Individual differences in posterior cortical volume correlate with proneness to pride and gratitude

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Proneness to specific moral sentiments (e.g., pride, gratitude, guilt, indignation) has been linked with individual variations in functional MRI (fMRI) response within anterior brain regions whose lesion leads to inappropriate behavior. However, the role of structural anatomical differences in rendering individuals prone to particular moral sentiments relative to others is unknown. Here, we investigated grey matter volumes (VBM8) and proneness to specific moral sentiments on a well-controlled experimental task in healthy individuals. Individuals with smaller cuneus, and precuneus volumes were more pride-prone, whereas those with larger right inferior temporal volumes experienced gratitude more readily. Although the primary analysis detected no associations with guilt- or indignation-proneness, subgenual cingulate fMRI responses to guilt were negatively correlated with grey matter volumes in the left superior temporal sulcus and anterior dorsolateral prefrontal cortices (right > left). This shows that individual variations in functional activations within critical areas for moral sentiments were not due to grey matter volume differences in the same areas. Grey matter volume differences between healthy individuals may nevertheless play an important role by affecting posterior cortical brain systems that are non-critical but supportive for the experience of specific moral sentiments. This may be of particular relevance when their experience depends on visuo-spatial elaboration.

Keywords: social cognition; emotion; neuroanatomy; individual differences; moral emotion

INTRODUCTION

Individuals differ in their proneness to experience moral emotions that are associated with blaming (guilt, indignation) or praising (pride, gratitude) themselves or others (Zahn et al., 2009b). We will refer to moral emotions as sentiments following philosophers of the Scottish enlightenment who pointed to their role as key motivators of moral behaviour (Bishop, 1996). As internalized motivations they play an important role in explaining the human ability to act cooperatively independently of external reward and punishment. Human cooperation is increasingly recognized as a factor that may carry evolutionary fitness advantages by enhancing group survival (Gintis et al., 2008). Brain structure variations are strongly influenced by hereditary factors (Schmitt et al., 2008; Kremen et al., 2010) and are therefore likely to be directly shaped by evolutionary selection pressures. The question whether individual differences in brain structure and variations in proneness to specific types of moral sentiments are related is therefore crucial for understanding the mechanisms through which evolution and individual brain development may have shaped our moral abilities.

Functional MRI (fMRI) in healthy participants has recently been used to identify neurocognitive components of specific moral sentiments (Moll et al., 2007) and individual differences in functional activation emerged (Zahn et al., 2009a, b). These individual difference effects were reproducible for guilt which was associated with septal/subgenual cingulate (SSC) regional blood-oxygenation-level-dependent effect (BOLD) (Zahn et al., 2009a, b; Basile et al., 2011) and functional coupling increases (Green et al., 2010). This finding concurs with patient lesion studies. Loss of guilt was reported by carers of patients with ventromedial (PFC) lesions (Koenigs et al., 2007) and neurodegeneration in this area, which included the subgenual cingulate cortex, was associated with loss of interpersonal warmth (Sollberger et al., 2009). Ventral PFC lesions have been proposed to cause changes in moral character since the 19th century (Welt, 1888) and this association has been directly shown since the advent of CT brain imaging (Eslinger and Damasio, 1985). Recently, septal neurodegeneration was selectively associated with loss of experimentally probed guilt and pity, but not disgust, anger or embarrassment (Moll et al., 2011). However, individual differences on fMRI activation patterns in these regions may reflect state rather than trait markers of neurocognitive architecture.

Regional grey matter (GM) structure on the other hand was shown to be determined to a large degree by genetic factors. When comparing mono- and dizygotic twins, differences in regional GM structure depended to around 50% on genetic factors with regional variation (Schmitt et al., 2008; Kremen et al., 2010). Interestingly, part of the remaining environmental variance in regional GM volume may be accounted for by learning (Draganski et al., 2004; Mechelli et al., 2005) and remained stable in regions that were not specifically required for an intensely trained task used in one study (Draganski et al., 2004). There is growing evidence for individual differences in regional GM to be associated with differences in emotional styles using different measures (Benetti et al., 2010; Giuliani et al., 2011; Hartley et al., 2011; Kuhn et al., 2011; Takeuchi et al., 2011). To our knowledge, the relationship of variation between healthy individuals on proneness to respond with specific moral feelings and individual differences in structural neuroanatomy has not been investigated so far. This question is of particular importance for understanding whether individual variation in proneness to moral sentiments is solely related to functional anatomical differences or whether those functional anatomical differences are strongly influenced by brain structural variability.

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Proneness to moral sentiments

Here, we used a recently refined voxel-based observer-independent method that uses high dimensional warping for spatial registration, Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra (DARTEL) (Ashburner, 2007), to investigate GM volume variations in healthy participants and a novel experimental task to probe proneness to specific moral sentiments with carefully controlled stimulus material (Zahn et al., 2009b).

As described above, there is evidence that individual variations in proneness to specific moral sentiments are associated with individual differences in brain functional measures in regions known to be necessary for moral functioning from patient lesion studies. Based on these findings, we derived the following hypotheses for our investigation of structural variations: (1) there are associations of brain structural variations and individual differences in proneness to specific moral sentiments in healthy people. We further aimed to determine whether these structural variations occur (a) predominantly in brain regions not necessary for moral sentiments, because these may modulate proneness to specific moral sentiments without affecting moral faculties to a degree that would hamper psychosocial functioning, or (b) in brain regions necessary for these specific types of moral sentiments, because high psychosocial functioning could be achieved in different social niches with a relatively wide variation of proneness to specific moral sentiments.

Favouring hypothesis 1(b), we made the following specific predictions: based on evidence from patient lesion studies (Moll et al., 2011) and fMRI (Takahashi et al., 2004; Moll et al., 2007; Kedia et al., 2008; Zahn et al., 2009b), we hypothesized associations of frontopolar GM volume with guilt-proneness. Based on recent studies, we further expected the importance of subgenual parts of the anterior cingulate (Zahn et al., 2009a, b) and the septal region (Zahn et al., 2009b; Moll et al., 2011) for individual variation on guilt-proneness. In contrast, we expected lateral orbitofrontal/insular areas to be associated with indignation-proneness based on an fMRI study directly probing indignation (Zahn et al., 2009b), a study in which this region showed activation for decisions based on moral anger (Moll et al., 2006), and evidence that a lateral orbitofrontal region was selectively more activated for other-critical feelings (anger and disgust) vs prosocial moral feelings including guilt (Moll et al., 2007). Our hypotheses for pride- and gratitude-proneness were less well supported due to a relative scarcity of evidence. Our main expectations were that pride-proneness and gratitude-proneness should be related to differences within mesolimbic and basal forebrain areas, specifically the hypothalamus, ventral tegmental area (VTA) and septal area (Zahn et al., 2009b).

Half of the investigated sample had previously taken part in our fMRI study of individual differences in value-related moral sentiments (Zahn et al., 2009b). This allowed us to examine whether previously reported individual differences in functional activations were associated with GM volume differences. Greys matter volume differences are an established confounding factor in explaining resting-state functional imaging findings (Drevets and Savitz, 2008), but they are usually not considered in the fMRI literature. However, when investigating individual differences, it is important to consider to what degree functional anatomical and structural differences are associated. We focussed the correlation of fMRI effects and GM volume on guilt, because this was the only sentiment for which reproducible individual difference effects on fMRI were previously found (Zahn et al., 2009a, b).

METHOD

Subjects

Sixty-four healthy participants N = 64 subjects (33 men, age: mean = 28.1 ± 7.7 years, education: mean = 17.3 ± 2.1 years) took part in the voxel-based morphometry and neuropsychological study, 29 of these participants had also taken part in a previously published fMRI study on social value-related moral sentiments (Zahn et al., 2009b), 26 had participated in an unrelated fMRI study on the neuroanatomy of social concepts (Zahn et al., 2007). Data from one participant had to be excluded prior to the image analysis because of incomplete coverage of the brain, leaving N = 63 for the final analyses. All were strongly right-handed and native English speakers, underwent a neurological examination and a clinical screening MRI during the previous 12 months, had normal or corrected-to-normal vision, no history of psychiatric or neurological disorders or psychopharmacological treatment, were not taking centrally active medications and had not consumed alcohol 24h prior to scanning. Informed consent was obtained according to procedures approved by the NINDS Internal Review Board. Participants were compensated according to the NINDS standards.

Experimental task design

Here, we used an adaptation of an experimental task originally developed for fMRI (Zahn et al., 2009b) and recently validated in a study of major depressive disorder (Green et al., 2013), the value-related moral sentiment task (VMST, which can be obtained at http://www.translational-cognitive-neuroscience.org/start/test-materials), to measure proneness to experience experimentally induced moral sentiments associated with moral and social values (e.g. ‘generosity’, ‘honesty’). The stimuli for the VMST are based on previous normative studies (Zahn et al., 2007, 2009b). The VMST allowed us to directly compare self-praising (pride), self-blaming (guilt), other-praising (gratitude) and other-blaming emotions (indignation/anger). Participants were shown written descriptions of positive or negative interactions between themselves and their best friends in which either themselves (self-agency, N = 90), or their best friend (other-agency, N = 90) acted in accordance with (N = 90) or counter (N = 90) to social and moral values. The resulting four conditions of the task measuring proneness to experimentally induced moral sentiments were (i) positive self-agency (e.g. ‘Yourself acting in a generous way towards [name of best friend: e.g. Sam]’, POS_S-AG, N = 45), (ii) positive other-agency (e.g. ‘Sam acting in a generous way towards you’, POS_O-AG, N = 45), (iii) negative self-agency (e.g. ‘Yourself acting in a stingy way towards Sam’, NEG_S-AG, N = 45), and (iv) negative other-agency (e.g. ‘Sam acting in a stingy way towards you’, NEG_O-AG, N = 45).

The best friend was chosen in order to equate familiarity with the agents and recipients in each condition, but at the same time to measure interactions with a person who has no kinship relationships that could directly affect the participants’ evolutionary fitness. Before the experiment they had to enter the nickname of their best friend who was of the same gender and not genetically or otherwise related, nor someone that they had had a sexual relationship with. The same social concepts (e.g. ‘tactless’, ‘honest’) were used in the self- and other-agency conditions. Participants were required to select the word that was the best label for the emotion that they would experience most strongly in response to the social behaviour. This instruction was given to enhance differentiation between these emotions. The choice of feelings included pride, gratitude, embarrassment, guilt, indignation/anger, and none/other. Participants rated how strongly they would experience pleasant or unpleasant feelings using a −4 to +4 bipolar visual analogue Likert scale (−4 = extremely unpleasant, +4 = extremely pleasant). Details about the stimulus selection and design have been described previously (Zahn et al., 2007, 2009b). The order of stimuli was fully randomized for each participant with all conditions mixed.

Relevant psycholinguistic variables from the MRC Psycholinguistic database (Coltheart, 1981): word familiarity, Kucera Francis word frequency, imageability and concreteness in addition to number of
syllables were matched across conditions (http://cercor.oxfordjournals.org/content/19/2/276/suppl/DC1). The sentence structure and word number were identical for all stimuli.

The percentage of trials that were rated as guilt-, pride-, gratitude- and indignation/anger-evoking in each condition was reported previously (http://cercor.oxfordjournals.org/content/19/2/276/suppl/DC1), confirming the prediction that guilt was the most frequent feeling in the NEG_S-AG, pride in the POS_S-AG, gratitude in the POS_O-AG and indignation/anger in the NEG_O-AG condition, respectively (http://cercor.oxfordjournals.org/content/19/2/276/suppl/DC1). This was the basis for choosing the percentage of trials rated as evocative of the condition-specific moral sentiment (% guilt in NEG_S-AG, % pride in POS_S-AG, % gratitude in POS_O-AG, % indignation/anger in NEG_O-AG) as a measure of prouneness towards that sentiment in each individual.

To assess global self-esteem, the Rosenberg self-esteem scale (Rosenberg, 1989) was administered. We rescaled the scoring of this scale from 1 to 4 instead of 0–3. As a standard measure of positive and negative affective style we used the positive and negative affect schedule (Watson et al., 1988).

Image acquisition

High resolution T1-weighted 3D magnetization-prepared rapid acquisition gradient echo structural images were collected (1 mm slice thickness, 0.98 mm spatial resolution, 128 slices, matrix: 224 x 224, TR = 7.6 ms, TE = 2.964, inversion time = 725 ms; FOV: 220 mm x 222 mm) on the same 3 tesla general electric scanner equipped with a standard head coil.

Image preprocessing and DARTEL analysis

Images were inspected for artefacts (motion, high level of inhomogeneities) before and after normalization. T1-images were normalized and segmented into GM, white matter (WM) and cerebrospinal fluid using the new features of the VBM8 toolbox, version 359 (http://dbm.neuro.uni-jena.de/vbm): segmentation without tissue priors, labelling voxels according to their tissue types using partial volume estimation, de-noising with non-local means filter and integration of DARTEL normalization (Ashburner, 2007). After pre-processing, images (1.5 x 1.5 x 1.5 mm³ voxel size) were smoothed with a Gaussian kernel of FWHM = 8 mm. The ‘non-linear modulation only’ option (i.e. with no affine component) was selected to create volumetric GM and WM partitions. This option is recommended to obtain relative volume after correcting for differences in brain size and replaces earlier methods of using total intracranial volume or total GM + WM (http://dbm.neuro.uni-jena.de/vbm/segmentation/modulation/) as nuisance covariates. A 0.2 absolute threshold masking was used to select voxels for the subsequent statistical analysis.

RESULTS

Behavioural data

Rated valence was equal (t(62) = 0.95, P = 0.35) between guilt (mean = −2.6 ± 0.7) and indignation (mean = −2.6 ± 0.6) trials and between pride (mean = 2.4 ± 0.6) and gratitude trials (mean = 2.4 ± 0.6, t(62) = −0.5, P = 0.62). But the emotional intensity of negative moral sentiments (mean for guilt and indignation = 2.6 ± 0.6) was higher (t = 2.3 [62], P = 0.02) than that of positive moral sentiments (mean for pride and gratitude = 2.4 ± 0.5). Supplementary Table S1 reports cross-correlations of experimental measures of moral sentiments and standard measures for exploratory purposes. These cross-correlations show that rated emotional valence in the positive conditions was positively associated with standard measures of positive affectivity and global self-esteem. Rated valence in the negative self-agency condition was negatively associated with self-esteem. Although pride and gratitude-proneness were positively associated with rated valence in the positive conditions, they were independent of standard measures of self-esteem and positive affectivity. There were medium associations between the different moral sentiment measures, but no critical multicollinearity (variance inflation factors < 1.34).

Stimulus sentences in each condition and participant were randomly assigned to two lists based on alphabetical order of words used to describe social values (e.g. stingy) to create a split into two unbiased sublists of stimuli of the task. Split-half reliability between the two sublists of stimuli was computed using the Spearman–Brown formula (Wilson, 2010). There were high split-half reliability coefficients for all VMST measures: POS_S-AG pride: 0.92, POS_O-AG gratitude: 0.82, NEG_S-AG guilt: 0.88, NEG_S-AG embarrassment: 0.90, NEG_O-AG indignation/anger: 0.90, POS_S-AG valence: 0.93, POS_O-AG valence: 0.91, NEG_S-AG valence: 0.88 and NEG_O-AG valence: 0.90. This concords with results obtained in a different version of the
VMST using the negative conditions only, recently validated in a sample of people with major depressive disorder (Green et al., 2013).

**Neuroimaging results**

**Associations of individual differences on moral sentiments with GM volumes**

Whereas there were no effects of moral sentiments in any of the predicted regions, we observed large clusters of GM volume variation within the precuneus and cuneus to be negatively associated with pride-proneness and within the right inferior temporal cortices positively with gratitude-proneness (see Figure 1 and Table 1).

We further carried out Supplementary data analyses to rule out that these results could have resulted from multicollinearity between moral sentiment variables used within the same model (see Supplementary Results, Supplementary Tables S2 and S3, and Supplementary Figure S1).

**Associations of individual differences in guilt-related BOLD responses with GM volumes**

In our previous fMRI study, we found strong effects for guilt-proneness on individual activation patterns within the SSC (Zahn et al., 2009b). We therefore used the SSC-BOLD response to guilt of each participant from that study (N=29) and explored its effect on GM volume variation across the brain. Interestingly, there was no effect on local GM within the SSC itself, but instead individuals with high BOLD response to guilt within the SSC showed relatively lower GM volume within the anterior dorsolateral PFC (right > left) and the left STS. There were no negative associations of SSC-BOLD-response to guilt and GM volume. Interestingly, guilt- and gratitude-proneness were both associated with lower GM volume within the right anterior dorsolateral PFC area identified as also being associated with higher SSC-BOLD response to guilt. The latter analysis remains exploratory, because the results did not survive correction for multiple comparisons across independent a priori ROIs (Figure 2 and Table 2).

**DISCUSSION**

We sought to determine whether individual differences in proneness to specific moral sentiments (1) are associated with GM volume variations and whether this occurs (a) in brain regions that are not necessary for appropriate interpersonal behaviour in patients with brain lesions, or (b) in brain regions known to be necessary for moral...
sentiments and appropriate interpersonal behaviour from patient lesion studies. Although individual differences in proneness to specific moral sentiments were indeed associated with regional variation in GM volumes thereby confirming our general prediction, these effects occurred in brain areas that were not implicated specifically in the experience of these moral sentiments before and thus refuted our more specific predictions (1b). The non-predicted regional effects were that cuneus and precuneus volumes were reduced in pride-prone individuals and right inferior temporal volumes were increased in gratitude-prone participants. These results were obtained using a gold standard method of measuring GM volume recently shown to be of equally high specificity and sensitivity in detecting neurodegeneration in these areas as cortical thickness analyses (Guignet et al., 2011).

The result of a lack of association of proneness to specific moral sentiments with GM volume variation in areas such as the ventral and anterior PFC known to impair moral behaviour and emotions in patients with structural lesions (Beer et al., 2003; Koenigs et al., 2007; Moll et al., 2011) could be interpreted in different ways. One possibility is that we lacked the statistical power to detect individual differences in GM volumes in these areas. This is unlikely in that we detected significant effects in non-predicted areas even when correcting for multiple comparisons across the whole brain and had more power for detecting effects in our a priori ROIs. Another possibility is that we lacked the statistical power to detect individual differences in moral feelings as relevant to behaviour in patients observed in lesion studies. Although this possibility could only be ruled out with certainty by directly showing the relationship of our moral sentiment measure with moral behaviour in patients, our previous fMRI study (Zahn et al., 2009b) showed that individual differences on this measure (pride-, guilt-, gratitude-proneness) were

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Table 1 Associations of individual proneness to moral sentiments with regional GM volumes

<table>
<thead>
<tr>
<th>Between-subject covariate of interest</th>
<th>Direction of effect</th>
<th>Hemi-sphere</th>
<th>Brodmann area</th>
<th>Anatomical description</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>T-score</th>
<th>FWE-corrected P-value</th>
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</thead>
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<tr>
<td>Guilt-proneness</td>
<td>Negative</td>
<td>R</td>
<td>46</td>
<td>Anterior dorsolateral prefrontal cortex</td>
<td>35</td>
<td>45</td>
<td>4</td>
<td>2.85</td>
<td>0.05*</td>
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<tr>
<td>Gratitude-proneness</td>
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<td>R</td>
<td>46</td>
<td>Anterior dorsolateral prefrontal cortex</td>
<td>54</td>
<td>39</td>
<td>10</td>
<td>3.55</td>
<td>0.03*</td>
</tr>
<tr>
<td>Gratitude-proneness</td>
<td>Positive</td>
<td>R</td>
<td>20</td>
<td>Inferior temporal gyrus</td>
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<td>3.87</td>
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<td>Pride-proneness</td>
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<td></td>
<td></td>
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All analyses were performed using an uncorrected P = 0.005 and minimum cluster size of 4 voxels. Only areas that survived correction for multiple comparisons (voxel- or cluster-based FWE) at P = 0.05 over a priori ROIs or the whole brain are discussed in the text and reported in the tables as definite results. Coordinates are in Montreal Neurological Institute Standard Space. Areas surviving voxel-based FWE-corrected P = 0.05 over first tier a priori ROIs are marked with *. No significantly positive effects were found.

Table 2 Associations of individual differences in guilt-related SSC-BOLD with regional GM volumes

<table>
<thead>
<tr>
<th>Between-subject covariate of interest</th>
<th>Direction of effect</th>
<th>Hemi-sphere</th>
<th>Brodmann area</th>
<th>Anatomical description</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>T-score</th>
<th>FWE-corrected P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SSC-BOLD effect guilt vs indignation</td>
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<td>R</td>
<td>46</td>
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<td>3</td>
<td>5.30</td>
<td>0.02*</td>
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<td></td>
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<td>5.21</td>
<td>0.02*</td>
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</table>

All analyses were performed using an uncorrected P = 0.005 and minimum cluster size of 4 voxels. Only areas that survived correction for multiple comparisons (voxel- or cluster-based FWE) at P = 0.05 over a priori ROIs or the whole brain are discussed in the text and reported in the tables as definite results. Coordinates are in Montreal Neurological Institute Standard Space. Areas surviving voxel-based FWE-corrected P = 0.05 over first tier a priori ROIs are marked with *. No significantly positive effects were found.

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Fig. 2 Individual differences were depicted as decreases (blue) in GM volume that were associated with individual SSC-BOLD responses to guilt vs indignation on an fMRI task in a subgroup of N = 29 participants (panels (a) and (b)). Statistical maps were depicted at an uncorrected voxel-level significance threshold of P = 0.005 and a minimum cluster size of 4. Only areas that survived comparison for multiple comparisons (voxel- or non-stationary cluster-based FWE-correction) at P = 0.05 over a priori ROIs or the whole brain are discussed in the text and reported in the tables as definite results. The colour scale is identical to Figure 1.
indeed associated with variance in BOLD response within specific brain regions (septal area, subgenual cingulate, hypothalamus) known to be critical for moral behaviour from patient lesion studies (Moll et al., 2005). These results render lack of power an unlikely explanation for our finding of lack of association between variability in brain structure and our measure of moral sentiments. An alternative explanation which we favour is that structural variability in brain regions critical for specific moral sentiments is low between healthy participants, because high psychosocial functioning may not allow for large variations in structural anatomy within brain systems critical for moral motivations.

This interpretation is in keeping with marked associations between structural differences in subgenual and frontopolar cortices and Factor 1 of Hare’s psychopathy checklist, which captures empathic sensitivity and remorse, in patients with developmental psychopathy (de Oliveira-Souza et al., 2008) who showed regional volumetric differences when compared as a group against a healthy control sample. This implies that structural variability within brain areas critical for moral sentiments may be more informative of psychopathology than of individual differences within the range of healthy functioning.

Despite this lack of structural variability within predicted areas, there were extensive associations of positive moral sentiments with areas leading to visual-spatial deficits when affected by lesions in patients. In posterior cortical atrophy, focal neurodegeneration is observed within the cuneus, precuneus and right posterior temporal brain areas (Nestor et al., 2003), thus encompassing all those areas to be primarily associated with pride- and/or gratitude-proneness in our study. Interestingly, changes in personality or social behaviour are not typically seen in these patients (Nestor et al., 2003; McMonagle et al., 2006). Furthermore, damage to the precuneus consistently and distinctively occurs in Alzheimer’s disease at an early stage (Salmon et al., 2003) even on an individual case basis (Zahn et al., 2005) and patients typically lack consistent and common neuropsychiatric symptoms (Bozat et al., 2000) to be expected if the precuneus were necessary for the experience of moral sentiments such as gratitude or pride.

The precuneus has been linked to visual imagery during retrieval of episodic memories (Fletcher et al., 1996) including autobiographical episodes (Gardini et al., 2006) using functional imaging in healthy populations. This concords with the pronounced impairments of episodic memory in early Alzheimer’s disease (Salmon and Bondi, 2009) as well as with the direct connections of the precuneus with the posterior cingulate cortex (Cavanna and Trimble, 2006) which is directly connected to medial temporal lobe structures in primates (Kobayashi and Amaral, 2007). The precuneus/posterior cingulate region has been suggested to be of importance for processing self-relatedness of stimuli via its link with retrieving episodic autobiographical memories (Northoff and Bermpohl, 2004). Further, an fMRI study in a healthy sample led to the postulate that by supporting mental imagery the precuneus is involved in distinguishing agency of self and other (Ruby and Decety, 2001). Agency role (self vs other) was shown to predict the experience of pride relative to gratitude (Zahn et al., 2009b) and may be supported by visuo-spatial representations.

The specific association of right posterior inferior temporal volumes and gratitude-proneness was intriguing. Disruption of the integrity of this region was associated with both acquired (Barton, 2008) and developmental propagandism (Dinkelacker et al., 2011). Interestingly, a similar right temporal region showed GM volume increases in healthy individuals with higher competence in interpreting other’s intentions (Lewis et al., 2011). Further, WM volume in a right posterior temporal area, superior to the one identified here, was associated with autism spectrum traits in healthy participants (von dem Hagen et al., 2011). These studies suggest that individual differences in right posterior temporal lobe development are associated with differences in social cognitive styles in healthy populations.

We interpret the finding that individuals with higher GM volume within posterior cortical areas showed lower proneness to respond with pride and higher proneness to respond with gratitude as possibly being related to differences in reliance on visuo-spatial representations of morally salient scenes associated with these different types of feelings. A well-developed posterior cortical system may facilitate construction of detailed scenes which could play a more important role for experiencing gratitude than pride. This is if more elaborate sensory imagery is required to experience feelings that may counter the self-serving attributional bias reliably found in people with no psychiatric history (Mezulis et al., 2004). Self-serving bias favours the experience of pride which is associated with self-praising attributions (Weiner, 1985). We speculate that posterior cortical networks involved in visual imagery, although not necessary for moral sentiments, may play a supportive role in that they may allow for more lively and detailed scenic representations of social behaviour and hence more intense emotional experience when visuo-spatial memories or mental models are required. Rich visuo-spatial representations may also facilitate the experience of moral sentiments without relying on elaboration of associated knowledge of social behaviour in anterior tempororo-frontal networks (Moll et al., 2008). We have previously reported a high correlation between visual imagery, autobiographical episodic retrieval and emotional intensity on our task (Zahn et al., 2009b). It appears that structural variations within the visual imagery system have less influence on negative moral sentiments, which may be due to their overall heightened emotional intensity in keeping with previous research (Baumeister et al., 2001) and may make them more independent of further scenic elaboration.

We found no GM variations to be directly associated with guilt- or indignation-proneness in our primary data analysis. In a secondary data analysis, we therefore related the fMRI BOLD effect for guilt vs indignation in the SSC with GM variations in a whole brain analysis. Interestingly, this revealed that individuals with high SSC-BOLD responses to guilt exhibited lower GM volumes in the anterior dorsolateral PFC (right > left) and the left STS, but that there were no volume differences in the SSC region. An exploratory analysis revealed that guilt- and gratitude-prone individuals showed lower GM volumes in a subregion of the right anterior dorsolateral PFC region resulting from our secondary data analysis.

These findings rule out that individual differences in the SSC-BOLD response to guilt were due to partial volume effects (i.e. higher BOLD being due to more GM volume rather than higher levels of activation within the same volume). It is intriguing that left posterior STS, thought to be involved in social sensory information (Allison et al., 2000), and right anterior dorsolateral PFC GM volumes were decreased in individuals with high SSC-BOLD, because both areas are not directly connected with the SSC (Ongur and Price, 2000). An additional left anterior STS area of decreased volume (Figure 1, panel b), previously linked with social conceptual knowledge (Zahn et al., 2007), did not survive correction for multiple comparisons, but could be mediating the effects seen in the posterior STS, because it is directly connected with both posterior STS (Markowitsch et al., 1985) and SSC (Kondo et al., 2003). Further, the right hemispheric homologue of the anterior STS area was shown to exhibit selective increases in functional con connectivity with the SSC for guilt compared with indignation, an effect that increased with individual guilt-proneness (Green et al., 2010). It is unclear how GM variation in one area may be associated with functional activation differences in another area, but it may be analogous to von Monakow’s mechanism of diaschisis effects observed in patients with structural brain lesions in one area leading to remote functional changes in connected areas (Zahn et al., 2006).
The finding of right anterior dorsolateral PFC volumes being decreased in individuals with high guilt-proneness and gratitude-proneness remains preliminary and is further discussed in the Supplementary data. Although our positive and negative moral sentiment measures showed associations with standard measures of positive affectivity and self-esteem, we were able to rule out that the reported effects were due to effects of valence or emotional intensity. This is because we used a moral sentiment variable of equal valence and emotional intensity as a covariate of no interest in all of our analyses.

CONCLUSIONS
Taken together, these results support the view that individual variations in functional activations within critical areas for moral sentiments were not due to GM volume differences in the same areas. Grey matter volume differences between healthy individuals may nevertheless play an important modulatory role by affecting posterior cortical brain systems that are non-critical but supportive for the experience of specific moral sentiments. This may be of particular relevance when the experience of a moral sentiment depends more strongly on visuo-spatial elaboration. Future studies in patients with damage to posterior cortical networks such as Alzheimer’s disease and posterior cortical atrophy are needed to confirm their role in enabling visuo-spatial elaborations of planned or appraised moral behaviours, thereby supporting the experience of moral sentiments such as gratitude. Impairments of the ability to experience moral sentiments could be present in these patients without leading to changes in moral conduct, because moral sentiments could still be experienced normally in direct interpersonal exchanges which are richer in visuo-spatial cues than emotional responses to being told about a moral situation without witnessing it directly.

SUPPLEMENTARY DATA
Supplementary data are available at SCAN online.

REFERENCES
Bozat, S., Gregory, C.A., Ralph, M.A.L., Hodges, J.R. (2000). Which neuropsychiatric and gravitational proneness remains preliminary and is further discussed in the Supplementary data. Although our positive and negative moral sentiment measures showed associations with standard measures of positive affectivity and self-esteem, we were able to rule out that the reported effects were due to effects of valence or emotional intensity. This is because we used a moral sentiment variable of equal valence and emotional intensity as a covariate of no interest in all of our analyses.

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Proneness to moral sentiments


