

Examining gray matter structures associated with individual differences in global life satisfaction in a large sample of young adults

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Although much attention has been directed towards life satisfaction that refers to an individual's general cognitive evaluations of his or her life as a whole, little is known about the neural basis underlying global life satisfaction. In this study, we used voxel-based morphometry to investigate the structural neural correlates of life satisfaction in a large sample of young healthy adults ($n = 299$). We showed that individuals' life satisfaction was positively correlated with the regional gray matter volume (rGMV) in the right parahippocampal gyrus (PHG), and negatively correlated with the rGMV in the left precuneus and left ventromedial prefrontal cortex. This pattern of results remained significant even after controlling for the effect of general positive and negative affect, suggesting a unique structural correlates of life satisfaction. Furthermore, we found that self-esteem partially mediated the association between the PHG volume and life satisfaction as well as that between the precuneus volume and global life satisfaction. Taken together, we provide the first evidence for the structural neural basis of life satisfaction, and highlight that self-esteem might play a crucial role in cultivating an individual's life satisfaction.

Keywords: life satisfaction; precuneus; parahippocampal gyrus; self-esteem; voxel-based morphometry

INTRODUCTION

Over the decades, an increasing amount of attention has been devoted to positive psychology (Seligman and Csikszentmihalyi, 2000). A central construct within the positive psychology literature is global life satisfaction. Global life satisfaction is defined as an individual's general cognitive evaluations of his or her life as a whole, which, along with positive and negative affect, is regarded as three primary components of subjective well-being that reflects the experience of pleasure (Diener *et al.*, 2003). This type of well-being was termed as hedonia by Aristotle, which is differentiated from the notion of eudaimonia—the highest human good involving virtue and the realization of one's potential (Aristotle, 1925). Contemporary psychological research has continued to distinguish between eudaimonic well-being and hedonic well-being (e.g. Ryan and Deci, 2001; Urry *et al.*, 2004), with empirical studies demonstrating that these two types of well-being are related but independent constructs using confirmatory factor analysis techniques (Gallagher *et al.*, 2009; Linley *et al.*, 2009).

Life satisfaction has been increasingly recognized as an important domain in individual differences (Diener *et al.*, 2003). For instance, life satisfaction tends to reflect relatively stable, long-term judgments of subjective well-being, whereas affect measures reflect more short-term reports of subjective well-being and show situational variability (Kim-Prieto *et al.*, 2005). Life satisfaction is heritable (Stubbe *et al.*, 2005) and a lack of satisfaction with life acts as a risk factor for depression (Green *et al.*, 1992). Higher life satisfaction has also been linked to higher self-esteem, better physical health, better psychological health, higher eudaimonic well-being, more positive affect and stronger social relationships, and linked to lower neuroticism, fewer stressful life events and fewer negative affect (Ryff and Keyes, 1995; Zullig *et al.*,

2005; Ring *et al.*, 2007; Abdel-Khalek, 2010; Kong *et al.*, 2012a, b, 2014a, b; Kong and You, 2013; Zhao *et al.*, 2014). In this study, we used structural magnetic resonance imaging to investigate the brain structures underlying individual differences in life satisfaction.

Although life satisfaction has drawn continuous attention in the past few decades (e.g. Diener *et al.*, 2003), little work to date has directly addressed the structural basis of life satisfaction. To our knowledge, the only study directly exploring the neural correlates of life satisfaction has found that higher left than right superior frontal activation under resting electroencephalography is associated with individuals' global life satisfaction (Urry *et al.*, 2004). Although no study has used MRI techniques to investigate the structural correlates of life satisfaction, numerous studies have explored the neural correlates of constructs related to life satisfaction such as depression, neuroticism, eudaimonic well-being, perceived stress, physical health and psychological health. Specifically, depression, which is moderately negatively associated with life satisfaction (Swami *et al.*, 2007), is often found to be associated with structural changes or altered activation in the amygdala, hippocampus and insula in response to certain specific activation procedures (von Gunten *et al.*, 2000; Campbell *et al.*, 2004; Videbech and Ravnkilde, 2004; Hamilton *et al.*, 2008; Hwang *et al.*, 2010; Sprengelmeyer *et al.*, 2011; Bechdolf *et al.*, 2012). Neuroticism, which is moderately negatively associated with life satisfaction (Steel *et al.*, 2008), is reported to be mostly associated with several brain regions including the amygdala, hippocampus/parahippocampal gyrus (PHG), posterior cingulate cortex/precuneus, anterior cingulate cortex (ACC), dorsomedial prefrontal cortex (DMPFC) and dorsal lateral prefrontal cortex (LPFC) (Omura *et al.*, 2005; Wright *et al.*, 2007; DeYoung *et al.*, 2010; Kunisato *et al.*, 2011; Lu *et al.*, 2014a; Servaas *et al.*, 2014). Recently, using voxel-based morphometry (VBM), anxiety symptoms is found to be correlated with regional gray matter volume (rGMV) in the PHG (Wei *et al.*, 2014), and perceived stress is correlated with rGMV in the PHG and insular cortex (Li *et al.*, 2014a). Among the constructs positively related to life satisfaction, eudaimonic well-being is reported to associated with rGMV in the insula (Lewis *et al.*, 2014) and the activation of the ventromedial

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prefrontal cortex (VMPFC) in response to negative stimuli and dorsal LPFC in response to positive stimuli (van Reekum *et al.*, 2007; Heller *et al.*, 2013). Using VBM, better physical health, which is moderately associated with life satisfaction (Abdel-Khalek, 2010), is found to be associated with smaller rGMV in the rostral LPFC (Takeuchi *et al.*, 2014a) and the amygdala (Song *et al.*, 2014), whereas psychological health, which is moderately associated with life satisfaction (Abdel-Khalek, 2010), is associated with smaller rGMV in the ACC (Takeuchi *et al.*, 2014a). On the basis of these studies, we speculated that structural differences in these regions may be associated with life satisfaction.

After reviewing the literature on life satisfaction, among the constructs, self-esteem has been demonstrated to be a strong correlate of life satisfaction in many studies. For example, Campbell (1981) found self-esteem was the strongest predictor of life satisfaction (with a correlation of 0.55) in a national sample of American adults. Neto (1993) further confirmed that self-esteem was the strongest predictor of life satisfaction in adolescents. Subsequently, Diener and Diener (1995) found a correlation of 0.47 between these two variables in college student samples from 31 countries (see also Kwan *et al.* 1997; Kong *et al.*, 2012a; Kong and You, 2013). Recently, a cross-lagged study further revealed that self-esteem predicted life satisfaction 8 months later, whereas the effect of life satisfaction on subsequent self-esteem was not found (Ye *et al.*, 2012), suggesting that self-esteem plays a causal role in life satisfaction. This causal relationship can be explained by the bottom-up theories of subjective well-being. The theories propose that life satisfaction judgment is based on an assessment of satisfaction in a relatively small number of life domains such as family, friends and oneself (Brief *et al.*, 1993; Schimmack, 2002; Heller *et al.*, 2004) and thus the correlation between life satisfaction and domain satisfaction reflects a causal influence of domain satisfaction on life satisfaction. According to Diener and Diener (1995), self-esteem reflects one's judgment and evaluation of oneself, while life satisfaction involves evaluations of one's life as a whole. From the life satisfaction perspective, self-esteem is considered as a component of life satisfaction, which involves evaluations of different life domains such as family and oneself (Huebner *et al.*, 1999). Taken together, self-esteem likely plays a causal role in life satisfaction. Thus, another important goal of this study was to test whether individual differences in self-esteem may account for the association between brain structure and life satisfaction.

To probe these questions, we used well-validated assessments of life satisfaction and self-esteem, and VBM methodology, which can be used to explore the structural neural correlates of interindividual differences in behavior (e.g. those related to stable personality characteristics) (Kanai and Rees, 2011; Takeuchi *et al.*, 2011, 2014a; Kong, *et al.*, 2014c; Lewis *et al.*, 2014). Specifically, we measured participants' levels of life satisfaction using the Satisfaction with Life Scale (SWLS, Diener *et al.*, 1985), which has been widely used to assess individual differences in life satisfaction in previous studies (e.g. Neto, 1993; Ring *et al.*, 2007; Kong *et al.*, 2012a,b; Kong and You, 2013). On the basis of previous neuroscience findings on constructs related to life satisfaction (e.g. Urry *et al.*, 2004; van Reekum *et al.*, 2007; Heller *et al.*, 2013; Lewis *et al.*, 2014; Takeuchi *et al.*, 2014a), we hypothesized that individual differences in life satisfaction would be associated with rGMV of the prefrontal (i.e. DMPFC, VMPFC and LPFC), ACC, the precuneus, PHG, amygdala, hippocampus and insula. Furthermore, given the important role of self-esteem in life satisfaction (Campbell, 1981; Neto, 1993; Diener and Diener, 1995; Kwan *et al.* 1997; Kong *et al.*, 2012a; Ye *et al.*, 2012; Kong and You, 2013), we further examined whether self-esteem would be able to mediate the relationship between brain structures and life satisfaction.

METHODS

Participants

Two hundred and ninety-nine college students [159 females; mean age = 21.55 years, standard deviation (s.d.) = 1.01] participated in this study as a part of an ongoing project investigating associations among brain imaging, cognitive functions and genetics (Wang *et al.*, 2012; Huang *et al.*, 2014; Kong *et al.*, 2014c; Li *et al.*, 2014b; Lu *et al.*, 2014b; Song *et al.*, 2014). Data that are irrelevant to the scope of this study were not reported here. All participants were college students from Beijing Normal University, Beijing, China. Participants were screened to confirm their healthy development by a self-report questionnaire before the study, and thus, those who had past or current psychiatric illness or a history of neurological illness were excluded. The majority of the participants were right-handed ($n = 280$) based on a single-item handedness questionnaire ('Are you (a) right-handed, (b) left-handed, (c) mixed-handed?'). Both behavioral and MRI protocols were approved by the Institutional Review Board of Beijing Normal University. Written informed consent was obtained from all participants prior to study onset.

Assessment of global life satisfaction

The SWLS (Diener *et al.*, 1985) was administered to assess global life satisfaction, which is the cognitive component of subjective well-being. The SWLS reflects global cognitive evaluations of one's life, rather than summing across their satisfaction with specific domains (e.g. family, friends, school, self and living environment), for obtaining an index of overall life satisfaction. In their review of the SWLS, Pavot and Diener (1993) concluded that it is a one-dimensional, internally consistent measure. The SWLS has also high criterion-related validity with related constructs of optimism, loneliness, positive affect, negative affect, self-esteem, self-concept, anxiety and depression (Diener *et al.*, 1985; Neto, 1993; Kong *et al.*, 2012a, b; Kong and You, 2013; Kong and Zhao, 2013). The scale consists of five statements, such as, 'I am satisfied with my life' and 'In most ways my life is close to my ideal'. Participants were instructed to indicate the extent to which they agree or disagree with each statement using a 5-point Likert scale. Higher scores reflect higher levels of global life satisfaction. The Chinese version of the SWLS has been demonstrated to be a reliable and valid measurement in assessing life satisfaction in Chinese adults (e.g. Kong *et al.*, 2012a,b, 2014a; Kong and You, 2013; Kong and Zhao, 2013). In this study, the SWLS exhibited adequate reliability ($\alpha = 0.82$).

Assessment of self-esteem

Self-esteem was measured by the Rosenberg Self-esteem Scale (RSES; Rosenberg, 1965), which is a 10-item self-report measure of global self-esteem. Each item is answered on a 6-point Likert type scale ranging from 1 = strongly disagree to 6 = strongly agree. It includes items such as, 'I am able to do things as well as most other people' and 'I take a positive attitude toward myself'. Scale scores are the sum of items with reverse coding of relevant items. A meta-analysis of the scale by Schmitt and Allik (2005) found that the scale was a very popular test whose validity and reliability tests are used in 53 countries. The RSES has also high criterion-related validity with related constructs of extraversion, neuroticism, social support, positive affect, negative affect, life satisfaction, loneliness and depression (Rice *et al.*, 1998; Schmitt and Allik, 2005; Çivitci and Çivitci, 2009; Kong *et al.*, 2012b; Kong and You, 2013; Zhao *et al.*, 2012, 2013). The Chinese version of the RSES has been found to be a reliable and valid measurement in assessing self-esteem in Chinese populations (Kong *et al.*, 2012b; Zhao *et al.*, 2012; Kong and You, 2013). In the study, the SWLS exhibited adequate reliability ($\alpha = 0.89$).

Assessment of positive and negative affect

The affective component of subjective well-being was assessed by a general version of the Positive and Negative Affect Schedule (PANAS-Gen; Watson *et al.*, 1988). The PANAS-Gen consists of a word list describing two different affect states (10 positive and 10 negative), for example, 'excited' and 'upset'. Participants are instructed to indicate the extent to which they generally feel each affect using a 5-point Likert scale. Positive and negative affect scores are calculated separately, with higher scores indicating that participants feel more of that affect. The scale has high internal consistency, test-retest reliability and criterion-related validity with related constructs of extraversion, neuroticism, anxiety, depression, hope, stress and life satisfaction (Watson *et al.*, 1988; Lucas *et al.*, 1996; Crawford and Henry, 2004; Steel *et al.*, 2008; Kong and Zhao, 2013). The Chinese version of the scale has been demonstrated to be a reliable and valid measurement in assessing positive and negative affect in Chinese population (e.g. Kang *et al.*, 2003; Kong and Zhao, 2013; Sun and Kong, 2013). In this study, the positive affect scale ($\alpha = 0.81$) and negative affect scale ($\alpha = 0.78$) exhibited adequate reliability.

MRI acquisition

Participants were scanned using a Siemens 3T scanner (MAGENTOM Trio, a Tim system) with a 12-channel phased-array head coil at BNU Imaging Center for Brain Research, Beijing, China. MRI structural images were acquired using a 3D magnetization prepared rapid gradient echo T1-weighted sequence (TR/TE/TI = 2530/3.39/1100 ms, flip angle = 7°, FOV = 256 × 256 mm²). One hundred and twenty-eight contiguous sagittal slices were acquired with 1 × 1 mm² in-plane resolution and 1.33-mm slab thickness for whole brain coverage.

Image processing for VBM

VBM was performed using SPM8 (Statistical Parametric Mapping, Wellcome Department of Imaging Neuroscience, London, UK), with an optimized VBM protocol on T1-weighted structural MRI images. First, image quality was assessed by manual visual inspection. Six participants whose images had excessive scanner artifacts or showed gross anatomical abnormalities were excluded. Second, the origin of the brain was manually set to the anterior commissure for each participant. Third, images were segmented into gray matter, white matter and cerebrospinal fluid using the unified segmentation approach (Ashburner and Friston, 2005). Fourth, gray matter images were rigidly aligned and resampled to 2 × 2 × 2 mm³ and normalized to a study-specific template in MNI152 space using the Diffeomorphic Anatomical Registration through Exponential Lie algebra registration method (Ashburner, 2007). Fifth, gray matter voxel values were modulated by multiplying the Jacobian determinants derived from the normalization to preserve the volume of tissue from each structure after warping. The modulated gray matter images were then smoothed with an 8-mm full-width-at-half-maximum isotropic Gaussian kernel.

Statistical analysis of VBM

Statistical analyses of the gray matter volume (GMV) data were performed using SPM8. In the whole-brain analyses, we used a multiple linear regression analysis to detect the neuroanatomical correlates of individual differences in life satisfaction. In the analysis, the self-reported life satisfaction score was used as the covariate of interest and age, sex and total GMV were as the confounding covariates. To exclude boundary effects between gray matter and white matter, an absolute threshold masking of 0.2 was used. For all analyses, the cluster-level statistical threshold was set at $P < 0.05$, and corrected at the non-stationary cluster correction (Hayasaka *et al.*, 2004) according to the random field theory with an underlying voxel level of $P < 0.0025$.

In this test, a relatively higher cluster-determining threshold combined with high smoothing values of more than six voxels has been found to lead to appropriate conservativeness in real data (Silver *et al.*, 2011). With high smoothing values, an uncorrected threshold of $P < 0.01$ appears to bring about anticonservativeness, whereas that of $P < 0.001$ appears to result in slight conservativeness (Silver *et al.*, 2011).

Furthermore, small-volume corrections (SVCs) were performed in regions with a priori hypothesis. The regions of interest (ROIs) were chosen from previous structural and functional imaging studies that might play an important role in life satisfaction. The Wake Forest University Pick Atlas (Maldjian *et al.*, 2003) was used to define the regions of the ACC, VMPFC, DMPFC, dorsal and rostral LPFC, hippocampus, parahippocampus, amygdala and insula, based on the automated anatomical labeling template. The significance of correlation coefficients between life satisfaction and the rGMV of these ROIs were examined at a corrected threshold of $P < 0.05$, using the non-stationary cluster correction for multiple comparisons.

Mediation analysis

To test whether self-esteem can reliably explain the relationships between brain anatomy and life satisfaction, we conducted a mediation analysis, using the SPSS macro programmed by Preacher and Hayes (2008). It is based on a three-variable mediation model that investigates whether a predictor variable (X , brain anatomy) affects an outcome variable (Y , life satisfaction) through a mediator (M , self-esteem). Variable M is a mediator if X significantly predicts M (Path a), X significantly predicts in Y (Path c; representing the total effect), M significantly predicts in Y (Path b) when controlling for X , and the effect of X on Y reduces significantly when M as well as X simultaneously predicts Y (Path c'; representing the direct effect). In order to test statistical significance of the indirect effect through M , bootstrapping tests were used (Preacher and Hayes, 2008). We used 10 000 bootstrap samples to generate bootstrap confidence intervals (99%) for the indirect effects. An empirical 99% confidence interval do not include 0, signifying that the indirect effect is significant at the 0.01 level.

RESULTS

VBM of life satisfaction

Table 1 lists the characteristics of demographics of the total sample. Behaviorally, we replicated the previous finding that life satisfaction is moderately positively correlated with positive affect ($r = 0.28$, $P < 0.001$, in our dataset), and negatively with negative affect ($r = -0.26$, $P < 0.001$, in our dataset), suggesting that these components of subjective well-being are related but distinct constructs. Neurally, in whole-brain analysis, multiple regression analysis revealed that life satisfaction was significantly and negatively correlated with GMV in an anatomical cluster that primarily included the left precuneus (MNI coordinate: -8, -62, 22; $t = 4.66$; Cluster size = 13 712; $P < 0.05$) (Figure 1; Table 2).

SVC analysis revealed a significant negative correlation between life satisfaction and rGMV in an anatomical cluster that mainly included the left VMPFC (MNI coordinate: -4, 50, -18; $t = 3.86$; Cluster size = 952; $P < 0.05$) (Figure 2; Table 2). A significant positive correlation between life satisfaction and rGMV was also identified in an anatomical cluster that included the right PHG (MNI coordinate: 36, -18, -24; $t = 3.46$; Cluster size = 728; $P < 0.05$) (Figure 3; Table 2). No significant relationships were observed in the ACC, DMPFC, dorsal and rostral LPFC, hippocampus, amygdala and insula. Because of the problem of multiple comparisons across nine ROIs, Bonferroni corrections were made to reduce the risk of Type I errors. We extracted

the rGMV of the three aforementioned clusters from MRI scans of the participants and performed a correlation analysis between rGMV and life satisfaction. The results revealed that life satisfaction was negatively correlated with rGMV in the left precuneus ($r = -0.32$; $P < 0.001$, Bonferroni corrected) and left VMPFC ($r = -0.22$, $P = 0.001$, Bonferroni corrected), and positively with the rGMV in the right PHG ($r = 0.21$, $P = 0.004$, Bonferroni corrected).

To examine whether these results are specific to life satisfaction, we also excluded a confounding factor of the affective component of subjective well-being (i.e. positive and negative affect). An additional model examining the association of life satisfaction with rGMV was tested with age, sex, global GMV and positive and negative affect as covariates. All correlations remained significant after age, sex, global GMV and positive and negative affect had been controlled (Left precuneus: MNI coordinate: $-8, -62, 22$; $t = 5.22$; Cluster size = 8699; $P < 0.05$; right PHG: MNI coordinate: $26, -28, -16$; $t = 3.51$; Cluster size = 1304; $P < 0.05$; Left VMPFC: MNI coordinate: $-2, 64, -8$; $t = 3.48$; Cluster size = 920; $P < 0.05$). Although there were small variations in cluster size, significant regions were identical to those identified in initial analyses.

Brain structures mediated the relationship between self-esteem and life satisfaction

To test our hypothesis about the relationships between self-esteem, life satisfaction and brain structure, we collected the RSES measure from a

Table 1 Demographic and psychometric measures ($n = 293$)

Variables	Mean	s.d.	Range	<i>r</i>
Sex	–	–	–	0.25**
Age	21.56	1.01	18–25	–0.06
Total GMV	0.49	0.04	0.39–0.60	–0.16*
Positive affect	34.15	4.78	20–48	0.28**
Negative affect	24.40	4.69	12–40	–0.26**
Life satisfaction	20.03	5.34	6–35	1

Total GMV, Total gray matter volume. *r*, Pearson bivariate correlations with life satisfaction. * $P < 0.01$. ** $P < 0.001$.

subset ($n = 274$) of the participants studied in previous analysis and first performed a correlation analysis between self-esteem and life satisfaction. We replicated the previous finding that self-esteem has a strong correlation with life satisfaction ($r = 0.45$, $P < 0.001$, in our dataset). Next, we examined whether the rGMV of the regions related to life satisfaction could predict individual differences in self-esteem. The results showed that the rGMV in the right PHG ($r = 0.23$, $P < 0.001$, Bonferroni corrected) and left precuneus ($r = -0.19$, $P = 0.003$, Bonferroni corrected) was significantly correlated with self-esteem, even after adjusted for age, sex and total GMV. Furthermore, after age, sex, global GMV and positive and negative affect had been controlled, all correlations remained significant (right PHG: $r = 0.24$, $P < 0.001$, Bonferroni corrected; Left precuneus: $r = -0.16$, $P = 0.021$, Bonferroni corrected).

The results above indicated that self-esteem, life satisfaction and brain structure were linked closely to one another, but the exact relationships among these variables remain unknown. Here, we further performed two mediation analyses to examine whether self-esteem is able to mediate the relationship between brain structure and life satisfaction. Age, sex and total GMV were used as covariates in the mediational model. The results showed that the effect of the PHG volume on life satisfaction was not significant ($\beta = 0.12$, $P > 0.05$) after self-esteem was added as a mediator in the model. In contrast, the direct relationship was significant ($\beta = 0.25$, $P = 0.001$). Bootstrap simulation ($n = 10\,000$) further confirmed that the indirect effect through self-esteem was significant (99% confidence interval = $[0.26, 1.25]$, $P < 0.01$). Thus, self-esteem partially mediated the association between the PHG volume and life satisfaction (see Figure 4).

Same procedure was also implemented for the mediating effect of the precuneus. The results showed that the effect of the precuneus volume on life satisfaction reduced, though still significant ($\beta = -0.41$, $P < 0.001$) after self-esteem was added as a mediator in the model. In contrast, the direct relationship was significant ($\beta = -0.54$, $P < 0.001$). Bootstrap simulation ($n = 10\,000$) further confirmed that the indirect effect through self-esteem was significant (99% confidence interval = $[-1.47, -0.21]$, $P < 0.01$). Thus, self-esteem partially mediated the association between the precuneus volume and life satisfaction (see Figure 5).

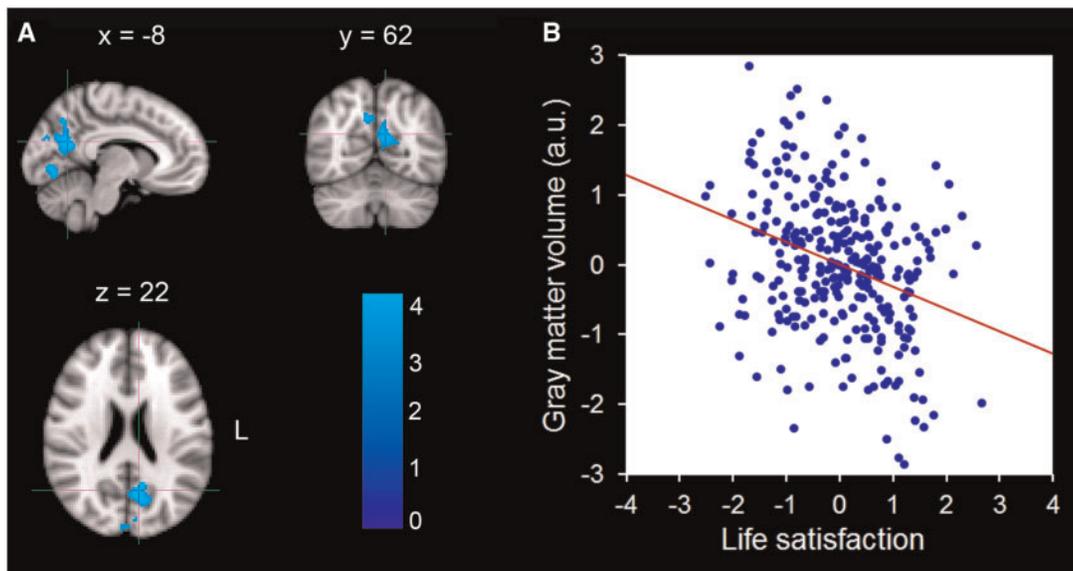


Fig. 1 Brain regions that negatively correlated with life satisfaction. (A) The rGMV of the left precuneus was negatively correlated with life satisfaction. The coordinate is shown in the MNI stereotactic space. (B) Scatter plots depicting correlations between rGMV of the precuneus and individual variability in life satisfaction ($r = -0.32$, $P < 0.001$).

DISCUSSION

The aim of this study was to investigate the structural neural correlates of global life satisfaction in a large sample of young healthy adults. Behavioral results showed that life satisfaction was positively correlated with self-esteem, which is consistent with previous studies (Campbell, 1981; Neto, 1993; Diener and Diener, 1995; Kwan *et al.*, 1997; Kong *et al.*, 2012a; Ye *et al.*, 2012; Kong and You, 2013). The VBM analysis revealed that individuals' life satisfaction was positively correlated with the rGMV in the right PHG, and negatively correlated with the rGMV in the left VMPFC and left precuneus. Furthermore, mediation analyses indicated that self-esteem mediated the association between the rGMV in the precuneus and PHG and life satisfaction. Taken together, our study provides the first evidence on the structural neural basis of life satisfaction, and highlight that self-esteem may play a crucial role in cultivating an individual's life satisfaction.

In accordance with our expectation, our study revealed a significant negative correlation between life satisfaction and the rGMV in the left precuneus. The negative association between life satisfaction and regional structures is not surprising, because recent studies have often observed negative correlations between a range of cognitive functions (e.g. emotional intelligence) and the rGMV of brain regions (e.g. the medial prefrontal cortex) (Takeuchi *et al.*, 2011, 2014a; for a review, see Kanai and Rees, 2011). The negative relationships are believed to be relevant to the intracortical myelination and synaptic pruning during

development (Huttenlocher *et al.*, 1982; Sowell *et al.*, 2001; Paus, 2005). Previous studies have shown that the precuneus is involved in the controlling and switching of attention among objects and object features (Barber and Carter, 2005; Cavanna and Trimble, 2006). Furthermore, the region is also reported to play a central role in a range of highly integrated tasks, including visuo-spatial imagery (Knauff *et al.*, 2002; Simon *et al.*, 2002; Vanlierde *et al.*, 2003; for a review, see Cavanna and Trimble, 2006), episodic memory retrieval (Wiggs *et al.*, 1998; Lundstrom *et al.*, 2003, 2005; Wagner *et al.*, 2005) and self-processing operations such as self-consciousness, autobiographical memory, sense of agency and self-reflection (Kircher *et al.*, 2002; Lou *et al.*, 2004; Vogeley *et al.*, 2004; Den Ouden *et al.*, 2005; Freton *et al.*, 2014; for a review, see Cavanna and Trimble, 2006), all of which seems consistent with the notion that the precuneus plays a central role in the modulation of conscious processes (Cavanna and Trimble, 2006; Cavanna, 2007). Precuneus dysfunction has been linked with sleep, vegetative state, drug-induced anesthesia and neuropsychiatric disorders including epilepsy, Alzheimer's disease and schizophrenia characterized by impaired consciousness (Vogt and Laureys, 2005; Cavanna, 2007). Thus, pruning of ineffective synapses during development may lead to less regional gray matter in the region, and increases in efficiency of conscious processes, both of which help individuals retrieve a positive self-image from positive episodic/autobiographical memories and lead to higher levels of life satisfaction.

We also revealed a significant negative correlation between life satisfaction and the rGMV in the left VMPFC. Previous studies have shown suggested that the VMPFC encodes the value of external rewards from various modalities including juice (Kim *et al.*, 2011), faces (Smith *et al.*, 2010; Lin *et al.*, 2012) and non-monetary goods such as snack foods (Chib *et al.*, 2009) and the affective value of emotional stimuli (Wincoff *et al.*, 2013). Furthermore, the region is also shown to play an important role in emotional regulation, emotional perspective taking, sympathy, social decision making and collaborative attention and goals (Mitchell *et al.*, 2005; Amodio and Frith, 2006; Saxe *et al.*, 2006; Etkin *et al.*, 2011; Rilling and Sanfey, 2011; Takeuchi *et al.*, 2014b), which has immense value for social behavior and well-being. VMPFC dysfunction has been associated with psychopathy (Motzkin *et al.*, 2011), depression (Brassen *et al.*, 2008), schizophrenia (Park *et al.*, 2008) and generalized social anxiety disorder (Evans *et al.*, 2008). Thus, the highly developed

Table 2 Brain structures correlating with life satisfaction

Region	Side	MNI coordinate			<i>T</i>	Cluster size (mm ³)
		<i>x</i>	<i>y</i>	<i>z</i>		
<i>Positive correlation</i>						
PHG	R	36	-16	-24	3.36	728*
<i>Negative correlation</i>						
Precuneus	L	-8	-62	22	4.66	13 712*
VMPFC	L	-4	54	-14	3.58	952*

MNI = Montreal Neurological Institute; L = left; R = right. All *z*-scores reflect a VBM threshold of $P < 0.0025$ (uncorrected). * $P < 0.05$ corrected at the non-stationary cluster level.

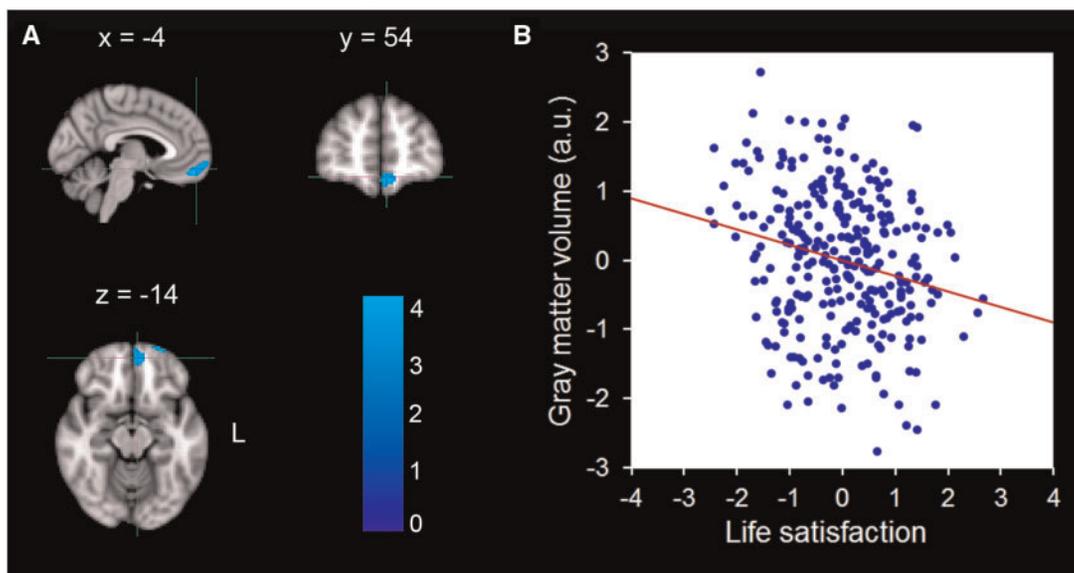


Fig. 2 Brain regions that negatively correlated with life satisfaction. (A) The rGMV of the left VMPFC was negatively correlated with life satisfaction. The coordinate is shown in the MNI stereotactic space. (B) Scatter plots depicting correlations between rGMV of the VMPFC and individual variability in life satisfaction ($r = -0.22$, $P < 0.001$).

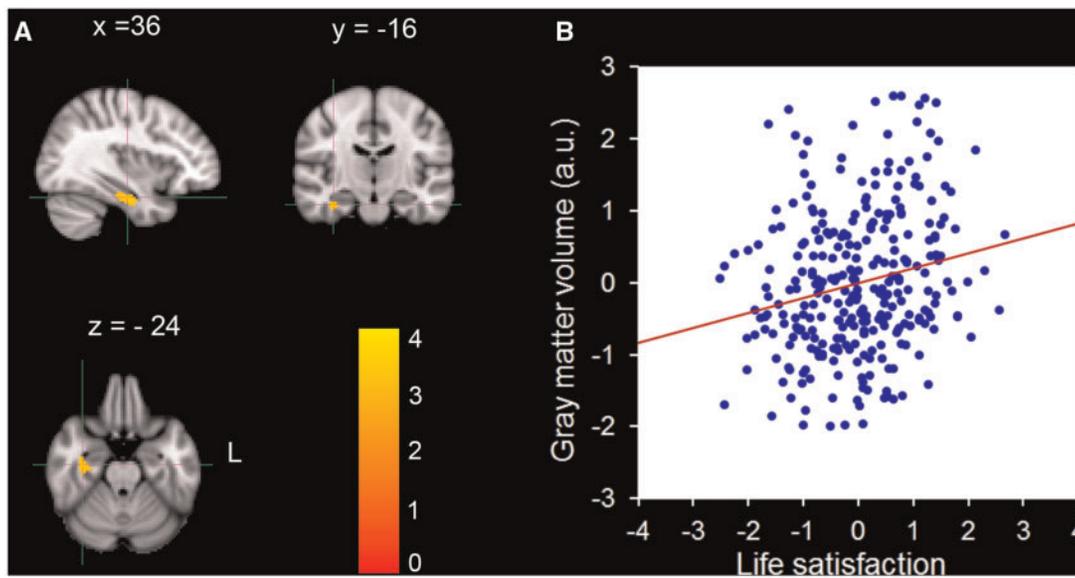


Fig. 3 Brain regions that positively correlated with life satisfaction. (A) The rGMV of the right PHG was positively correlated with life satisfaction. The coordinate is shown in the MNI stereotactic space. (B) Scatter plots depicting correlations between rGMV of the right PHG and individual variability in life satisfaction ($r = 0.21, P < 0.001$).

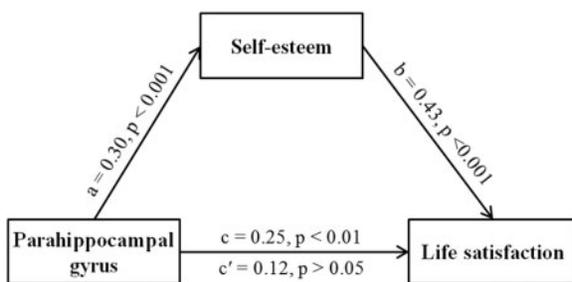


Fig. 4 The PHG mediates the impact of self-esteem on life satisfaction. Depicted is the path diagram (including standard regression coefficients) of the mediation analysis demonstrating that the rGMV of the PHG affects individuals' life satisfaction through self-esteem. All four requirements for a mediation effect are satisfied: Paths a–c are significant, and path c' is significantly smaller than path c.

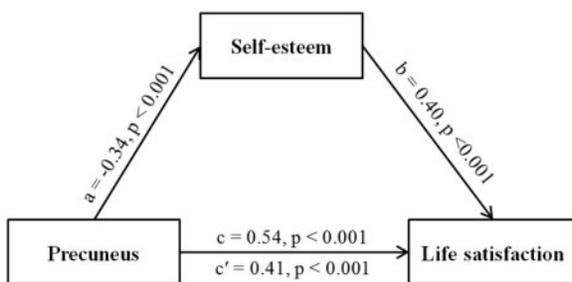


Fig. 5 The precuneus mediates the impact of self-esteem on life satisfaction. Depicted is the path diagram (including standard regression coefficients) of the mediation analysis demonstrating that the rGMV of the precuneus affects individuals' life satisfaction through self-esteem. All four requirements for a mediation effect are satisfied: Paths a–c are significant, and path c' is significantly smaller than path c.

VMPFC might help individuals to regulate emotional reactions jeopardizing valued relationships, sympathize with others' experience and value long-term benefits associated with cooperative relationships, thus leading to higher levels of life satisfaction.

Furthermore, we revealed that the rGMV in the right PHG was positively associated with individuals' life satisfaction, suggesting that the function of this structure contributes to life satisfaction. The PHG

has been involved in perceptual processing, encoding and retrieval of scenes and places (Epstein *et al.*, 1999; Hayes *et al.*, 2007; Epstein, 2008; Rudy, 2009), emotional memory encoding and retrieval (Alkire *et al.*, 1998; LaBar and Cabeza, 2006; Sterpenich *et al.*, 2006; Murty *et al.*, 2010) and emotional perceptual decision making (Pessoa and Padmala, 2005). This cortical region also plays an important role in stress regulation (Ulrich-Lai and Herman, 2009), and pain and stress perception (Cheng *et al.*, 2007; Li *et al.*, 2014a). PHG dysfunction has been linked with post-traumatic stress disorders (Etkin and Wager, 2007; Werner *et al.*, 2009; Meng *et al.*, 2014), anxiety disorders (Etkin and Wager, 2007; Goldin *et al.*, 2009) and schizophrenia (Gradin *et al.*, 2011). Therefore, higher levels of life satisfaction might be associated with larger rGMV in the right PHG through an array of capacities such as better emotional memory, more faithful pain/stress perception and improved stress regulation.

Interestingly, we found that self-esteem mediated the effect of the PHG volume on life satisfaction. The finding highlights that the PHG might play a crucial role in self-esteem, consistent with studies previously reporting the associations between measures related to self-esteem and hippocampal formation including the PHG and hippocampus (Pruessner *et al.*, 2005; Onoda *et al.*, 2010; Kubarych *et al.*, 2012; Miyamoto and Kikuchi *et al.*, 2012; Egenolf *et al.*, 2013; Frewen *et al.*, 2013). For example, individuals with low self-esteem showed greater activation in the PHG in response to social exclusion, relative to those with high self-esteem (Onoda *et al.*, 2010). Low self-esteem has been found to be associated with greater amounts of perceived daily hassles and chronic stressors (Abouserie 1994; Lo, 2002), and associated with high cortisol responses to stress (Kirschbaum *et al.*, 1995; Pruessner *et al.*, 2005) and cardiovascular and inflammatory responses (O'Donnell *et al.*, 2008). Furthermore, the hippocampus/PHG is also reported to be associated with cortisol responses to stress (Pruessner *et al.*, 2005; Cunningham-Bussel *et al.*, 2009; Root *et al.*, 2009) and cardiovascular responses (Critchley *et al.*, 2000). Therefore, given the role of the PHG in emotional memory (Alkire *et al.*, 1998; LaBar and Cabeza, 2006; Sterpenich *et al.*, 2006; Murty *et al.*, 2010), stress regulation (Ulrich-Lai and Herman, 2009) and pain and stress perception (Cheng *et al.*, 2007; Li *et al.*, 2014a), it is not surprising that the PHG engagement can lead to higher levels of life satisfaction through striving for high self-esteem as a buffer for stressful life events.

We also found that self-esteem supported the association between the precuneus volume and life satisfaction. Numerous studies have demonstrated that the precuneus/posterior cingulate cortex is a central part of the default mode network (DMN; Fox *et al.*, 2005; Fransson, 2005; Buckner *et al.* 2008; Fransson and Marrelec, 2008) and it serves as a functional core of the DMN (Utevsky *et al.*, 2014). The DMN that consists of the precuneus/posterior cingulate cortex, medial prefrontal cortex, medial temporal lobe and posterior lateral cortices has been shown to be involved in self-referential processes such as conscious awareness of the internal and external environment (Buckner *et al.* 2008). These self-referential processes are believed to form the core of our self and are critical for elaborating experiential feelings of self (Northoff *et al.*, 2006). Previous neuroimaging studies have demonstrated the importance of the precuneus in self-esteem (Onoda *et al.*, 2010; Rameson *et al.*, 2010; Eisenberger *et al.*, 2011; Miyamoto and Kikuchi *et al.*, 2012; Oikawa *et al.*, 2012). In particular, self-esteem is found to be positively associated with the activity of the precuneus in the processing of positive self-face evaluation (Oikawa *et al.*, 2012). Therefore, the highly developed precuneus seems to facilitate the cognition of self-referential processes, and thus help individuals get high positive self-evaluations (i.e. high self-esteem) from positive episodic/ autobiographical memories, which in turn increases levels of life satisfaction.

In conclusion, we employed the VBM approach to investigate the structural neural correlates of individual differences in life satisfaction. We found that rGMV of the right PHG, left MPFC and left precuneus was related to life satisfaction. These findings were maintained even after controlling for individual differences on measures of positive and negative affect. As such, this research demonstrated a unique structural basis for individual differences in life satisfaction. Moreover, we also substantiated that self-esteem acted as a potential mechanism that accounted for the association between right PHG volume and life satisfaction as well as that between right precuneus volume and life satisfaction. The present findings seem to provide valuable guidance for how to implement psychological (self-esteem intervention) or neural-based interventions (e.g. neurofeedback training) aimed at enhancing an individual's life satisfaction. Despite these strengths in our study, this sample was drawn from a college student population. The narrow age range may limit the generalizability of our findings, although it is common to choose college students as participants (Takeuchi, *et al.*, 2011, 2014a; Kong *et al.*, 2014c; Li *et al.*, 2014a; Lewis *et al.*, 2014; Song *et al.*, 2014). In addition, we cannot determine the direction of causation between self-esteem, life satisfaction and brain structure. The implementation of longitudinal or experimental studies will help to elucidate these complex relationships in the future.

Conflict of Interest

None declared.

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