuroticism) is associated with a more positive response only to pleasant stimuli and situations that contain a reward element, and not to pleasant stimuli and situations that do not contain a reward element (Smillie et al., 2012). Moreover, reward associations have been shown to facilitate performance on a reward-modulated Stroop task (Krebs et al., 2010, 2011; Villablanca, 2010). Good performance on the Stroop task represents adaptive and efficient ability to solve attentional conflicts. Likewise, good performance on the two subtests of the WAIS is indicative of high concentration and fast mental processing, respectively.

In line with our suggestion that PACS assesses the individual tendency to adaptively maintain positive affect via reward-based conflict solving, PACS was mostly related to the connectivity between the amygdala and a network of regions related to reward and attention. For instance, PACS positively predicted the connectivity between the right amygdala and both the bilateral thalamus and the caudate, meaning that this connection was stronger for high PACS scores. This is consistent with data positing that this connection facilitates reward processing and increased attention (Davis, 1997; Roy et al., 2009). Amygdalar-striatal connectivity was found to be altered in pathological gambling (Peters

et al., 2013), where gamblers attend to the same gamble for hours on end, which has been linked to an altered reward system similar to that seen in other addictions. Furthermore, consistent with the scope of the PACS, the caudate has also been associated with approach–attachment behavior (Villablanca, 2010), and has also been proposed to be involved in the recruitment of the motor system to support working memory performance by the mediation of sensory–motor transformations (Postle and D'Esposito, 2003). PACS also positively predicted connectivity between the right caudate and bilateral dACC, and increased connectivity between the caudate and the ACC has been observed in MDD (Gabbay et al., 2013), alongside increased connectivity between other areas in striatum and PFC. Abnormalities in the gray matter of these regions have also been linked to OCD and other anxiety disorders (Radua and Mataix-Cols, 2009; Radua et al., 2010). PACS further negatively predicted connectivity between the right thalamus and the left dlPFC, meaning that this connection was stronger for low PACS scores. This is in line with an increase in connectivity between these regions that was linked to reduced working memory among schizophrenic patients (Anticevic et al., 2012) as well as among patients with mild cognitive impairment (Liang et al., 2011).

In summary, we suggest that PACS assesses the individual ability to maintain positive affect by focusing on rewarding information. In line with this assumption, PACS was related to the strength of connectivity in a neural network that included the amygdala, the thalamus, the caudate, the dACC and the dlPFC that has previously been observed in studies on reward, emotion and attention.

The third factor

Our analyses revealed a third factor, which indicated an inverse relationship between the executive functions of attention, concentration and processing speed on the one hand and trait negative affect on the other. High negative affect has previously been linked to decreases in these executive functions, for instance in OCD (Shin et al., 2014) but also in healthy controls (Melcher et al., 2011). This third factor negatively predicted the strength of connectivity between the left amygdala and right IPL and between the right amygdala and bilateral PCC, meaning that connectivity between these regions was lower for high scores in this factor. It has been suggested that parietal regions work in concert with prefrontal control mechanisms and support the down-regulation of the amygdala by (re-)directing attention (Ochsner et al., 2012). In line with this suggestion, Kanske et al. (2011) found IPL to be connected to the amygdala during distraction (i.e. shifting attention). A decrease in amygdalar-parietal connectivity was previously observed in OCD (Gottlich et al., 2014), and OCD patients are known to have deficits in shifting attention (e.g. Aycicegi et al., 2003) and in processing speed (Shin et al., 2014). It has been suggested that this decrease may explain why intrusive thoughts occur more in patients and people high on negative affect, as shifting attention away becomes more difficult (Gottlich et al., 2014).

Possible implications and future directions

Our findings support theoretical and empirical research suggesting that emotional traits and executive functions are not distinct but have common underlying factors. Moreover, these common factors are reflected in differential neural connectivity patterns that overlap in regions of cognitive control, emotion, attention and reward. These results corroborate findings of recent studies (Forbes et al., 2014; Forster et al., 2013) and models emphasizing the shared neural structures underlying cognitive and emotional functions (Okon-Singer et al., 2007, 2013, 2015; Pessoa et al., 2002b, 2005; Pessoa, 2009). It is plausible to hypothesize that the shared variance between executive functions and emotional traits is due to an underlying common mechanism other than those measured. For example, such a mechanism may be related to working memory, in line with recent views suggesting a role for working memory in emotion-related processes (Arend et al., 2015; Owens

et al., 2013) and/or to specific, subconscious conflict control processes (e.g., Cohen et al., 2014a). It has been suggested that exposure to emotional items inherently leads to activation of control processes, even when not asked to control the emotional reaction (e.g., Sabatinelli et al., 2011). Recent views also propose that negative affect is an integral part of cognitive control, and that cognitive conflicts constitute negative valence by their nature (see review in Inzlicht et al., 2015). Future studies may examine which underlying mechanism drives the relationship between executive functions and emotional traits by directly manipulating different factors.

To the best of our knowledge, this is the first study to carve out distinct neural mechanisms in the brain's resting state that are shared by multiple emotional traits and executive abilities. The results point to specific neural networks sub-serving the psychological mechanisms that control emotional behavior and may aid in informing us more thoroughly about how emotional traits and executive functions shape each other. While NATI and PACS may at first glance seem to be opposites, it is important to note that negative and positive affect are distinct constructs rather than extremes on the same scale (Rush and Hofer, 2014; Tellegen et al., 1999; Watson et al., 1999), and that neuroticism and extraversion are also distinct constructs rather than opposites (Marsh et al., 2013). Our results support the view that while NATI and PACS both draw on prefrontal, insular and striatal resources when amygdalar networks are queried, the resting-state functional connectivity patterns predicted by each factor are distinct. Specifically, NATI is predominantly reflected in connectivity patterns between the amygdala and a network of regions previously related to cognitive control of emotion and language-related interference effects. PACS, on the other hand, is predominantly reflected in connectivity patterns between the amygdala and a network of regions previously related to reward, attention, working memory and motor response.

It is important to note that our findings are limited to the descriptive scope of the measures that were included. Future studies may use different measures of emotional traits and executive functions to extend our understanding of the common underlying mechanisms. The PCA approach that we employed in combination with resting-state functional connectivity is based on the examination of individual differences. Recent studies focusing on individual differences show that taking individual differences into account can help elucidate the diversity and complexity of psychological phenomena and their neural underpinnings (Adelstein et al., 2011; Cox et al., 2012; Rohr et al., 2013). Our findings thus highlight new possibilities for gleaning insight into how the brain's functional wiring is associated with people's behavior and may serve as a basis particularly for future studies investigating psychiatric illnesses.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.06.049.

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