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ORIGINAL ARTICLE

Amygdala structure and core dimensions of the affective personality

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Abstract While biological models of human personality propose that socio-affective traits and skills are rooted in the structure of the amygdala, empirical evidence remains sparse and inconsistent. Here, we used a comprehensive assessment of the affective personality and tested its association with global, local, and laterality measures of the amygdala structure. Results revealed three broad dimensions of the affective personality that were differentially related to bilateral amygdala structures. Dysfunctional and maladaptive affective traits were associated with a global size and local volume reduction of the amygdala, whereas adaptive emotional skills were linked to an increased size of the left amygdala. Furthermore, reduced asymmetry in the bilateral global amygdala volume was linked to higher affective instability and might be a potential precursor of psychiatric disorders. This study demonstrates that structural amygdala measures provide a neural basis for all major dimensions of the human personality related to adaptive and maladaptive socio-affective functioning.

Keywords Amygdala · Personality · MRI · Voxel-based morphometry · Affect · Emotional intelligence

Sascha Frühholz and Katja Schlegel contributed equally to the study.

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Introduction

Socio-affective dispositions are central to biological models of human personality (Kennis et al. 2013), that largely agree on three-to-four core dimensions, including extraversion, neuroticism (or the fight–flight–freeze system), the behavioral inhibition system, and psychoticism. These models also share the perspective that human personality is associated with the structure and functioning of the neural system, especially of the amygdala as a central node of the emotional brain network (LeDoux 2012; Dricu and Fruhholz 2016; Fruhholz et al. 2014). The amygdala has frequently been shown to be specifically involved in recognizing important social (Adolphs 2009; Fruhholz et al. 2014) and emotional information (Vuilleumier 2009; Fruhholz et al. 2015, 2016) displayed by other individuals across many sensory modalities. While such processing of emotional information is largely indicated by increased functional activity in the amygdala and mainly refers to the perception and experience of rather short emotional events, the amygdala might also be involved in more persistent or habitual ways of how individuals respond to emotional information and emotional situations. The latter type of processing is linked to socio-affective dispositions or personality traits, and might not only be reflected in the level of activity of the amygdala, but also in its structural properties (Davidson 2001; Davidson and McEwen 2012). Supporting this notion, certain structural measures of the amygdala, such as its overall volume and its local grey matter (GM) volume and density, have been shown to correlate with some socio-affective traits such as extraversion (Cremers et al. 2011; Lewis et al. 2014), neuroticism (Omura et al. 2005), behavioral inhibition (Barros-Loscertales et al. 2006), fearfulness (van der Plas et al. 2010), aggressiveness (Whittle et al. 2008; Pardini et al. 2014), and impulsivity (Gopal et al. 2013).

While the previous studies provided the first evidence for a link between the amygdala structure and affective dispositions, the results are far from conclusive. First, the direction of the relationship is unclear, as both positive and negative correlations have been reported (Cremers et al. 2011; Lewis et al. 2014). Second, a systematic investigation of the broader dimensions underlying the affective personality still remains to be done, as the previous studies usually focused on narrow, specific traits that were measured with self-report questionnaires (Nostro et al. 2016). Notably, competencies such as emotion recognition ability and other components of emotional intelligence (Mayer et al. 2004) have largely been neglected in this line of research. However, these competencies are measured with performance-based tests that have objectively correct answers and might be more directly linked to structural properties of the amygdala than commonly used self-report questionnaires. Third, the previous studies differed with respect to their measures of the amygdala structure, mainly focusing on the global size of the amygdala (Nacewicz et al. 2006; Pedraza et al. 2004).

The aim of the present study was, therefore, to expand the previous findings by comprehensively assessing the socio-affective human personality and relating its major dimensions to a wider range of structural amygdala measures. Although interindividual differences in personality and socio-affective dispositions might be reflected in structural properties of several brain regions (Kennis et al. 2013; Nostro et al. 2016), the present study specifically focused on the amygdala for several reasons. First, the present study was concerned with the affective dimensions of personality, and the amygdala is supposed to underlie both temporary and persistent emotional responding. Second, as mentioned above, evidence for the role of the amygdala in personality is sparse and highly inconsistent, ranging from positive and negative findings to non-findings (Nostro et al. 2016).

Sixty-five adult human participants completed ten established questionnaires and performance-based tests consisting of 21 subscales (Fig. 1a; see Table S1), which were selected based on a taxonomy of socio-affective personality traits and affective skills relevant to effective social functioning (Schlegel et al. 2013), and which are established and internationally used instruments of personality assessments. T1-weighted structural images of each participant's brain were recorded, and volumetric and morphometric analyses were applied to assess the global and local volume in subregions of the amygdala, respectively (Padival et al. 2013; Davidson and McEwen 2012; Gopal et al. 2013).

Materials and methods

Participants

Seventy healthy participants took part in the experiment for payment. Participants were recruited through public advertisements and were either students, employees, or affiliates of the University of Geneva. Data from five participants had to be excluded because of insufficient quality of their anatomical brain images (see below). The final sample consisted of 26 male and 39 female participants with a mean age of 25.6 years (SD = 4.05, age range 18–35 years). Sixty-two participants reported being right-handed and three participants (4.6%) reported being left-handed. No participant presented a psychiatric or neurological medical history and the sample could, therefore, be expected to cover a normal range of personality traits.

In addition, we tested whether participants were in the normal range of psychological well-being or showed potentially clinical psychological distress by administering the short version of the General Health questionnaire (GHQ-12) (Goldberg and Williams 1988). Similar to the previous studies, the 12 four-point Likert scale GHQ items were recoded into binary variables and then summed to provide a total GHQ score that ranged from 0 to 12. In our sample, 41.5% had scores of 3 and higher and 29.2% had scores of 4 and higher, which is within the normal range of psychological distress in healthy individuals as reported in other studies (James et al. 2013; Moffat et al. 2004). Thus, the final sample covered a normal range of psychological well-being and showed no general signs of psychological disorders. The experiment was approved by the local ethics committee of the University of Geneva and informed written consent was obtained from each participant in accordance with the ethical and data security guidelines of the institution.

Assessment of affect-related personality traits and skills

Participants completed ten questionnaires and tests (presented on computers) and provided basic demographic information in the laboratory of the University of Geneva. The test battery (duration 45–60 min) covered a wide range

Fig. 1 **a** Three-component solution [principal component (PC) 1–3] of the principal component analysis on the 21 subscales (for numbering, see below) of the ten affective trait questionnaires and tests administered to 65 human participants (*left panel*). The *right panel* lists the single socio-affective scales (original questionnaires and tests in *parentheses*; see Table S1 for details). **b** Three components of the affective personality identified in the present study seem to overlap, first, with the three components of the classic model of personality proposed by Eysenck (extraversion, neuroticism, and psychoticism; *blue circles*) (Eysenck 1963) and, second, with emotional intelligence as an adaptive competence (*upper left panel*, *orange box*), respectively. *BEQ* berkeley expressivity questionnaire, *BFI* big five inventory, *BIS/BAS* behavioral inhibition system and behavioral activation system questionnaire, *GERT* Geneva emotion recognition test, *IRI* Interpersonal Reactivity Index, *UPPS* Impulsive Behavior Scale, *PANAS* positive and negative affect schedule, *STAI* state-trait anxiety inventory, *STAXI* state-trait anger expression inventory, *STEU* situational test of emotional understanding

of emotion-related personality traits, dispositions, and skills that are related to effective socio-emotional functioning in private and professional life (Schlegel et al. 2013). Besides the broad and general personality dimensions of the five-factor model (openness, conscientiousness, extraversion, agreeableness, and neuroticism), the present study included a wide range of more specific affect-related traits and skills, each of which captures a specific facet of individual differences in the way people attend to, process, respond to, or deal with socio-emotional information. The importance of such affect-related dispositions in human functioning has been emphasized in personality theories such as the Cognitive-Affective System Theory of Personality (Mischel and Shoda 1995), and more recently, in theories of emotional intelligence (e.g., Mayer et al. 2004). In particular, the present study included (1) affective maladaptive personality traits associated with clinical disorders (e.g., anxiety, anger, impulsivity, and negative affect), (2) adaptive affect-related traits (e.g., empathy, emotional expressivity, and positive affect), as well as (3) performance-based tests of emotional skills (emotion recognition ability and emotional understanding; see Fig. 1; Supplementary Table S1 for details). Each of these constructs has widely been studied in different domains of psychology and can be measured with established questionnaires or tests. Including all of these constructs in the present study allowed for a comprehensive assessment of the affective personality that cannot be achieved with one questionnaire alone, and that goes beyond the broad dimensions of the five-factor model.

All instruments were administered in French and presented to the participants on computer screens using the free Limesurvey survey application (Team and Schmitz 2012). The Geneva emotion recognition test (GERT) was administered via its own Web-based html application. In addition to these instruments, participants provided basic demographic information. The total duration of the study was between 45 and 60 min.

The ten tests and questionnaires yielded a total of 21 subscales, which we computed according to the respective instructions from the literature. We conducted a principal component analysis (PCA) in combination with parallel analysis to identify the main dimensions underlying these 21 subscales, which we intended to use as predictors of amygdala volume. Parallel analysis adjusts the number of components to be extracted in relation to the number of components that would be found in random data. This analysis, conducted with the R package "paran" (Dinno 2009), indicated the extraction of three dimensions from the data. We then performed a PCA with Varimax rotation, as our aim was to create orthogonal components to avoid collinearity of the predictors for the later analyses. The three extracted components explained 50.5% of the variance. Table 1 shows the component loadings of the PCA. Component scores for these three dimensions were computed using the regression method. We tested whether the component scores were normally distributed by computing the Shapiro–Wilk test and by examining skewness and kurtosis (Table 2). The Shapiro–Wilk test was not significant for the "Dysfunctional Affectivity and Instability" (DAI) dimension (PC1) nor for the "Adaptive Skills and Traits" (AST) dimension (PC2), indicating that the scores were approximately normally distributed. The Shapiro–Wilk test was significant for "Arousal Dependency and Disinhibition" (ADD, PC3), but its distribution can be considered sufficiently close to a Gaussian distribution,

Table 1 Mean values and component loadings of the 21 subscales on the three dimensions extracted through principal component analysis

Subscale	Mean (SD)	Component loadings		
		DAI (PC1)	AST (PC2)	ADD (PC3)
Neuroticism (BFI)	2.76 (0.73)	0.84		
Personal distress (IRI)	2.96 (0.64)	0.79		
Behavioral inhibition (BIS/BAS)	2.92 (0.52)	0.78		
Urgency (UPPS)	2.17 (0.51)	0.70		0.54
Negative affect (PANAS)	18.18 (6.28)	0.70		
Anger expression and control (STAXI)	35.12 (11.07)	0.66		0.37
Trait anger (STAXI)	20.37 (4.79)	0.48		0.44
Agreeableness (BFI)	4.01 (0.50)	−0.45		
Emotional expressivity (BEQ)	4.56 (0.83)	0.42	0.38	
Trait anxiety (STAI)	2.56 (0.21)	0.39	−0.39	
Emotion recognition ability (GERT)	0.64 (0.12)		0.75	
Emotional understanding (STEU)	0.59 (0.16)		0.74	
Empathy (IRI)	3.78 (0.49)		0.69	−0.32
Extraversion (BFI)	3.21 (0.74)		0.58	
Positive affect (PANAS)	34.69 (5.85)	−0.40	0.49	
Behavioral activation (BIS/BAS)	3.07 (0.34)		0.42	
Openness (BFI)	3.74 (0.63)	−0.36	0.41	
Lack of premeditation (UPPS)	1.97 (0.45)			0.76
Conscientiousness (BFI)	3.71 (0.56)			−0.68
Sensation seeking (UPPS)	2.63 (0.65)			0.62
Lack of perseverance (UPPS)	1.86 (0.39)		−0.35	0.58

Abbreviations in parentheses refer to the instrument that each subscale was taken from. For questionnaire and test abbreviations, see Supplementary Table S1. Component loadings < abs(0.30) are not reported

DAI dysfunctional affect and instability, *AST* adaptive skills and traits, *ADD* arousal dependency and disinhibition

Table 2 Shapiro–Wilk test, skewness, and kurtosis statistics for the three principal components derived from the principal component analysis as well as for the measure of amygdala volume

	Shapiro–Wilk test statistic	Skewness statistic	Kurtosis statistic
PC1: dysfunctional affect and instability (DAI)	0.97 ($p = 0.12$)	0.46 (SEM = 0.30)	−0.33 (SEM = 0.59)
PC2: adaptive skills and traits (AST)	0.98 ($p = 0.26$)	−0.50 (SEM = 0.30)	0.29 (SEM = 0.59)
PC3: arousal dependency and disinhibition (ADD)	0.95 ($p = 0.01$)	−0.76 (SEM = 0.30)	0.54 (SEM = 0.59)
Left amygdala volume	0.98 ($p = 0.26$)	0.18 (SEM = 0.30)	−0.80 (SEM = 0.59)
Right amygdala volume	0.98 ($p = 0.37$)	−0.12 (SEM = 0.30)	0.40 (SEM = 0.59)
Directional amygdala volume difference	0.99 ($p = 0.99$)	−0.18 (SEM = 0.30)	0.19 (SEM = 0.59)

given that skewness and kurtosis for these components scores were within the absolute range of "1" (Westfall and Henning 2013), which was also confirmed with visual inspection of the histogram.

Structural image acquisition, amygdala segmentation, and volumetric analysis

Structural brain images of each participant were acquired through a high-resolution, magnetization-prepared rapid acquisition gradient echo (MPRAGE) T1-weighted sequence (TR/TE/TI = 1900/2.27/900 ms, FoV = 296 mm, voxel size 1 mm^3, 192 slices), recorded on a 3T Siemens Tim TRIO System (Siemens, Erlangen, Germany). The native T1 anatomical images were first manually reoriented, such that the origin of the images was set to the anterior commissure (AC), the *y*-axis was oriented to match the AC-PC line, and the midline of the brain images matched the zero sagittal plane. The images were then subjected to a volumetric analysis that involved, first, an automated full brain cortical surface reconstruction and volumetric segmentation procedure as implemented in the FreeSurfer software (http://freesurfer.net/; Version 5.3.0). Segmentation of the amygdala subnuclei was not possible with the acquired T1 images, because subnuclei segmentation is not yet implemented in the segmentation software used, likely because such subnuclei are not visible in the T1 anatomical images. The segmentation algorithm first performed cortical white matter segmentation, a tessellation of the white matter/grey matter junction, and automatically corrected topological defects in the resulting segments. Following this process, a manual correction of amygdala segmentation errors was undertaken by two independent individuals trained on amygdala segmentations in line with common anatomical boundary landmarks of the amygdala (Chung et al. 2010; Bach et al. 2011). The differentiation of the amygdala and the adjacent hippocampus was especially done given the lateral anatomical landmarks of the lateral ventricles and based on medioventral landmarks given in a common anatomical atlas (Mai et al. 1997). Finally, a grey matter and white matter segmentation was performed using the new segment option implemented in the Statistical Parametric Mapping software (SPM, version 8; http://www.fil.ion.ucl.ac.uk/spm/software/spm8/).

The manual correction of amygdala segmentation errors was iterated until a segmentation overlap of at least 90% for both the left and right amygdala of a participant was reached (see Fig. S1). For three participants, this overlap could not be achieved due to insufficient T1 image quality, and the data of these participants were discarded from further analysis (for details, see "Materials and methods"). We additionally calculated the Dice similarity coefficient (Dice 1945) indicating the spatial overlap between segmentations done independently by the two individuals (A and B) according to the formula DSC $(A, B) = 2(A \cap B)/(A + B)$, where $\cap$ denotes the extent of the spatial overlap. Across the 65 participants, we revealed a DSC > 0.84 for the left amygdala and a DCS > 0.81 for the right amygdala, which is in the range of an excellent agreement (DCS > 0.70) between the two segmenters across all participants (Zijdenbos et al. 1994). Steps 1 and 2 yielded the mean left and right amygdala volume for each participant (see Fig. S1), which was divided by the total intracranial volume of each participant as derived from the segmentation in step 3 to obtain relative volumes of the left and right amygdala. Individual DARTEL flow fields were estimated based on segmented grey and white matter tissue classes (Ashburner and Friston 2005), which were then used for normalizing the T1 images and the amygdala segmentation masks to the Montreal Neurological Institute (MNI) standard space.

Multivariate regression analysis

To test the relationship between affective personality and amygdala structure, one multivariate regression analysis was conducted with the three affective personality dimensions (component scores) as independent variables and with four global structural amygdala features as dependent variables (relative left and right amygdala volume, directional volume difference [i.e., (left amygdala − right amygdala)], and non-directional amygdala volume difference [i.e., abs(left amygdala − right amygdala)]. The multivariate regression analysis was set up as a multivariate general linear model (GLM) using z-transformed dependent and independent variables, controlling for participant age. The directional volume difference provides directional information about a larger amygdala in the left or the right hemisphere, while the non-directional difference refers to amygdala volume difference irrespective of the laterality. Standardized regression coefficients (β values) were thresholded at $p < 0.05$.

Voxel-based morphometry: volume and density

The voxel-based morphometry (VBM) analysis was performed using the VBM8 toolbox (http://dbm.neuro.uni-jena.de/vbm/download/) for SPM8, which is based on DARTEL segmentation and normalization algorithms (Ashburner and Friston 2005). The VBM analysis was performed, first, on normalized grey matter images to investigate the effects of personality on regional brain density (Good et al. 2001). Second, the VBM analysis was performed on normalized images representing the relative differences in regional grey matter images corrected for the individual brain volume, such that these images were modulated for non-linear warping effects due to spatial normalization. The latter analysis computed the effects of personality on regional brain volume (Good et al. 2001). Based on an examination of the covariance between images and visual inspection, the data of two more participants were discarded because of insufficient image quality, resulting in a total dropout of five participants. The images of the remaining sample were spatially smoothed using an isotropic Gaussian kernel of 8 mm^3 full-width half maximum and subjected to a random-effects multiple regression group analysis with the three z-standardized personality component scores as independent variables and age as a control variable. To determine grey matter density effects in the left and right amygdala, we first thresholded the resulting static images at a voxel threshold of $p < 0.01$ and subsequently applied a small volume correction [$p < 0.05$, false discovery rate (FDR) corrected, cluster size $k > 5$]

inside a combined mean normalized left and right amygdala mask derived from the final sample of participants.

Results

Principal component analysis of personality subscales

In the first step of the analysis, we performed a PCA with Varimax rotation on the scores of the 21 test and questionnaires subscales to identify the general dimensions of the affective personality and emotional intelligence. This analysis revealed three major orthogonal dimensions (Fig. 1a). PC1 was characterized by scales related to negative affectivity, neuroticism, and dysfunctional traits such as anxiety and anger, and was labeled "Dysfunctional Affectivity and Instability" (DAI). This PC overlaps with the neuroticism and the psychoticism dimensions in classic personality models, especially with the anger-aggressive part of psychoticism (Eysenck 1963) (Fig. 1b). PC2 was labeled "Adaptive Skills and Traits" (AST) due to high loadings for emotion recognition ability and emotional understanding (assessed with objective performance-based tests) as well as for adaptive traits such as positive affect, empathy, and openness. This PC represents a combination of extraversion and the "socio-emotional sensitivity and emotional abilities" dimension found in the previous research on socio-affective functioning and emotional intelligence (Schlegel et al. 2013) (Fig. 1b). PC3 was labeled "Arousal Dependency and Disinhibition" (ADD) and displayed high loadings for scales related to impulsive behavior, sensation seeking, and low conscientiousness. PC3 also displayed high negative loadings on the behavioral inhibition scale of the BIS/BAS questionnaire and integrates parts of the extraversion dimension, both of which have been associated with active behavioral approach tendencies and the need for external stimulation as part of a habitual under-aroused inner state (Cloninger 2000) (Fig. 1b).

Volumetric amygdala analysis

In the second step of the analysis, we performed a global volumetric analysis of the entire amygdala based on combined automated and manual segmentation of the structural images, normalized by the individual total brain volume (see "Materials and methods"). There was substantial interindividual variation in the normalized left ($M_{\mathrm{vol}} = 1209$ mm^3, SD = 122, range 944–1468 mm^3) and right amygdala volumes ($M_{\mathrm{vol}} = 1216$ mm^3, SD = 122, range 964–1505 mm^3) as well as in the volume difference between participants' left and right amygdala (Fig. 2a, b; see also Table 2).

As determined by a mixed-effect ANOVA with the between-subject factor gender (male and female) and the within-subject factor laterality (left and right), we did not find a difference between the left and the right amygdala volume ($F_{1,63} = 0.288$, $p = 0.594$) or between male and female participants ($F_{1,63} = 0.288$, $p = 0.569$). There was no interaction between the factors ($F_{1,63} = 0.069$, $p = 0.793$). Left and right normalized amygdala volumes were correlated ($r = 0.61$, $p < 0.001$), and both left ($r = 0.44$, $p = 0.001$) and right normalized amygdala volume ($r = -0.44$, $p < 0.001$) were correlated with the directional volume difference score, but not with the non-directional volume difference score (left: $r = -0.18$, $p = 0.153$; right: $r = -0.06$, $p = 0.625$). All correlational analyses used Pearson correlations in line with the previous studies (Brierley et al. 2002). The mean volume of the bilateral amygdala did not correlate with the directional ($r = 0.00$, $p = 0.989$) or non-directional left–right volume asymmetry ($r = -0.13$, $p = 0.029$). There were no gender differences in directional ($t_{63} = 0.263$, $p = 0.793$; two-sample t test) and non-directional amygdala volume difference ($t_{63} = 1.507$, $p = 0.137$; two-sample t test).

Amygdala structure and affective personality

In the third step of the analysis, we examined the relationship between affective personality dimensions and amygdala structure. We ran a multivariate regression analysis with the three affective personality dimensions as independent variables and four structural amygdala features as dependent variables (i.e., left and right amygdala volume, and directional and non-directional left–right amygdala volume difference). The volume of the left ($F_{1,61} = 6.499$, $p = 0.013$, $\beta = -0.30$) and the right amygdala ($F_{1,61} = 6.672$, $p = 0.012$, $\beta = -0.30$) as well as the non-directional volume difference between the left and the right amygdala ($F_{1,61} = 4.193$, $p = 0.045$, $\beta = -0.25$) were negatively associated with the DAI dimension (PC1). The latter non-directional volumetric asymmetry was not significantly correlated with the mean normalized amygdala volume; thus, this asymmetry was not generally associated with larger or smaller volumes of the amygdala. The left amygdala ($F_{1,61} = 4.070$, $p = 0.048$, $\beta = -0.23$) was also negatively associated with the ADD dimension (PC3), while it was positively correlated with the AST dimension (PC2) ($F_{1,61} = 5.772$, $p = 0.019$, $\beta = 0.27$) (Fig. 2c).

The same multivariate regression analysis described above was run separately for male and female participants to explore any gender-related influences on the association

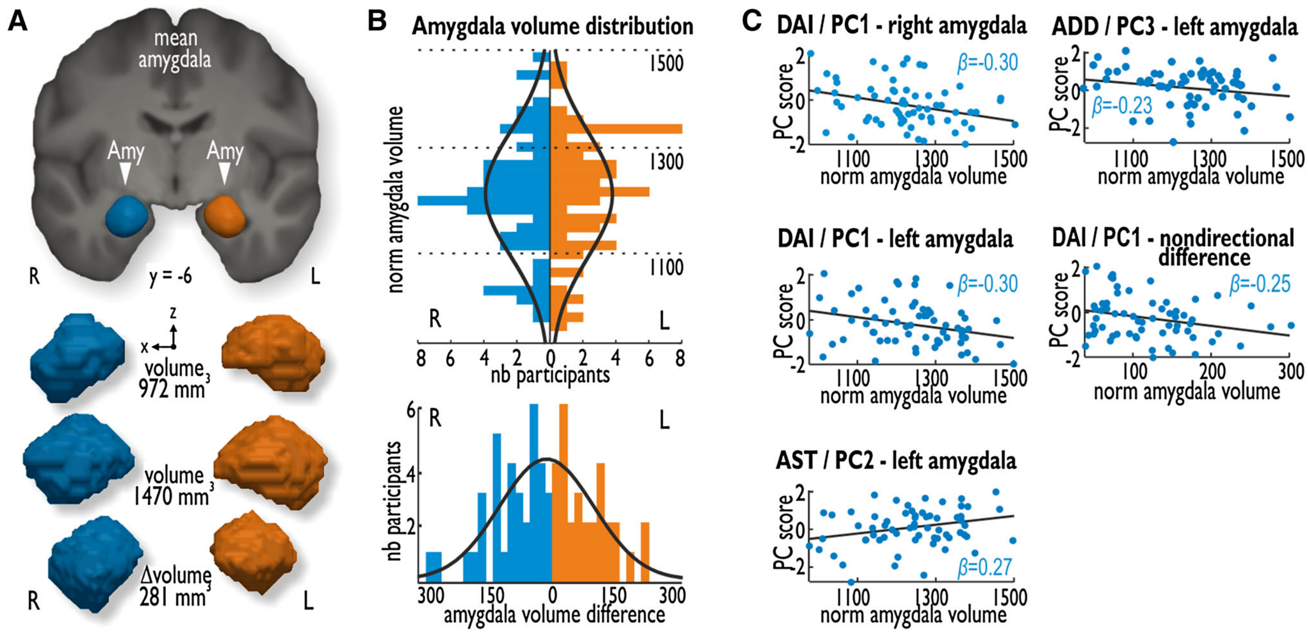

Fig. 2 **a** Average amygdala across all participants ($N = 65$) represented in Montreal Neurological Institute (MNI) space (*upper panel*). Note that the *left* and the *right* hemisphere are reversed. The *lower panel* shows the bilateral amygdala of the participants with the smallest mean normalized *left* and *right* amygdala volumes, the largest mean normalized amygdala volume, and the largest difference between the normalized *left* and *right* amygdala volume. **b** Distribution of the normalized *left* and *right* amygdala volume (*upper panel*) and of the *left–right* difference in the normalized amygdala volumes across all participants ($N = 65$, *lower panel*). **c** Volume of the left and the right amygdala as well as the non-directional *left–right* volume difference were negatively associated with the DAI dimension (PC1). The *left* amygdala was also negatively associated with the ADD dimension (PC3) and positively associated with the AST dimension (PC2). *L* left, *R* right

between the PC and the amygdala volume. For female participants, we found that the DAI dimension (PC1) was negatively associated with the left ($F_{1,35} = 5.701$, $p = 0.023$, $\beta = -0.32$) and right amygdala volume ($F_{1,35} = 4.179$, $p = 0.049$, $\beta = -0.36$); no other effects were significant [all F's < 3.566, all p's > 0.925, all β's $< -\text{abs}(0.26)$]. For male participants, no significant effects were obtained [all F's < 2.684, all p's > 0.116, all β's $< \text{abs}(0.30)$]. Although the DAI dimension (PC1) was significantly associated with the left and right amygdala volume, a statistical comparison in male and female participants based on the Fisher z-transformed β values revealed no significant difference between genders in the left ($z = -0.24$, $p = 0.810$) and right amygdala ($z = -0.25$, $p = 0.802$). Thus, when analyzed separately by gender, some regression coefficients were significant only for female participants, but none of these correlations statistically differed between genders. As there were no gender differences in the personality structure of the PCs and in the strength of their association with amygdala volume, gender was not included as a control variable in the analysis described above.

Finally, we found that individual differences in the ADD dimension (PC3) in particular showed associations with local measures of amygdala structure, as revealed from voxel-based morphometry analysis (VBM) of the structural images. Besides a global volume reduction of the left amygdala with increasing scores of the ADD dimension (PC3) (Fig. 2c), this dimension was specifically associated with a local grey matter volume reduction of the laterobasal (LB) nucleus of the left amygdala (Fig. 3). The assignment to the LB nucleus was based on the definition of amygdala subregions (Amunts et al. 2005) as provided by the SPM Anatomy toolbox implemented in SPM12, which differentiates between the laterobasal, superficial, and centromedial amygdala nucleus. We tested several boundary points of the grey matter cluster, and the probability was 58–93% of being located in the LB nucleus; otherwise, the probability indicated that the grey matter cluster is located most likely in its posterior extension into the hippocampus. Thus, the global volume reduction of the left amygdala might be specifically driven by an LB nucleus volume loss.

Discussion

Our results suggest that, first, the affective personality, comprehensively measured with a wide range of assessment tools, can be described by three superordinate

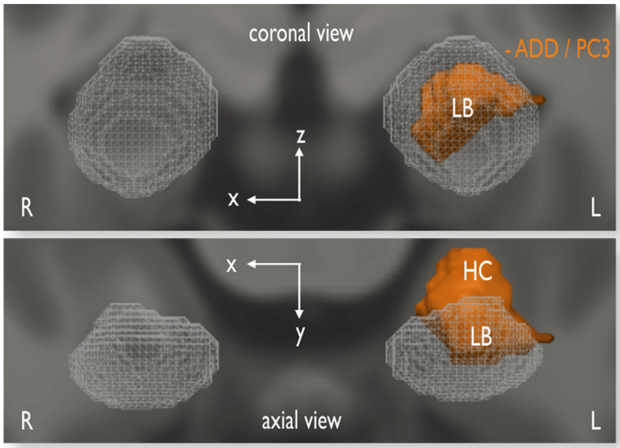

Fig. 3 GM volume of the *left* laterobasal (LB) nucleus showed a stronger negative association with the ADD dimension compared with the DAI and AST dimensions [$p < 0.05$, false discovery rate (FDR) corrected, cluster size $k > 5$] across the 65 participants (*left* and *right* are reversed). The *upper panel* shows a coronal view of the bilateral amygdala, while the *lower panel* shows an axial view of the *left* LB cluster extending into the anterior hippocampus (HC). *L* left, *R* right

dimensions, (PC1-1), referred to as Dysfunctional Affectivity and Instability (DAI), Adaptive Skills and Traits (AST), and Arousal Dependency and Disinhibition (ADD), respectively. Second, our data showed that both the maladaptive DAI personality dimension (PC1, comprising traits like distress, anxiety, anger, and impulsivity) and the positive AST dimension (PC2, comprising empathy, openness, emotion recognition ability, etc.) were associated with structural measures of the amygdala. In particular, smaller amygdalae were associated with higher levels of dysfunctional traits (DAI dimension, PC1), which is supported by the previous results for neuroticism (Omura et al. 2005) and aggression (Gopal et al. 2013). However, opposite effects have also been reported, especially in younger adolescents (Whittle et al. 2008). This discrepancy might be explained by an initial hypertrophy in response to early critical life events that influence the development of negative traits, leading to a positive correlation between these traits and amygdala volume. However, due to cellular atrophy and cell death, an initial hypertrophy eventually leads to amygdala shrinkage in adults (Nacewicz et al. 2006; Tottenham 2009). Hence, in adults, a negative correlation between maladaptive traits and amygdala volume can be expected.

Unlike this negative amygdala-DAI coupling, we found that adaptive emotional abilities and traits (AST dimension, PC2) were primarily associated with a larger volume in the left amygdala, which is in line with the previous results for extraversion (Omura et al. 2005) and positive emotionality (Lewis et al. 2014). As proposed by Davidson (2000), positive emotions are controlled by the left rather than the right hemisphere. Moreover, Dyck et al. (2011) suggested that the left hemisphere is involved in tasks that require conscious emotional processing which might also be linked to a more sustained activity in the left amygdala (Sergerie et al. 2008). Indeed, the AST dimension (PC2) included a better performance on tasks requiring conscious processing of non-verbal emotional expressions (emotion recognition) as well as emotional information from texts (emotional understanding).

In addition to these positive and negative relationships with the left or right amygdala volume, we found that lower asymmetry between the bilateral amygdala was correlated with higher levels of dysfunctional affect and instability (DAI dimension, PC1). This is corroborated by studies that found reduced hemispheric asymmetries across several brain regions in psychiatric disorders that involve high levels of negative affect and emotional instability, such as schizophrenia (Bilder et al. 1999) and autism (Rojas et al. 2002). Thus, reduced asymmetry of the amygdalae in healthy individuals might be a neural marker signaling maladaptive emotional functioning, and a precursor to psychiatric and personality disorders (Meyer-Lindenberg and Tost 2012). High scores on the ADD dimension (PC3) were also related to a reduced volume of the BL nucleus. The BL nucleus is an important input node because of its extensive connections with sensory cortical and subcortical regions (Fruhholz et al. 2014; Pannese et al. 2015), and its volume appears to be negatively associated with impulsivity control (Gopal et al. 2013). BL nucleus structure might thus be linked to individual differences in sensory distraction control and immediate behavioral impulse generation as represented by the ADD dimension (PC3). This might especially be the case for emotional stimuli (Winstanley 2004) or stimuli that are relevant to certain psychiatric disorders (Yang et al. 2009; Boccardi et al. 2011). Accordingly, studies have demonstrated that structural changes in the BL especially occur in response to repeated stress (Padival et al. 2013; Davidson and McEwen 2012), which at the same time shapes personality.

This study provides the first comprehensive investigation of the central dimensions of socio-affective traits and competencies, as well as their association with a central structure of the limbic system. The assessment of broad affective dimensions as opposed to narrow traits could be a promising avenue especially for social neuroscience, as these dimensions might better correspond to underlying brain mechanisms than very specific psychological constructs. Biological models of personality so far have linked only negative affect and behavioral inhibition to the structure and function of the amygdala (Kennis et al. 2013), but our results demonstrate that such relationships also exist for other dimensions that reflect more superordinate and also positive socio-affective dispositions. Specifically, our data show that, first, dysfunctional or maladaptive traits (e.g., distress, anxiety, anger, impulsivity) are associated with overall volume and local density reduction in the amygdala, whereas objectively assessed emotional abilities and adaptive traits (e.g., empathy, openness) are linked to an increased overall volume of the left amygdala. Second, an increased difference between the volume of the left and right amygdala is related to less dysfunctional affect and instability. Reduced asymmetry might thus be a risk factor for excessive emotional instability and related psychiatric disorders. Third, given that amygdala–personality relationships might be bidirectional (Lewis et al. 2014), heritable aspects of the amygdala structure could generate predispositions to the way in which emotionally important life experiences influence individual affective personality. This corroborates the central role of the amygdala in emotional processing, but also in explaining differences between people's affective personalities.

We finally have to note some limitations of the present study. First, the study included 65 healthy participants and is, therefore, somewhat limited in its sample size. Future studies might investigate even bigger samples to add to the present evidence that structural brain measures underlie the major dimensions of the affective personality. However, the scores pertaining to affective personality dimensions in the present study were normally distributed and presumably cover a wide range of individual differences in the normal population. Furthermore, studies including larger sample sizes in the past usually relied on an automated segmentation of the amygdala, which can introduce biases due to misaligned segmentations. We chose to take advantage of a combined automatic and labor-intensive manual segmentation of the amygdala, which supposedly led to more precise amygdala segmentation. Second, we used a multivariate regression analysis to compute the relationship between the core dimensions of the affective personality and the amygdala volume. Multivariate statistical testing is the recommended procedure if there is a moderate correlation between the dependent variables. This was the case for our amygdala volume measures as dependent variables, with only the directional and non-directional volume difference measures being perfectly correlated. Thus, some caution is warranted about the relationship of amygdala volume differences and the affective personality. However, since only the non-directional volume difference, but not the directional volume difference revealed significant relations to the affective personality dimensions, both measures, although correlated, might differ in their predictive nature concerning core dimensions of the affective personality. A final limitation of the present study is the focus on the general volume of the amygdala. Although the whole amygdala can be indicative of socio-affective functions (and dysfunctions), the volumetric quantification of amygdala subregions might be even more informative. The anatomical images recorded from our participants did not allow the segmentation of amygdala subnuclei, but future studies might use specialized brain anatomical scans for this purpose (Solano-Castiella et al. 2011). Amygdala subnuclei have different roles during temporary and habitual emotional responding (Fruhholz and Grandjean 2013), and they might, therefore, be differentially linked to socio-affective traits.

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Compliance with ethical standards

Conflict of interest All authors declare to have no conflict of interests.

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