Review article

Feelings of shame, embarrassment and guilt and their neural correlates: A systematic review

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A B S T R A C T

This systematic review aimed to provide a comprehensive summary of the current literature on the neurobiological underpinnings of the experience of the negative moral emotions: shame, embarrassment and guilt. PsychINFO, PubMed and MEDLINE were used to identify existing studies. Twenty-one functional and structural magnetic resonance imaging and positron emission tomography studies were reviewed. Although studies differed considerably in methodology, their findings highlight both shared and distinct patterns of brain structure/function associated with these emotions. Shame was more likely to be associated with activity in the dorsolateral prefrontal cortex, posterior cingulate cortex and sensorimotor cortex; embarrassment was more likely to be associated with activity in the ventrolateral prefrontal cortex and amygdala; guilt was more likely to be associated with activity in ventral anterior cingulate cortex, posterior temporal regions and the precuneus. Although results point to some common and some distinct neural underpinnings of these emotions, further research is required to replicate findings.

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1. Introduction

Humans experience moral emotions as early as two years of age (Barrett et al., 1993). The onset of this ability coincides with the development of self-evaluative processing, including being able to distinguish self from others. They can be either positive (e.g., pride and gratitude) or negative (e.g., shame, embarrassment and guilt) and most of these emotions can be considered ‘pro-social’ as they tend to promote adaptive social behaviors (Bowles and Gintis, 2005; Tangney et al., 2011). Negatively valenced ‘self-blaming’ moral emotions are particularly important for social functioning. These emotions are crucial for the development and maintenance of interpersonal relationships because they act as important social regulators by encouraging a balance between the individual’s urges and the rights and needs of others. Further, dysregulation in the experience of these emotions may lead to poor mental health. For example, it has been suggested that the excessive experience of self-blaming emotions like shame and guilt may have particularly adverse consequences in the realm of mood and anxiety disorders, such as depression (Andrews, 1995; Kim et al., 2011; O’Connor et al., 1999; Tangney et al., 1992a).

While a great deal of research has been conducted investigating the neural correlates of basic emotions (e.g., anger, fear, sadness, happiness), far less research has investigated the neural basis of the experience of the negative moral emotions, shame, embarrassment and guilt. Such research might be particularly useful for refining current conceptualizations of common and distinct features of these emotions. Indeed, shame, embarrassment and guilt have a number of broad characteristics in common; all three emotions occur when the rules, norms or social agreements, defining what is right or wrong, are broken. Conversely, these emotions are suggested to have distinct features. A generally accepted differentiation between shame and guilt, proposed by Tangney and colleagues, is that shame is associated with internal attributions while guilt is associated with behavioral attributions (Tangney et al., 1996). Guilt is generally referred to as ‘behavior-focused negative self-conscious emotion’ (Tangney et al., 2011). With guilt, the focus is on the ‘do’ (e.g., “I did something wrong”) (Tangney, 1995). Guilt may be associated with attributing a transgression, of social or inner moral norms, to external (rather than intrinsic) factors. Furthermore, the feeling of guilt often generates a sentiment of remorse, a desire to have behaved differently regarding the transgressed social norm, or a need to make up for a fault by confessing, taking reparative action (Tangney et al., 2007), or employing other methods for releasing guilty feelings (Lindsay-Hartz, 1984; Tangney et al., 2011). Guilt, more so than shame, may imply empathy toward others and a real concern about acting badly and hurting someone in the process (Tangney, 1992; Tangney et al., 2007). While a guilty person may feel emotional ‘pain’, it will unlikely become overwhelming (Tangney et al., 2011).

Shame, on the other hand, is generally referred to as ‘self-focused negative emotion’ (Tangney et al., 2011), and is experienced when a person believes that their transgression of certain rules defines who they are (Wong and Tsai, 2007). Shame is related to the way we perceive ourselves and how we believe others see us, and our failure or inadequacy to fulfill the desire to be a good person (e.g., “I am a bad person for lying to my friend”). People who experience shame may be concerned with their own evaluation and what others might think of them (Tangney et al., 1992b), even when experienced alone. Since shame refers to the entire self’s mal-function, negatively judging or questioning oneself as a person will likely directly affect one’s core identity (Wong and Tsai, 2007). Thus, feeling ashamed induces the sentiment of worthlessness, inferiority and incompetence, and often leads to a want to escape and withdraw socially (Tangney et al., 2011). As such, by directly affecting the self, shame is thought to generate greater pain and be a more distressing subjective emotion than guilt. As alluded to, shame and guilt have a different relationship to empathy, while guilt is associated to “other-oriented empathy”, shame’s connection to empathy appears to be disrupted and focuses on “self-oriented distress” (Tangney et al., 2007).

While Tangney’s operationalization of shame and guilt is popular, the similarities and differences between these emotions remains a topic of debate (Pulcu et al., 2013; Tangney et al., 1996; Wong and Tsai, 2007), especially between different fields (i.e., criminology, social and clinical psychology, philosophy, etc.) (Tangney et al., 2007; Tibbetts, 2003). In contrast to the above definitions, O’Connor (O’Connor et al., 1999) for example defines several classes of guilt as involving characterological self-blame.

Embarrassment has long been conceived as a dimension of shame (Kaufman, 1989; Lewis, 1971), generally assumed to vary on a range of factors including intensity, public exposure, and physical reaction (e.g., blushing). However, in more recent years, embarrassment has been suggested to be considered as a distinct emotional response (Tangney et al., 1996). Compared to shame and guilt, embarrassment appears to be associated with more sudden and accidental violation of social conventions with a motivational response directed towards the preservation of one’s social reputation, rather than a concern for others’ well-being and a need to make amends as in guilt or with a concern for oneself with a need to hide as in shame (Eisenberg, 2000; Tangney et al., 1996). Embarrassment is always directly related to the response of the presence of an “audience” (real or imagined), in which the person worries about their social image as a result of their behavior being directly witnessed. Embarrassment appears to be less negative, generating less emotional pain, only affecting one’s presented self, and can therefore be perceived as a less ‘damaging’ emotion by playing a more adaptive role than shame in social interactions.

As such, although there is some debate about their differences (Tangney et al., 1996), shame, embarrassment and guilt are theoretically separable constructs that can be differentiated on the basis
of factors such as interpersonal context of experience, appraisal and resulting action, behavioral or situational emotional trigger and coping mechanisms, etc. (Tangney et al., 1996). While shame, embarrassment and guilt are emotions often used interchangeably in colloquial terms, and empirically, measurement of these emotions as separate constructs is more difficult (Gibson, 2013), recent neuroimaging research has attempted to differentiate them in order to understand their distinct neurobiological correlates. There is now growing evidence that shame and guilt can be partly differentiated in terms of their primary brain structural and functional correlates. However, this literature has not been summarized to date. As such, the intention of this paper is to conduct a systematic review in order to reconcile the available brain imaging literature on the subject to date. The aim of the review is to a) provide a descriptive overview of the current literature on the neural correlates of the experience of shame, guilt and embarrassment, b) provide a preliminary quantitative analysis of the common and unique neural correlates of these emotions, c) critically appraise study methods and their potential impact on results, and d) highlight gaps in the literature for future research.

2. Methods

This literature review of neuroimaging studies was conducted under the PRISMA guidelines. Fig. 1 presents the PRISMA Flow Diagram detailing the different phases of the literature search (Liberati et al., 2009).

Studies were included if they reported the direct association between brain structure or function and the experience of guilt, shame and/or embarrassment. Studies were included if the experience of these emotions was inferred by the authors (based on theoretical reasoning), based on participant self-report or observational techniques. Studies employing structural magnetic resonance imaging (sMRI), functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) were included. Studies including either or both healthy and psychiatric participants were included. Only studies with adult population were included. Furthermore, only studies using human subjects and written in English were included. Document types were limited to peer-reviewed journal articles.

Studies were excluded if they did not investigate (or purport to investigate) experiential aspects of shame, embarrassment or guilt (e.g., studies were excluded if they investigated decision-making or other cognitive processes associated with moral emotions). Studies referring more broadly to ‘self-blaming emotions’ or ‘negative moral emotions’ without specifying/measuring shame, embarrassment or guilt, specifically, were excluded. In addition, in order to facilitate comparison across studies, studies whose subjects had neurodegenerative disorders or focal brain lesions were also excluded. Exceptions were made, however, for studies including patients with neurodegenerative disorders if the findings were reported separately for a healthy control group. Finally, and again to facilitate comparison across studies, studies were excluded if they only reported associations between moral emotions and functional connectivity.

Studies that were published or in press as of October 2014 were retrieved in from three databases: PsyCINFO (American Psychological Association), PubMed (US National Library of Medicine National Institute of Health) and MEDLINE (Wolters Kluwer Health OvidSP). The database searches were conducted by combining keywords through Thesaurus (PsyCINFO); MeSH term (PubMed); Search Tools (MEDLINE); and free text. While some of the papers mentioned in their abstract investigating specific emotions such as guilt; shame and/or embarrassment; they did not always report specific results related to them and were therefore excluded during the full text stage of the review. Details of study screening and eligibility assessment are presented in more detail in Fig. 1.

As a result of discrepancies and inconsistencies in the way that similar brain regions were labeled across studies, peak voxel locations (for each cluster reported in each study) were initially checked and labeled using the Anatomical Automatic Labeling (AAL) atlas in SPM8, and in the case of any ambiguities, a consensus was reached by three of the authors (CB, SW, BH). Further, if necessary, regions were relabeled to present a more unified scheme. For instance, brain regions reported as medial orbitofrontal cortex (mOFC) were relabeled to ventromedial prefrontal cortex (vmPFC). A description of the anatomical relabeling employed in this review can be found in the legend of Fig. 3.

3. Results

The first brain imaging study of negative moral emotions was published fifteen years ago, and since there has been a steady growing interest in the neurobiological underpinning of these emotions. Twenty-one studies were included in this review spanning the years 2000–2014. Search results were screened independently by two co-authors (CB and SW) and any uncertainties about inclusion/exclusion criteria were discussed until consensus was reached. Table 1 summarizes the main characteristics of each study in terms of methodology, sample and results. It is of note that while studies often investigated several emotions, for clarity, the results are discussed for each emotion under separate headings.

3.1. Methodology

Studies differed substantially in terms of the methodologies and statistical contrasts/analyses used. Differences are summarized briefly here, but are also mentioned in Sections 3.2–3.4, below. Only three fMRI studies reported using imaging sequences optimized for coverage of areas where signal loss is common (i.e., ventral temporal lobe and orbitofrontal cortex) (Moll et al., 2007; Morey et al., 2012; Zahn et al., 2009). Upon inspection, however, it does not appear that the three studies using optimized sequences reported more activity in these regions as compared to other studies (see Fig. 2). All but one study (Zahn et al., 2014) presented findings from whole brain analyses, although many used a combination of whole brain and region of interest (ROI) analyses. The majority of fMRI/PET studies employed script driven tasks (8/19) with instructions for participants to imagine themselves in the situation described (or remembered, in the case of autobiographical recall paradigms) and including ratings of stimuli or own affect (6/19). Five other studies involved other types of participation such as photo-driven tasks involving active rating of stimuli (3/19) and two studies employed more active participation by the using a game or combining the use of words and faces. An assessment of results based on the different induction techniques used in studies was conducted and the induction method did not seem to affect the results (see Fig. S1 in Supplementary material). In terms of statistical analysis, eight studies reported brain activity associated with one of the target negative moral emotions compared to a neutral (non-emotional) condition (Fourie et al., 2014; Michl et al., 2014; Moll et al., 2007; Morey et al., 2012; Roth et al., 2014; Shin et al., 2000; Takahashi et al., 2004; Wagner et al., 2011). Four studies reported brain activity associated with one of the target negative moral emotions compared to at least one other of these emotions (Michl et al., 2014; Pulcu et al., 2014; Takahashi et al., 2004; Wagner et al., 2011). Five studies reported brain activity associated with one of the target negative moral emotions compared to another negative moral emotion (e.g., guilt > indignation) (Basilie et al., 2011; Green et al., 2012; Kédia et al., 2008; Morey et al., 2012; Wagner et al., 2011), three studies
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<td>Shin et al. (2000)</td>
<td>8 healthy individuals (All males) (Mean 50)</td>
<td>PET</td>
<td>Auto-biographical recall</td>
<td>Guilt</td>
<td>Guilt &gt; Neutral: dACC, MCC, AIC/vIPFC, anterior STC, M1: primary motor cortex</td>
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<tr>
<td></td>
<td>Mean (SD) age: 25.0 (±4.4)</td>
<td></td>
<td>(precentral gyrus), lateral cerebellum</td>
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<td>Neutral &gt; Guilt: PIC, M1: precentral gyrus, precuneus, visual cortex (cuneus,</td>
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<td>fusiform gyrus)</td>
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<td>Takahashi et al. (2004)</td>
<td>19 healthy individuals (10 M) (Mean 30.8 (±6.2)</td>
<td>fMRI</td>
<td>Emotion induction statements</td>
<td>Guilt</td>
<td>Guilt &gt; Embarrassment: dmPFC</td>
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<td></td>
<td>Mean (SD) age: 25.1 (±3.2)</td>
<td></td>
<td>(script-driven, instructed to read the</td>
<td>Embarrassment</td>
<td>Guilt &gt; Neutral: dmPFC, posterior MTC, visual cortex (calcarine)</td>
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<td>sentences, post scan guilt and</td>
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<td>Embarrassment &gt; Guilt: hippocampus, anterior MTC, dorsal midbrain, visual cortex</td>
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<td>embarrassment ratings)</td>
<td></td>
<td>(calcarine, lingual gyrus, inferior occipital)</td>
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<tr>
<td>Finger et al. (2006)</td>
<td>16 healthy individuals (Gender/age not specified)</td>
<td>fMRI</td>
<td>Emotion induction statements</td>
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<td>Embarrassment/Shame (moral = social with audience) &gt; (social without audience =</td>
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<td></td>
<td></td>
<td></td>
<td>(script-driven, instructed to imagine</td>
<td>Shame</td>
<td>neutral): dmPFC, vIPFC, posterior STS (posterior MTC, anterior ITC,</td>
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<td>hippocampus, visual cortex (calcarine, lingual gyrus)</td>
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<td>Embarrassment (Shame (male &gt; female) &lt; audience &gt; no audience): amygdala</td>
</tr>
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<td>Moll et al. (2007)</td>
<td>12 healthy individuals (6 M, 6 F) (Mean 28.59 (±9.6)</td>
<td>fMRI</td>
<td>Emotion induction statements</td>
<td>Guilt</td>
<td>Guilt &gt; Neutral: dmPFC, vIPFC, dorsal midbrain, anterior STC, posterior STS, M1:</td>
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<tr>
<td></td>
<td>Mean (SD) age: 26.0 (±4.0)</td>
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<td>(script-driven, instructed to imagine</td>
<td>Embarrassment</td>
<td>primary motor cortex (frontal operculum/precentral gyrus)</td>
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<td>oneself in situation)</td>
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<td>Embarrassment &gt; neutral: dmPFC, dACC, AIC, posterior STS, TPJ/posterior STC</td>
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<td>Morita et al. (2008)</td>
<td>19 healthy individuals (9 M and 10 F) (Mean 30.8 (±6.2)</td>
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<td>Self-reported embarrassment as parametric modulator of self-face condition:</td>
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<td></td>
<td>Mean (SD) age: 26.0 (±4.0)</td>
<td></td>
<td>(Photogenic ratings of self- and other-faces, post scan</td>
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<td>Kédia et al. (2008)</td>
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<td>Note: similar regions were more active for other-anger and compassion &gt; self-anger</td>
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<td></td>
<td>Mean (SD) age: 21 (±1.98)</td>
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<td>(script-driven, instructed to imagine</td>
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<td>29 healthy individuals (15 M, 9 F) (Mean 27.9 (±7.3)</td>
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<td>Negative self-agency (guilt condition) &gt; fixation: no significant effect</td>
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<td></td>
<td>Mean (SD) age: 27.9 (±7.3)</td>
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<td>(script-driven, instructed to judge</td>
<td>Pride</td>
<td>Individual differences in the percentage of trials where guilt was experienced</td>
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<td>pleasantness of own feeling, post-scan</td>
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<td>was positively correlated with activation in the vmPFC and vACC during negative</td>
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<td>Deontological + altruistic guilt &gt; Basic emotions (anger &amp; sadness); vACC, dACC,</td>
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<td>(script-driven, instructed to imagine</td>
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<td>guilt rating)</td>
<td>emotions (i.e.,</td>
<td>(Altruistic guilt &gt; sadness) &gt; (Deontological &gt; anger): no significant effect</td>
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<td>Wagner et al. (2011)</td>
<td>15 healthy individuals (All females) age range: 25–30</td>
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<td>Guilt ≥ Neutral: dIPFC, vIPFC, dmPFC, PIC, anterior ITC, anterior MTC, anterior STC, posterior STS, preSMA, parahippocampal gyrus, IPC (supramarginal gyrus; angular gyrus), SPC (parietal operculum), basal ganglia (putamen), precuneus, visual cortex (calcarine), cerebellum (vermis) Guilt &gt; Shame + Sadness: dmPFC, vIPFC Guilt &gt; Shame: dIPFC, dmPFC, vIPFC, dACC, amygdala, basal ganglia (putamen, caudate, pallidum), AIC, anterior MTC, cerebellum Guilt &gt; Sadness: vIPFC Shame &gt; Neutral: dmPFC, AIC, anterior ITC, anterior MTC, IPC (angular gyrus), precuneus, visual cortex (lingual gyrus), cerebellum (vermis) Shame &gt; Guilt: no significant effect</td>
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<td>Morita et al. (2012)</td>
<td>15 high-functioning ASD (14 M, 1 F) Mean (SD): age: 23.7 (± 4.3)</td>
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<td>Within ASD group Self-reported embarrassment as parametric modulator of self-face condition: (positive correlation) vIPFC (negative correlation) AIC</td>
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<td>Morey et al. (2012)</td>
<td>16 healthy individuals (All males) Mean (SD): age: 22.41 (±2.69)</td>
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<td>Emotion induction statements (script-driven, instructed to imagine oneself in situation, in-scan guilt ratings)</td>
<td>Guilt-self</td>
<td>Guilt-other &gt; Guilt-self: posterior MTC, dmPFC, precuneus, visual cortex (calcarine) Guilt-self &gt; Guilt-other: no significant effect Main effect of guilt: (positive correlation with guilt ratings) dmPFC, vIPFC, IPC (supramarginal gyrus) Main effect of guilt: (negative correlations with guilt ratings) dIPFC, vIPFC, MCC, PIC, posterior MTC, S1: first somatosensory cortex (postcentral gyrus), SPC, precuneus, visual cortex (cuneus) Across groups (HC &amp; remitted MDD) Guilt &gt; Indignation: vACC (pregenual &amp; subgenual), basal ganglia (caudate) HC &gt; remitted MDD Guilt &gt; Indignation PIC, parietal-occipital junction Remitted MDD &gt; HC Guilt &gt; Indignation no significant effects Within HC group Guilt &gt; Indignation: dACC, anterior MTC, posterior MTC, preSMA, S1: first somatosensory cortex (postcentral), visual cortex (cuneus) Within remitted MDD group Guilt &gt; Indignation: no significant effect</td>
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<td>Green et al. (2012)</td>
<td>25 remitted MDD participants 22 healthy controls (HC)</td>
<td>fMRI</td>
<td>Emotion induction statements (script-driven, unpleasantness ratings, post-scan individual classification of trials)</td>
<td>Guilt</td>
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<td>Both across groups (bvFTD &amp; HC) and within each group Embarrassment (physiological reactivity and observed self-conscious behavior) associated with larger right vACC gray matter (after controlling for sadness associated reactivity/behavior)</td>
</tr>
<tr>
<td>Morita et al. (2013)</td>
<td>32 healthy individuals (16 M and 16 F) Mean (SD) age: 21.3 (±2.4)</td>
<td>fMRI</td>
<td>Facial emotion induction (Photogenic ratings of self- and other-faces, post scan embarrassment ratings)</td>
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<td>Self-reported embarrassment as a parametric modulator of self-face condition: (positive correlation) AIC</td>
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<td>Michl et al. (2014)</td>
<td>14 healthy individuals (7 M, 7 F) Mean (SD) age: 29 (±2.95)</td>
<td>fMRI</td>
<td>Emotion induction statements (script-driven, instructed to imagine oneself in situation)</td>
<td>Guilt</td>
<td>Guilt &gt; Neutral: dlPFC, dmPFC, anterior MTC, anterior STC, posterior MTC, M1: primary motor cortex (frontal operculum, precentral gyrus), visual cortex (fusiform gyrus, calcarine, lingual gyrus), cerebellum Guilt &gt; Shame: thalamus, posterior MTC, visual cortex ( fusiform gyrus) Shame &gt; Neutral: dlPFC, dmPFC, hippocampus (parahippocampal gyrus), AIC, anterior STC, presMA, visual cortex (middle occipital gyrus, calcarine, cerebellum Shame &gt; Guilt: dlPFC, dACC, PCC, hippocampus (parahippocampal gyrus), dorsal (anterior) midbrain, AIC Interpersonal guilt (self-incorrect &gt; both-incorrect contrasts values): anterior MCC, AIC Interpersonal guilt: Positive correlation between gray matter (GM) volume in an anterior MCC cluster and compensation behavior during interpersonal game paradigm. Across groups (HC &amp; OCD) Guilt (DG &gt; AG) &gt; Basic emotions No significant effect HC &gt; OCD Guilt (DG &gt; AG) &gt; Basic emotions (anger + sadness): dmPFC, dACC, AIC, preSMA, precuneus HC &gt; OCD Guilt (DG only) &gt; anger: AIC, preSMA, precuneus HC &gt; OCD Guilt (AG only) &gt; sadness: no significant effect</td>
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<tr>
<td>Yu et al. (2014)</td>
<td>27 healthy graduate &amp; undergraduate students</td>
<td>fMRI sMRI using voxel-based morphometry (VBM)</td>
<td>Interpersonal game paradigm (dot estimation task, pain administered to other if self-incorrect, post-scan guilt ratings for each condition)</td>
<td>Interpersonal guilt</td>
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<tr>
<td>Basile et al. (2014)</td>
<td>13 OCD patients (10 M, 3 F) Mean (SD) age: 37.0 (11.1) 19 healthy controls (8 F &amp; 11 M) Mean (SD) age: 26.2 (±2.1)</td>
<td>fMRI</td>
<td>Emotion induction statements associated with facial expressions (script-driven, instructed to imagine oneself in situation + forced choice guilt rating)</td>
<td>Deontological (DG) &amp; Altruistic guilt (AG) Basic emotions (i.e., anger and sadness)</td>
<td>Across groups (HC &amp; OCD) Guilt (DG &gt; AG) &gt; Basic emotions No significant effect HC &gt; OCD Guilt (DG &gt; AG) &gt; Basic emotions (anger + sadness): dmPFC, dACC, AIC, preSMA, precuneus HC &gt; OCD Guilt (DG only) &gt; anger: AIC, preSMA, precuneus HC &gt; OCD Guilt (AG only) &gt; sadness: no significant effect</td>
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<td>Fourie et al. (2014)</td>
<td>22 healthy low-prejudice individuals Mean (SD) age: 19.32 (±1.11)</td>
<td>fMRI</td>
<td>Implicit Association Test (written and facial stimuli) (categorization task followed by prejudice, egalitarian or neutral written feedback, post-scan emotion ratings)</td>
<td>Guilt</td>
<td>Guilt (prejudice feedback) &gt; Neutral (neutral feedback): dmPFC, dACC, dorsal PCC, thalamus, AIC, precuneus Guilt (Prejudice Feedback) &gt; Pride (Egalitarian Feedback): dmPFC, PCC, basal ganglia (caudate nucleus), AIC, posterior STS Negative correlation between individual guilt ratings and vACC activity during prejudice condition (controlling for other negative emotions)</td>
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### Table 1 (Continued)

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<tr>
<th>Study</th>
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<th>Moral Emotions</th>
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<td>Pulcu et al. (2014)</td>
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<td>fMRI</td>
<td>Emotion induction statements (script-driven, unpleasantness ratings, post-scan individual classification of trials)</td>
<td>Shame</td>
<td>MDD &gt; HC</td>
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<td>Shame &gt; Guilt: amygda, PIC</td>
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<td>HC &gt; MDD</td>
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<td>Shame &gt; Guilt: no significant effect</td>
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<td>MDD</td>
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<td>Shame &gt; Guilt: amygdala, PIC</td>
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<td>Guilt &gt; Shame: HC: positive correlation of unpleasantness of shame trials with PIC signal for shame vs. guilt.</td>
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<td>Roth et al. (2014)</td>
<td>25 healthy individuals (9 M, 16 F)</td>
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<td>Negative (shame/guilt)</td>
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<td>Mean (SD) = 31.9 (±10.2)</td>
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<td>63 healthy individuals (33 M, 30 F)</td>
<td>sMRI</td>
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<td>Investigated structural variations and individual differences in proneness to specific moral emotions:</td>
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<td></td>
<td>Mean (SD) = 28.1 (±7.7)</td>
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<td>Guilt-proneness associated with reduced volume in dlPFC*</td>
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Structural magnetic resonance imaging (sMRI), functional magnetic resonance imaging (fMRI).

Dorsolateral prefrontal cortex (dLPFC), dorso-medial prefrontal cortex (dmPFC), ventromedial prefrontal cortex (vmPFC), subgenual anterior cingulate cortex (sACC), pregenual anterior cingulate cortex (pACC), dorsal anterior cingulate cortex (dACC), mid-cingulate cortex (MCC), posterior cingulate cortex (PCC), insula cortex (IC), anterior insula cortex (Roth et al., 2014), posterior insula cortex (PIC), anterior temporal lobe (ATL), inferior temporal cortex (ITC), middle temporal cortex (MT), superior temporal cortex (STC), superior temporal sulcus (STS), temporoparietal junction (TPJ), supplementary motor cortex (SMA), pre-supplementary motor cortex (preSMA), primary motor cortex (M1/PMC), first somato-sensori cortex (S1), superior parietal cortex (SPC), inferior parietal cortex (IPC).

Healthy control (HC), Major Depression Disorder (MDD), Obsessive Compulsive Disorder (OCD), Autism Spectrum Disorder (ASD), behavioral variant frontotemporal dementia (bvFTD).

* Study reported using optimized fMRI sequence for full brain coverage.

* Result only found using a ROI analysis.
reported findings using a ‘basic’ negative emotion contrast condition (Basile et al., 2014, 2011; Wagner et al., 2011), and three studies reported contrasting a target negative moral emotion with either a positive moral emotion (e.g., pride) (Fourie et al., 2014; Roth et al., 2014) or a matched ‘social’ condition (Finger et al., 2006). Finally, ten studies reported correlations between individual differences in a target negative moral emotion and either brain function or structure (Fourie et al., 2014; Morey et al., 2012; Morita et al., 2008, 2012, 2013; Pulcu et al., 2014; Sturm et al., 2012; Yu et al., 2014; Zahn et al., 2014, 2009).

Arguably, the most robust approach to support specific shame-, embarrassment- and guilt-related brain activity is to compare these emotions with one another. However, only four studies reported such contrasts in healthy populations (Michl et al., 2014; Pulcu et al., 2014; Takahashi et al., 2004; Wagner et al., 2011). Findings from these studies are illustrated in Fig. S2 in the Supplementary material and discussed below in the sections describing shame-, embarrassment-, and guilt-related brain activity compared to a specific emotion control condition. Note that the results of these studies are included in Figs. 2 and 3.

3.2. The neurobiology of shame

Only four functional studies specifically reported shame related brain activation: three using fMRI in healthy populations (Michl et al., 2014; Roth et al., 2014; Wagner et al., 2011) and one looking
at patients with remitted Major Depressive Disorder (MDD) (Pulcu et al., 2014). Michl et al. (2014) used a paradigm involving the presentation of short sentences designed to evoke shame and other emotions (adapted from Takahashi et al., 2004), Roth et al. (2014) and Wagner et al. (2011) both used an autobiographical recall task where participants were instructed to remember personal events that elicited shame among other emotions.

3.2.2. Shame compared to a neutral control condition

In these studies, shame compared to a neutral condition, was associated with increased activation in prefrontal areas including the dorsolateral prefrontal cortex (dlPFC) (Michl et al., 2014; Roth et al., 2014), the ventrolateral prefrontal cortex (vlPFC) (Roth et al., 2014) and the dorsomedial prefrontal cortex (dmPFC) (Michl et al., 2014; Wagner et al., 2011). Increased activation was also found in the anterior inferior temporal (aITC), the anterior middle
temporal (aMTC) (Wagner et al., 2011) anterior superior temporal cortices (aSTC) (Michl et al., 2014), and anterior insula cortex (AIC) (Michl et al., 2014; Roth et al., 2014; Wagner et al., 2011). In addition, Wagner et al. (2011) found shame to be associated with increased activation in parietal regions including the angular gyrus and the precuneus whereas Michl et al. (2014) and Roth et al. (2014) reported activation in the posterior cingulate cortex (PCC) and subcortical involvement, including the parahippocampal gyrus (Michl et al., 2014), basal ganglia (pallidum and caudate head; Roth et al., 2014). Increased brain activation was also reported in sensorimotor areas (Michl et al., 2014; Roth et al., 2014), the visual cortex (Michl et al., 2014; Wagner et al., 2011) and the cerebellum (Michl et al., 2014; Roth et al., 2014; Wagner et al., 2011). Further Roth et al. (2014) reported shame to be associated with decreased activity in the superior parietal cortex (SPC) and supramarginal gyrus.

3.2.2. Shame compared to a (basic or moral) negative emotion control condition

Three studies compared shame to another (basic or moral) negative emotion in healthy populations (Michl et al., 2014; Pulcu et al., 2014; Wagner et al., 2011), but only two studies reported significant shame-related activation (Michl et al., 2014; Wagner et al., 2011). Wagner et al. (2011) reported increased activation in the primary motor cortex (precentral gyrus) when comparing shame to sadness but no significant effect when comparing shame to guilt. Michl et al. (2014), on the other hand, found increased activation for shame compared to guilt in the dlPFC, the AIC, the dorsal anterior cingulate cortex (dACC), the PCC, and in subcortical areas including the parahippocampal cortex and the dorsal anterior midbrain.

While the current neuroimaging on shame in healthy individuals is still extremely limited, it is notable that among the four studies reported, one investigated the neural correlates of individual differences in shame and reported a positive correlation of unpleasantness ratings for shame trials with posterior insula cortex (PIC) signal for shame versus guilt in healthy individuals (Pulcu et al., 2014).

3.2.3. Psychiatric population findings

With regard to results from studies of psychiatric populations, Pulcu et al. (2014) examined shame in remitted MDD participants using a script-based paradigm consisting of statements describing actions counter to social/moral standards, and requiring participants to rate their level of unpleasantness experienced. When looking at the effects of shame (shame > guilt trials based on individual post-scan classification), only in the remitted-MDD group was shame associated with activation in the right amygdala and right posterior insula cortex, whereas in the control group there were no significant effects (Pulcu et al., 2014).

3.3. The neurobiology of embarrassment

More research has examined the neurobiological underpinning of embarrassment than shame. Embarrassment is arguably a more readily grasped moral emotion: it is a self-conscious emotion directly related to the presence of a public audience, and has been investigated in six fMRI studies to date. Five studies used healthy subjects (Finger et al., 2006; Moll et al., 2007; Morita et al., 2008, 2013; Takahashi et al., 2004) and one investigated the neural correlates of embarrassment in high-functioning Autism Spectrum Disorder (ASD) (Morita et al., 2012). In addition, structural MRI has been used to investigate embarrassment in patients suffering from behavioral variant frontotemporal dementia (bvFTD) and controls (Morita et al., 2012).

The majority of these studies used statements or short scenarios to induce embarrassment. Takahashi et al. (2004) used three types of short sentences as stimuli designed to trigger embarrassment and other feelings. Finger et al. (2006) used written short stories depicting social situations moderated by the presence vs. absence of an audience to trigger embarrassment, and Moll et al. (2007) used written scripts in a moral sentiment task to elicit the emotional experience of embarrassment. Three studies from the same group used facial feedback images of the self and others to induce embarrassment (Morita et al., 2008, 2012, 2013). Finally, one study induced embarrassment using video recordings of a karaoke singing task (Sturm et al., 2012).

3.3.1. Embarrassment compared to a neutral control condition

Out of the six fMRI studies, two looked at embarrassment in relation to a neutral condition and found embarrassment to be associated with increased brain activation in the dmPFC (Moll et al., 2007; Takahashi et al., 2004), the vlPFC (Takahashi et al., 2004), the dACC (Moll et al., 2007), the AIC (Moll et al., 2007), the anterior temporal lobes (ATL: aITC and aMTC; Takahashi et al., 2004), the posterior superior temporal sulcus (STS) (Moll et al., 2007; Takahashi et al., 2004) and the temporoparietal junction (TPJ) (Moll et al., 2007). In addition, Takahashi et al. (2004) also found increased brain activation in the left hippocampus and visual cortex (calcarine and lingual gyri).

3.3.2. Embarrassment compared to an emotion control condition

Two studies investigated embarrassed-related brain activity when compared to another emotion (Finger et al., 2006; Takahashi et al., 2004). Comparing embarrassment to guilt, increased brain activation was reported in the dmPFC, aMTC, bilateral hippocampus, dorsal midbrain and visual cortex (calcarine, lingual gyrus and inferior occipital gyrus; Takahashi et al., 2004). Comparing an embarrassment condition to a matched non-embarrassment social condition, Finger et al. (2006) found embarrassment to be associated with activation in the dmPFC, vlPFC and the amygdala.

3.3.3. Individual differences in self-reported embarrassment

Two studies by Morita and colleagues looked at individual differences in self-reported embarrassment in healthy populations (Morita et al., 2008, 2013). While Morita et al. (2013) showed a positive correlation between self-reported embarrassment and activity in the AIC, Morita et al. (2008) found the opposite pattern with a negative correlation between AIC activity and embarrassment. In addition, Morita et al. (2008) reported self-reported embarrassment to be negatively correlated with activity in the dlPFC.

3.3.4. Psychiatric population findings

Only one study examined the emotional experience of embarrassment in psychiatric population. Using the same paradigm as in studies described above (Morita et al., 2008, 2013), Morita et al. (2012) found embarrassment to be positively correlated with activity in the vlPFC and AIC in individuals with Autism Spectrum Disorder (ASD).

3.3.5. Structural MRI findings

One sMRI study to date has investigated the neuroanatomical correlates of embarrassment. Sturm et al. (2012) induced embarrassment using a karaoke singing task and found that across both healthy controls and patients with frontotemporal dementia (FTD), as well as within each group, larger right pregenual anterior cingulate cortex (pACC) gray matter volume was associated with higher levels embarrassment observed during the task.

3.4. The neurobiology of guilt

Fifteen studies have investigated the neurobiological correlates of guilt, with one using PET, thirteen using fMRI, and one combining fMRI and sMRI. The most common methodology for eliciting guilt
in participants was to use emotion induction statements (Finger et al., 2006; Green et al., 2012; Kédia et al., 2008; Michl et al., 2014; Moll et al., 2007; Morey et al., 2012; Pulcu et al., 2014; Takahashi et al., 2004; Zahn et al., 2009). Other studies used alternate methods such as emotion induction statements paired with facial expressions (Basile et al., 2014, 2011), autobiographical recall (Shin et al., 2000; Wagner et al., 2011), an interpersonal game paradigm (Yu et al., 2014), and an implicit-association test (IAT) (Fourie et al., 2014). The latter was a dual categorization task involving feedback indicating that the participant was prejudiced based on their performance. While most of these studies looked at healthy controls, some looked at mental disorders such as remitted MDD and Obsessive Compulsive Disorder (OCD).

3.4.1. Guilt compared to a neutral control condition

Studies have found the experience of guilt to be associated with function and structure of prefrontal, temporal, cingulate, and subcortical brain regions. Studies examining guilt in relation to a neutral condition found increased guilt-related activity in prefrontal areas of the brain (dmPFC; Fourie et al., 2014; Michl et al., 2014; Moll et al., 2007; Takahashi et al., 2004; Wagner et al., 2011) (vPFC; Moll et al., 2007; Wagner et al., 2011) (dIPFC; Michl et al., 2014; Wagner et al., 2011). Activation in the temporal lobes was also commonly associated with guilty feelings, with studies reporting increased activation in anterior (Michl et al., 2014; Moll et al., 2007; Shin et al., 2000; Wagner et al., 2011) and posterior (Michl et al., 2014; Moll et al., 2007; Takahashi et al., 2004; Wagner et al., 2011) temporal regions. Increased guilt-related brain activation was also reported in a number of studies in both the anterior (AIC; Fourie et al., 2014; Shin et al., 2000) and posterior (PIC; Wagner et al., 2011) regions of the insula cortex. Increased guilt-related brain activation was reported in a number of cingulate regions including the dACC (Fourie et al., 2014; Shin et al., 2000), middle cingulate cortex (MCC; Shin et al., 2000), and dorsal PCC (Fourie et al., 2014) and parietal regions including the supramarginal gyrus (Wagner et al., 2011), angular gyrus and parietal operculum (Wagner et al., 2011), and precuneus (Fourie et al., 2014; Wagner et al., 2011). An increase in brain activation in relation to guilt was also reported in several subcortical regions including the thalamus (Fourie et al., 2014; parahippocampal gyrus (Wagner et al., 2011), dorsal midbrain (Moll et al., 2007), and basal ganglia (Wagner et al., 2011). Finally, activation in several areas of the sensorimotor cortex (Michl et al., 2014; Moll et al., 2007; Shin et al., 2000; Wagner et al., 2011), the visual cortex (Michl et al., 2014; Takahashi et al., 2004; Wagner et al., 2011) and the cerebellum (Michl et al., 2014; Shin et al., 2000; Wagner et al., 2011) were associated with guilt. In addition, guilt was associated with decreased activity in the PIC, precuneus, sensorimotor cortex (precentral gyrus) and visual cortex (Shin et al., 2000).

3.4.2. Guilt compared to an emotion control condition

Thirteen studies investigated the experience of guilt in relation to other emotions, or investigated the experience of specific types of guilt. Some studies explored guilt by contrasting it to the experience of shame (Michl et al., 2014; Pulcu et al., 2014; Wagner et al., 2011), embarrassment (Takahashi et al., 2004), ‘basic negative’ emotions (e.g., anger, sadness) (Basile et al., 2011; Kédia et al., 2008; Wagner et al., 2011), indignation (Green et al., 2012), and indignation and pride (Zahn et al., 2009). Less frequently, guilt conditions were contrasted with other conditions that were designed to eliminate variance associated with the experience of moral emotions more generally (Fourie et al., 2014; Yu et al., 2014), or specific types of guilt were contrasted, such as guilt related to others versus the self (Morey et al., 2012) and deontological guilt versus altruistic guilt (Basile et al., 2011).

Findings from these studies showed guilt-specific activation in the dmPFC (Basile et al., 2011; Finger et al., 2006; Fourie et al., 2014; Morey et al., 2012; Takahashi et al., 2004; Wagner et al., 2011), as well as other areas of the prefrontal cortex including the vIPFC and dIPFC (Wagner et al., 2011). Activation in cingulate regions were also commonly associated with guilt-specific feelings, especially in the dACC (Basile et al., 2011; Green et al., 2012; Wagner et al., 2011) and ventral ACC (Basile et al., 2011), but also in the MCC (Yu et al., 2014) and PCC (Fourie et al., 2014). A number of studies also reported an increase in activation in the AIC (Basile et al., 2011; Fourie et al., 2014; Wagner et al., 2011; Yu et al., 2014) during the experience of guilt. In terms of temporal lobe, activation in the posterior MTC (Finger et al., 2006; Green et al., 2012; Kédia et al., 2008; Michl et al., 2014; Morey et al., 2012) appeared to be most frequently reported in relation to guilt, with some studies also reporting increased brain activation in the anterior MTC (Green et al., 2012; Wagner et al., 2011), anterior STC (Finger et al., 2006), posterior STS (Fourie et al., 2014) and TPJ (Kédia et al., 2008). Increased activation in the precuneus (Basile et al., 2011; Kédia et al., 2008; Morey et al., 2012) was also commonly associated with guilty feelings. In addition, increased guilt-related activation was reported in several subcortical regions including the thalamus (Michl et al., 2014), the amygdala (Wagner et al., 2011) and basal ganglia (Fourie et al., 2014; Wagner et al., 2011). Finally, guilt-related activation was also reported in areas of the sensorimotor cortex (Green et al., 2012; Kédia et al., 2008) the visual cortex (Green et al., 2012; Michl et al., 2014; Morey et al., 2012) and the cerebellum (Wagner et al., 2011).

3.4.3. Individual differences in self-reported guilt

Three studies investigated individual differences in self-reported guilt in healthy individuals. The experience of guilt was found to be positively correlated with activity in the ventromedial PFC (Zahn et al., 2009), dmPFC and vIPFC (Morey et al., 2012), the vACC (Zahn et al., 2009) and the inferior parietal cortex (IPC; Morey et al., 2012). On the other hand, guilt ratings were also found to be negatively correlated with activity in the dIPFC and vIPFC (Morey et al., 2012), the MCC (Morey et al., 2012) and vACC (Fourie et al., 2014), the PIC, the posterior MTC, the SPC and precuneus, as well as the postcentral gyrus cortex and cuneus (Morey et al., 2012).

3.4.4. Psychiatric population findings

With regard to results from studies of psychiatric populations, all studies examined guilt-relatedness to specific mental disorders (Basile et al., 2014; Green et al., 2012; Pulcu et al., 2014). Both Pulcu et al. (2014) and Green et al. (2012) examined guilt in remitted MDD patients using a script based paradigm consisting of statements describing actions counter to social/moral standards, and requiring participants to rate their level of unpleasantness experienced. The third study, by Basile et al. (2014), investigated the experience of guilty feelings in OCD patients using an emotion induction statements paired with facial expressions where they were instructed to imagine oneself in a situation and rate their level of guilt experienced. One of these studies reported significant results for guilt across patient and control groups (remitted MDD and HC: guilt × indignation) with increased activation in the ventral ACC and basal ganglia (Green et al., 2012). Reduced guilt-related activation was found for patients compared to controls in other regions. Basile et al. (2014) found reduced guilt-related activity in OCD compared to control participants in a range of regions (Basile et al., 2014) while Pulcu et al. (2014) appeared to find reduced guilt-related activity in the amygdala and PIC in remitted MDD patients compared to controls (Pulcu et al., 2014).
3.4.5. Structural MRI findings

One sMRI study conducted to date reported a positive correlation between gray matter volume in the anterior MCC and sensitivity to guilty feelings (Yu et al., 2014). Fig. 2 and 3 present a simplified summary of the results of the reviewed studies.

4. Discussion

To date, the majority of brain imaging research investigating emotional processes has focused on basic emotions such as anger, sadness, fear and happiness. While this research has been useful in providing information about the neural substrates of these emotions in mental health and illness, neuroimaging research that aims to characterize the neural basis of more complex social emotions is paramount. The identified neuroimaging studies of self-blaming negative moral emotions differed in terms of methodologies and statistical analyses employed (discussed further below). Some studies reported brain function or structure that was associated with shame, embarrassment or guilt without testing for specificity (e.g., variance in brain function/structure associated with the experience of negative affect more generally was not controlled for). In order to provide a meaningful interpretation of the shared and unique neural correlates of shame, embarrassment and guilt, only results from analyses that attempt to test specificity (i.e., by controlling for the experience of another basic or moral emotion) are discussed below. Results in healthy controls are discussed in Sections 4.1 and 4.2. Results in psychiatric populations are discussed in Section 4.4.

4.1. Common and distinct neural circuitry underlying self-blaming negative moral emotions

A number of brain regions were associated with more than one self-blaming emotion. Shame and guilt appeared to share an association with ACC function (see Figs. 2 b and 3). The insula cortex is known to contribute to diverse mental functions such as motor control, interoceptive awareness and emotion. The role of the insula in emotion is broad, and the function of the insula have been linked to the experience of a number of positive and negative emotions. The insula is known to play a role in representing emotional states, especially in relation to processing subjective feelings, empathy and uncertainty (Singer et al., 2009). Furthermore, the ACC has been shown to be involved in the experience of interoceptive awareness (Craig, 2009). These functions are all likely to contribute to the reported role of the insula in negative moral emotions, generally. Additionally, there is evidence from lesion studies for the role of the ACC in disgust, and it has been suggested that disgust toward the self may be present in negative moral emotions (Calder et al., 2001). The association between ACC activity, shame and guilt (but not embarrassment) may echo previous association of the ACC’s sensitivity in relation to emotional and cognitive aspects of pain (Pavuluri and May, 2015; Wiech et al., 2014), and the definition of shame and guilt as more painful and damaging negative emotions compared to embarrassment (Tangney et al., 1996).

Shame and guilt were also both associated with dACC function. Different ACC regions have previously been involved in a range of functions including the experience of negative affect (Mayberg et al., 2014), the experience of social pain (Eisenberger and Lieberman, 2004) and interoceptive awareness (Khalsa et al., 2009). The known role of the dACC, in the experience of distress and particularly social pain (Masten et al., 2011) may explain its common role in the experience of these emotions. Shame and embarrassment were both associated with hippocampal and midbrain function. While the hippocampus has been associated with several brain functions such as memory, emotion processing and regulation of stress (Brody et al., 2001; Morgane et al., 2005), the report of hippocampus-related activation with both shame and embarrassment is interesting. The role of the hippocampus in responding to psychosocial stress (Dranovsky and Hen, 2006; McEwen, 2001) may be particularly important for the experience of shame and embarrassment given that both of these emotions (perhaps more so than guilt) are associated with threat from the external environment to the self (Tangney, 1996; Tangney et al., 1992b).

Embarassment and guilt were both associated with dmPFC, vlPFC and anterior temporal lobe function. The dmPFC plays a role in self-referential processing (Northoff et al., 2006) and mentalizing, also commonly referred to as the Theory of Mind (ToM) and the ability to infer others’ feelings, thoughts and intentions (Isoda and Norieske, 2013; Kang et al., 2013). The aptitude to estimate others’ intentions may parallel the necessary skills to read social cues and emotional states of others in order to experience self-blaming emotions when social/moral rules are broken. ToM may play more of a role in embarrassment and guilt than shame, given that shame is less likely to be associated with perceiving others’ feelings and more likely to be associated with self-focused cognition (Wong and Tsai, 2007).

The vlPFC has frequently been implicated in moral decision-making and disturbances (Harrison et al., 2012). The anterior temporal lobe is suggested to play a role in social conceptual knowledge, where it is required to understand social concepts and rules (Ross and Olson, 2010) and to be aware of situations that are likely to elicit moral emotions (Olson et al., 2007; Zahn et al., 2007). It is unclear why these regions may be specifically associated with guilt and embarrassment, but not shame. Given the few studies focusing on shame, further research is required to confirm any emotion specificity.

Shame, embarrassment and guilt were also found to have some neurobiological specificity. From the small number of studies (i.e., four) directly comparing shame, guilt and embarrassment with at least one other of these emotions, there was only evidence for guilt-specific activity in the dmPFC, posterior MTC, amygdala, basal ganglia, thalamus, and cerebellum (see Fig. S1 in Supplementary material). However, the review of studies that attempted to assess specificity in some way (either by controlling for negative affect or moral affect), provide some evidence that these three emotions might have different underlying neuronal circuitry. Shame appeared to be uniquely associated with dIPFC, PCC and sensorimotor cortex function. Considering previous findings showing the role played by the lateral PFC in the engagement of both cognitive and emotions regulation processes (Gray et al., 2002), it might be hypothesized that shameful feelings may require “harder mental work” to regulate the associated negative affect in comparison to guilt and embarrassment. This assumption is in line with the theoretical definition of shame describing it as a more damaging and distressful emotional experience. This explanation is consistent with the literature on depression (commonly associated with elevated shame, Andrews, 1995; Andrews et al., 2002; Kim et al., 2011: Pulcu et al., 2014)) that shows greater lateral PFC activation during emotion regulation in depressed patients (Johnstone et al., 2007). Recent studies have demonstrated the importance of the PCC in self-representation (Leech et al., 2011), a mental process related to moral reflection and again in line with the definition of shame as an emotion associated with strong concern with one’s own evaluation and a particular focus on the self (Tangney et al., 2011; Wong and Tsai, 2007).

A number of brain regions appeared to be ‘guilt-specific’ including the ventral (pregenual and subgenual) ACC, posterior temporal areas including the TPJ, the precuneus and premotor cortex. While activation of the vACC has long been associated with negative
affect (Drevets et al., 2008), its role in emotion regulation has more recently been acknowledged. In particular, the vACC has been associated with the inhibition of emotions (particularly fear), and it has been suggested that its activation may be associated with emotion regulation by facilitating planning of adaptive response (Etkin et al., 2011). This is in line with theoretical definition of guilt describing it as an introspactive emotion linked to the fear of punishment and the need for related-reparative actions. Further, guilt-specific association with the vACC is consistent with lesion studies showing that patients with ACC lesions experience reduced levels of guilt (Krajbich et al., 2009). Finally, posterior temporal regions, associated in previous studies with aspects of social cognitive and emotional processing (Decety and Lamm, 2007; Schilbach et al., 2008), were also reported to play a role in guilt. Guilt-specific activity in the TPJ and posterior MTC/STS is in line with the role of these regions in ToM, given that guilt has been particularly linked with other-processing including reading other’s state of mind/feelings/thoughts (Tangney, 1992; Tangney et al., 2007).

The precuneus, in close proximity to the PCC, has been demonstrated in recent studies to play a role in episodic memory retrieval, self-awareness-processing (Cavanna and Trimble, 2006; Kjaer et al., 2002; Morey et al., 2012) and emotional judgments (Morey et al., 2012). Given that shame was also found to be associated with precuneus activation (albeit only in studies that contrasted shame with a neutral condition), further research is required to understand whether and why precuneus function may be particularly linked to guilt experiences.

Finally, embarrassment appeared to be uniquely associated with vIPFC, amygdala and occipital function. The function played by the vIPFC in emotional processing (Stuss and Levine, 2002) and behavioral self-regulation (Beer et al., 2006; Goldstein, 1944), as well as the ventral pathway connection of this region to the amygdala in the limbic system may explain the involvement of both these regions during the experience of embarrassment. The increased functional coupling between the ventral PFC and the amygdala during reappraisal of negative emotion showing to result in reduced reported negative emotion (Banks et al., 2007; Schardt et al., 2010), whereas successful emotion regulation, is in line with the theoretical definition of embarrassment perceived as a less damaging and more adaptive emotion than shame. Additionally, the motivational response when feeling embarrassed being directed to self-preservation of one’s social reputation (Tangney et al., 1996) is consistent with the literature on lesion studies looking at the orbitofrontal cortex in the context of social behavior showing that damages to this region is associated with inappropriate social behavior (Beer et al., 2006). Shame on the other hand, as mentioned earlier, appeared to solicit a more dorsal pathway with shame-specific activation in the dmPFC and ACC. While both ventrolateral and dorsolateral PFC have previously been shown to play a role in processing negative emotions and reappraisal (Banks et al., 2007), the difference in PFC lateliness may lie in the specific nature of the definition of shame and embarrassment, with shame being more a distressing experience by affecting the entire self and therefore potentially requiring more complex cognitive processing during reappraisal of negative affects.

4.2. Self-blaming negative moral emotions and brain networks

It may be of relevance to interpret the neural correlates of shame, embarrassment and guilt in terms of brain networks. Parallels can be drawn between the regions implicated in each emotion and well-characterized brain networks including the default mode network (DMN), the ‘social brain’ network, and the mesolimbic network. The brain network of potentially most relevance is the DMN. The DMN demonstrates increased activity while an individual is at ‘rest’ compared to when performing demanding (and typically non-self-referential) cognitive tasks (Shulman et al., 1997). DMN areas include the PCC, dmPFC, inferior parietal cortices, precuneus (Buckner et al., 2008; Harrison et al., 2008) and the TPJ (Mars et al., 2012). While the DMN was first associated with passive or resting state tasks, it is now thought to play a role in self-regulatory mental processes, autobiographical memory, and thinking about the future. A number of studies have hypothesized about the importance of DMN function for moral decision-making (Greene et al., 2004, 2001; Harrison et al., 2008). Given these identified functions of the DMN, and the fact that many of the brain regions found to be associated with negative moral emotions overlap with DMN regions, it is reasonable to conclude that the DMN likely plays a role in the experience of guilt, shame, and/or embarrassment. The emotional experience of self-blaming emotion implies some sort of personal reflection and evaluation about the self, including reference to specific personal experiences; it takes into account social rules and moral expectations from others and society.

Parallels can also be drawn between brain regions whose activation was found to be associated with self-blaming negative moral emotions and a network of brain regions identified to underlie social cognitive processes (i.e., the ‘social brain’). The expression “social brain” refers to a complex network of brain regions that are involved in social interaction and processing of information about others including mentalizing (Blakemore, 2008; Frith, 2007). The brain regions that have been found to play a role in social cognition include the medial PFC, the vmPFC, the ACC, the TPJ, the posterior STS, and the amygdala (Blakemore, 2008; Frith, 2007; Kennedy and Adolphs, 2012). The ability to be aware of one’s own emotional state and to differentiate it from others’ is an important skill for survival, allowing for improved interindividual interaction and communication, and has been referred to as the ToM or ‘mentalizing’ (Schilbach et al., 2008). In a majority of cases, negative moral emotions are experienced in response to a ‘wrong/amoral’ action that has affected others and/or witnessed by others, which therefore implies the agent’s ability to not only reflect on their own behavior and identity but to also be able to read and relate to others’ emotional states. The neural regions found to be involved in the experience of self-blaming emotions appear to overlap with several brain regions associated with social cognitive skills such as mentalizing (Zaki and Ochsner, 2012).

Correspondences can also be drawn between brain regions whose activation was found to be associated with self-blaming negative moral emotions and the mesolimbic emotional network. This network comprises a set of subcortical regions that have been found to play a role in various functions such as motivation, memory and emotion processing and regulation, including mood and stress responsiveness (Brody et al., 2001; Morgane et al., 2005). The overlap between the brain regions reported in the literature on self-blaming emotions and those recognized as part of the mesolimbic network include the amygdala, the hippocampus, the hypothalamus, the cingulate gyrus, and areas of the basal ganglia, the insula and the parahippocampal gyrus. This parallel between the functions of some of the brain regions involved in the mesolimbic system and negative moral emotions may be due (as mentioned above) to the role played by the mesolimbic system in the processing and experience of negative emotional states (Kelley and Berridge, 2002).

It is of note that some research (not included in the review) has investigated the neural basis of self-blaming negative emotions using network approaches (i.e., functional connectivity). Three studies by Green and colleagues investigated guilt-related functional connectivity when compared to indignation in healthy and remitted MDD populations (Green et al., 2013a, 2012, 2010). Green et al. (2010) reported selective functional integration between subgenual cingulate/septal regions (SCS) and superior ATL in healthy control (HC) individuals. Green et al. (2012) reported between
group (HC > remitted MDD) connectivity between right superior ATL seed region and SCNR, bilateral medial frontal cortex, lateral hypothalamus and hippocampus, as well as within group (HC) connectivity between the SCNR, hippocampus, hypothalamus, amygdala, dACC and occipital pole. Functional connectivity results specific to the MDD population did not show significant results (Green et al., 2013a, 2012). Based on these findings, future work should employ measures of connectivity to further elucidate the role of neural networks in the experience of shame, embarrassment and guilt.

4.3. Methodological considerations

The above summary of the available research on the neural correlates of shame, embarrassment and guilt offers preliminary insight into the brain substrates underlying the experience of negative moral emotions that are crucial for adaptive social functioning and that are commonly compromised in mental ill-health. As a result of the limited number of studies and the wide variety of methodology used, it is difficult to compare studies and draw confident conclusions. It is arguably difficult to illicit such emotions in experimental situations. For example, the ability of participants to project themselves into the situation presented by script-driven scenarios is uncertain, and as such validity of findings must be questioned. Although several studies collected post-scan (Basile et al., 2014, 2011; Finger et al., 2006; Green et al., 2012; Michl et al., 2014; Moll et al., 2007; Morita et al., 2008, 2012, 2013; Pulcu et al., 2014; Takahashi et al., 2004; Yu et al., 2014), or in-scanner (Basile et al., 2014, 2011) self-reported ratings of the emotions experienced during the experiment, others assumed that a specific emotion was elicited without validation with self-report measures. In some cases self-report of emotion was arguably redundant (e.g., autobiographical recall). However, in many cases, it could be argued that the reported brain activation was not necessarily associated with the emotion intended by the research.

Much neuroimaging research has utilized moral dilemmas to investigate the neural correlates of moral decision-making processes (Casebeer and Churchland, 2003; Greene et al., 2004; Heekeren et al., 2005, 2003). Typically, such studies employ paradigms using moral dilemmas, also called ethical dilemmas, which are hypothetical situations that require a decision to be made between two options that are equally balanced in terms of negative and positive outcomes. The process of decision-making in these types of dilemmas generally evokes strong conflict regarding justice, ethicality and morality. Defining whether moral dilemmas have a ‘right’ or ‘wrong’ answer can be a real philosophical debate depending on various factors, and where pros and cons can be found on both sides. Yet, it is this fragile balance between the two possible choices as well as the fact that there are always consequences (both positive and negative) of the decision made (Moll et al., 2005) that may suggest good grounds for using moral situations to build new innovative and controlled tasks to elicit self-blaming emotions such as guilt, shame and embarrassment. Whereas existing paradigms used to elicit moral emotions suffer from methodological limitations (as noted above), utilizing moral dilemmas in new paradigms could be useful as a tool to capture brain activity during the experience of moral emotions.

Another challenge in terms of study comparison is the variety of statistical contrasts used by researchers to look at specific negative moral emotions. The majority of studies compared one single emotion to a neutral condition, which is problematic given that one cannot be certain that results do not reflect activation related to the experience of negative affect. Furthermore, while several studies contrasted one specific emotion to another emotion (e.g., guilt versus indignation) or group of emotions (e.g., guilt versus basic emotions), and these were the results that formed the basis for our discussion, the specific control emotions used in contrasts varied widely (e.g., indignation, self-anger, group of basic emotions). Finally, some studies used regression analyses to assess linear associations between emotional ratings and brain function/structure, adding again to the complexity of comparing results between studies. There is therefore a need for replication and greater consistency between study methods. Ultimately, the definitions of these moral emotions have long been debated, and different studies may have drawn on different theoretical descriptions when designing stimuli. For example, emotions labeled as embarrassment in some work (Takahashi et al., 2004) were labeled as shame in other work (Michl et al., 2014). Further, the definitions of emotions were sometimes unclear. Thus, future work should be clear about the definitions of the emotions that they aim to probe, in addition to being clear about the rationale for using a specific paradigm to tap into those emotions.

4.4. Implications for psychopathology

While understanding the neurobiological underpinnings of self-blaming emotions in healthy individuals is paramount and there is still an undeniable need for more studies in this area, there is also a need for more neuroimaging research that investigates the neural correlates of negative moral emotions in individuals with mental health disorders, such as depression, anxiety and psychopathy. To date, the majority of brain imaging research examining shame, embarrassment and guilt has focused on healthy populations with only 4 studies including psychiatric populations. Among these, two studies examined shame and/or guilt in remitted MDD: one study reported a group by emotion (guilt, shame) effect for activation in the amygdala and posterior insula cortex (Pulcu et al., 2014). The second study found reduced guilt-related activity in patients in the PIC and parietal-occipital junction (Greene et al., 2012). Another study examined individual differences in self-reported embarrassment in individuals with ASD and found a positive correlation with activity in the VLPFC and AIC (Morita et al., 2012). Finally, one study investigated guilt-related activity in patients with OCD (Basile et al., 2014), and found reduced activity in patients across a number of regions.

The small number of studies and different methodologies/statistical contrasts used makes these findings difficult to integrate, but given that these emotions are known to be experienced ‘abnormally’ in a number of mental disorders, further research is clearly warranted. Guilt has for a long time been recognized to play an important role in depression, more recently, researchers have found that both shame and guilt are strongly associated with depressive disorders (Pulcu et al., 2014, 2013). It however remains uncertain whether and how shame and guilt are uniquely associated with depression or whether one has stronger links to the onset and maintenance of this disorder. One of the characteristics of depressed patients is their tendency to blame themselves for negative events (internal attribution), to generalize the situations (global attribution) and to perceive consistency in the cause of the event (stable attribution) (Abramson et al., 1989). It has been shown that both shame and guilt involve the tendency to make internal attributions for negative situations (Pineles et al., 2006). These characteristics resonate with the dysfunctional experience of self-blaming emotions: to blame the entire self for what happened (shame) and to blame one’s own behavior for something bad happening (guilt). It has been shown in recent researches that people suffering from depression are more likely to experience self-blaming emotions than emotions associated with blaming others, suggesting a more specific negative emotion tendency directed towards the self (Green et al., 2013b; Zahn et al., 2015). Furthermore, this relationship between the experience of self-blaming emotions such as shame/guilt and depression...
6. Conclusions

Negative moral emotions, particularly shame, embarrassment and guilt, are important emotions for adaptive functioning in society: they play a particularly important role in the maintenance and development of social relationships. This systematic review summarized the current knowledge about neural correlates of these emotions, and highlighted the similarities and differences between them. All three emotions were suggested to be associated with function of neural systems underlying emotional processing, self-referral processing and social cognition. Further research is needed to comprehensively understand the neural correlates of these emotions (particularly shame and embarrassment, which have received the least study), and future research should be mindful of the methodological difficulties in inducing these kinds of moral emotions. Finally, the fact that self-blaming emotions can become dysfunctional when inappropriately experienced, and therefore contribute to the development and progression of mental disorders, suggests the need for more research in this area.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.neubiorev.2016.09.019.

References


