Article

The Neural Signatures of Shame, Embarrassment and Guilt: A Voxel-based Meta-analysis on Functional Neuroimaging Studies

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Abstract: Self-conscious emotions, such as shame and guilt, play a fundamental role in regulating moral behavior and in promoting the welfare of the society. Despite their relevance, the neural bases of these emotions are uncertain. In the present meta-analysis, we performed a systematic literature review in order to single out functional neuroimaging studies on healthy individuals specifically investigating the neural substrates of shame, embarrassment and guilt. Seventeen studies investigating the neural correlates of shame/embarrassment, and seventeen studies investigating guilt brain representation met our inclusion criteria. The analyses revealed that both guilt and shame/embarrassment were associated with the activation of the left anterior insula, involved in emotional awareness processing, and arousal. Guilt specific areas were located within the left temporo-parietal junction, which is thought to be involved in social cognitive processes. Moreover, specific activations for shame/embarrassment involved areas related to social pain (dorsal anterior cingulate, insula, thalamus), behavioral inhibition (premotor cortex) networks. This pattern of results might reflect distinct action tendencies associated with the two emotions.

Keywords: self-conscious emotions; shame; embarrassment; guilt; moral emotions; anterior insula

1. Introduction

Moral emotions are crucial in regulating social interactions, as they promote the welfare of the society or of other people (Haidt et al., 2003). Indeed, they provide the emotional drive to properly behave in social interactions (Kroll and Egan, 2004; Piretti et al., 2020; Grecucci et al., 2021), forcing individuals to implement strategies that are optimal over a long period, even though they do not appear functional in the short period (Ridley, 1996; Sober and Wilson, 1998).

It has been proposed that moral cognition depends on prefrontal, temporal and the limbic circuits, associated with the integration of context- independent and -dependent information with the associated emotional reactions (event-feature-emotion complexes model, EFEC) (Moll et al., 2005; 2008). Specifically, the prefrontal cortex seems to be responsible for representing context-dependent knowledge of event sequences (Grafman, 1995; Wood and Grafman, 2003), the temporal lobes for perceiving social cues and for representing context-independent social semantic knowledge (Lambon Ralph et al., 2017; Olson et al., 2013; Haxby et al., 2000), and the limbic system for the generation of emotional and motivational states (Saper et al., 2000). Hence, according to the EFEC model, the generation of moral emotions, including self-conscious emotions, relies on integrity of a network including prefrontal, temporal and limbic areas (Moll et al., 2005; 2008).

Several studies investigating the neural substrates of moral cognition (Eres et al., 2017; Bzdok et al., 2012), confirmed the anatomical predictions of this model and better defined the topography of the brain areas associated with moral processing. Indeed, they showed that ventromedial and dorsomedial prefrontal cortices (vmPFC and dmPFC), temporo-parietal junction (TPJ), precuneus, posterior cingulate cortex, left amygdala, anterior temporal lobes (ATL) and lateral orbitofrontal cortex were consistently found activated in neuroimaging studies investigating moral processing (Bzdok et al., 2012; Eres et al., 2017; Grecucci et al., 2021; Piretti et al., 2020).

Among moral emotions, a sub-group of emotions (e.g., shame, embarrassment, guilt and pride), defined as self-conscious emotions, helps individuals to navigate in the complexities of fitting into groups (Haidt, 2003), satisfying the human need of belonging to social groups (Baumeister and Leary, 1995). Self-conscious emotions are evoked by self-reflection and self-evaluation (Tangney et al., 2007) and occur when social norms, or agreed-upon social rules, are violated (Bastin et al., 2016). The provide an immediate feedback that promote inhibition or reinforcement of behaviour based on their positive or valence (Tangney et al., 2007; Grecucci et al., 2021; Piretti et al., 2020). One case in point, is shame that has been proposed as an algorithm the brain uses to inhibit socially and morally unwanted behaviors (Piretti et al., 2020; Grecucci et al., 2021).

While the EFEC model might explain the cognitive processes underlying all self-conscious emotions, which are all induced by moral and social norm violation (Bastin et al., 2016), it does not make any prediction about the different processes that might occur in different types of emotions such as the negative self-conscious emotions.. Indeed, even though shame, embarrassment and guilt are often (but culpably) used interchangeably, they appear to be substantially different (Gibson, 2015). Shame is typically elicited by the belief that the individual's violation of standards of morality, aesthetics or competence, defines who the individual is (Wong and Tsai, 2007). Hence, it involves the way the individuals perceives themselves and how they believe other people see them and their inadequacy to fulfil social standards (Tangney et al., 1992). The distinction between shame and embarrassment is still a matter of debate (for review see Crozier, 2014). If on the one hand, embarrassment might be considered as a dimension of shame (Probyn, 2005), on the other, it might represent a distinct emotional entity (Keltner and Buswell, 1997; Tangney et al., 1996). Embarrassment seems related to trivial social transgressions, occurring suddenly and in public contexts, especially in presence of individuals with equal or higher hierarchical social status. (Keltner & Buswell, 1996; Tangney et al., 1996; Buss, 2001; Haidt, 2003; Tangney, 2003). Conversely, shame emerges when one perceives personally the serious violation of a moral norm, that might be also experienced in private situations (Tangney et al., 1996; Tangney, 2003). Furthermore, shame and embarrassment are also distinct in the intensity (i.e., shame is more intense than embarrassment) (Rochat, 2009), in the duration (i.e., shame is more persistent than embarrassment) (Scheff, 1994) and in the focus of attention (i.e., shame affects the self, embarrassment affects the persona, the apparent self). However, these two emotions have also some features in common. They are associated with the same specific physiological reactions (e.g., blushing) (Sabini and Silver, 2005) and the same action tendency, leading people to hide and reduce their social presence and making movement and speech more difficult and less likely (Asendorpf, 1990, Keltner and Buswell, 1997, Lewis, 1993; Miller, 1996). However, it has also been reported that, differently from shame, embarrassment leads to reparative behaviours to re-gain social approval (Feinberg et al., 2011; Keltner and Buswell, 1997; Leary et al., 1996). At the neural level, shame was selectively associated with with dlPFC, posterior cingulate cortex and sensory-motor cortex, whereas embarrassment with vlPFC, amygdala and occipital areas, and both emotions with hippocampus and midbrain (Bastin et al.,2014). However, it must be acknowledged that, since the distinction between shame and embarrassment is not sharp, being classified according to the private-public, moral-conventional or low-high intensity dimensions, it is not easy to establish which brain areas are involved in processing these emotions, and which areas might selectively process one of the two emotions.

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If the difference between shame and embarrassment is not as clear-cut, the distinction between guilt and the other two emotions is more evident. Guilt occurs when the violation of social norms induces harm or suffering to other individuals (Hoffman, 1982; Grecucci et al., 2021; Piretti et al., 2020), typically in a relationship or among members of the same group (Fiske, 1991). Differently from shame and embarrassment in which, respectively, the self and the persona are perceived as defective, in guilt a specific action is typically perceived as wrong (Hoffman, 1982; Lewis, 1971; Lewis et al., 1993). The occurrence of guilt induces remorse and behavioural responses that aim to repair the wrong action (Tangney et al., 2007). This difference in the focus, self-oriented and other-oriented, for shame and guilt respectively, has important consequences on empathy for other people: while guilt tends to increase the empathic concern towards other people, empathic responses seem to be disrupted by self-oriented distress associated with shame (Tangney et al., 2007).

Table 1. Differences between shame and guilt.

	SHAME	GUILT
Target	What we are: related to the entire self. "I'm bad"	What we do: related to specific behaviours "What I did has been bad"
Level	Interpersonal – it occurs only with others	Intrapsychic – it occurs alone
Emotional activation	Painful	Less painful
Emotional perception	Difficult to recognize	Easy to recognize
Action tendency	Motivates hiding and inhibition	Motivates reparation to the situation
Relation with aggression, hostility, violence, externalization	Increased for shame-proneness individuals	Decreased for guilt- proneness individuals
Scapegoat	Blame mainly others	Blame myself
Responsibility	Deflected outward	Accepted

In a review, Bastin and collaborators (2014) suggested that guilt processing was selectively associated with ventral ACC, precuneus, premotor and posterior temporal areas. In addition, both guilt and shame processing were associated with anterior insula and dACC, and that both guilt and embarrassment processing with dorsomedial prefrontal cortex (dmPFC), vlPFC and anterior temporal lobe (ATL) (Bastin et al., 2014). In addition, a recent meta-analysis (Gifuni et al., 2017) partially confirmed the guilt neural substrates proposed by Bastin and collaborators (2014), reporting the activation of precuneus, dorsal ACC, dmPFC, and posterior temporal areas, in association with guilt processing (Gifuni et al., 2017).

However, it is worth noting that studies investigating self-conscious emotions used heterogeneous methods that prevent any firm conclusions from being drawn. For this reason, we run a meta-analysis study including neuroimaging research on the neural substrates of negative self-conscious emotions, i.e., to pinpoint brain areas consistently associated with shame, embarrassment and guilt processing. We predicted that shame, embarrassment and guilt may show different brain activations mirroring behavioural differences related to the emotions, together with some shared activations in light of their moral-self-conscious nature.

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2. Materials and Methods

In order to find studies investigating the neural underpinnings of shame, embarrassment and guilt we conducted a research on PubMed (https://www.ncbi.nlm.nih.gov/pubmed/) using the terms ((“fMRI” OR “functional magnetic resonance imaging” OR “PET”) AND (“shame” OR “embarrassment” OR “guilt” OR “moral emotions” OR “self-conscious emotions” OR "moral violations" OR "social standard violation")), and setting a range of dates between January 1st 1995 and December 14th 2018. This research identified 123 studies.

Subsequently, we refined our research by applying the following criteria:

1) paper originally published in English;

2) fMRI or PET studies including task-related whole brain analyses. Studies reporting region of interest (ROI analyses, resting-state fMRI analyses, diffusion tensor imaging (DTI) or voxel-based morphometry (VBM) were excluded;

3) participants were healthy adults: In case of studies involving neurological or psychiatric patients, children or adolescents, we considered only contrasts involving healthy controls, if reported;

4) Studies investigating the neural underpinnings of shame and guilt were included into two different sets, for two distinct meta-analyses. Specifically, we included studies contrasting shame/embarrassment vs. neutral or other emotional conditions and guilt vs. neutral or other emotional conditions. Studies failing to distinguish embarrassment/shame and guilt were excluded.

Since the difference between shame and embarrassment is not clear-cut, as they can be classified according to different criteria, and since the same physiological reactions and the same action tendencies, and their distinction is still a matter of debate, we decided to include in the same set both shame and embarrassment.

This method allowed us to identify 15 studies for the shame/embarrassment set (168 foci, 373 total subjects) and 17 studies for the guilt set (123 foci, 367 total subjects) (see Table 3). The most used paradigm in the studies analysed was emotion induction through verbal scripts (shame/embarrassment = 5; guilt = 7), pictures (shame/embarrassment = 5), both scripts and pictures (guilt = 3), vignettes (shame/embarrassment = 3) or movies (guilt = 1), while a few studies used the recollection of autobiographical memories through verbal scripts (shame/embarrassment = 1; guilt = 3), interpersonal games (shame/embarrassment = 1, guilt = 3), or implicit association task (guilt = 1).

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Table 2. Studies investigating shame/embarrassment and guilt brain processing.

Subset	*Authors*	*Paradigm*	*Stimulus type*	*Contrasts*	*Foci*	*Subjects (Females)*
Shame/ embarrassment	Bas-Hoogendam et al. 2017	Induction	Verbal scripts	Unintentional violations > neutral	5	21(15)
	Berthoz et al. 2002	Induction	Verbal scripts	Unintentional violations > normal	15	12(0)
	Finger et al. 2006	Induction	Verbal scripts	Moral and social with audience > social and neutral without audience	2	16(-)
	Krach et al. 2011	Induction	Vignettes	Vicarious embarrassment > neutral	9	32(17)
	Krach et al. 2015	Induction	Vignettes	Social pain > social neutral	17	16(0)
	Laneri et al., 2017	Induction	Vignettes	Empathic embarrassment > neutral	14	51(21)
	Melchers et al. 2015	Induction	Pictures	Vicarious embarrassment > neutral	6	60(39)
	Michl et al. 2012	Induction	Verbal scripts	Shame > neutral	10	14(7)
	Morita et al. 2008	Induction	self- and other-faces	Self-face > other-face	9	19(10)
	Morita et al. 2012	Induction	self- and other-faces	Self-face > other-face	29	15(2)
	Morita et al. 2014	Induction	self- and other-faces	Self-face > other-face	17	32(16)
	Morita et al. 2016	Induction	self- and other-faces	Self-face > other-face	13	18(0)
	Paulus et al. 2015	Induction	Vignettes	Positive correlation of vicarious embarrassment	11	32(17)
	Paulus et al. 2018	Induction	Vignettes	Fremdscham > neutral	15	34(0)
	Takahashi et al. 2004	Induction	Verbal scripts	Embarrassment > neutral	10	19(9)
	Wagner et al. 2011	Recollection	Verbal scripts	Shame > neutral	10	15(15)
	Zhu et al., 2018	Interpersonal game	Pictorial stimuli (dots)	Shame > happiness	2	30(17)
Guilt	Basile B et al. 2011	Induction	Verbal and facial stimuli	Guilt > anger and sadness	3	22(13)
	Finger et al. 2006	Induction	Verbal scripts	Moral > social and neutral	5	16(-)
	Fourie et al. 2014	implicit association task	verbal and facial stimuli	Prejudice feedback > neutral feedback	5	22(22)
	Gilead et al. 2016	Induction	Verbal scripts	Guilt > anger, joy, pride	10	19(14)
	Gradin et al. 2016	Interpersonal game	Verbal	Defection > cooperation	6	25(17)
	Green et al. 2012	Induction	Verbal scripts	Guilt > indignation (Within HC)	7	22(18)
	Kédia et al. 2008	Induction	Verbal scripts	Guilt > self-anger	4	29(14)
	Michl et al. 2012	Induction	Verbal scripts	Guilt > neutral	19	14(7)
	Molenberghs et al., 2015	Induction	Video	Civilians > Soldiers	3	48(24)
	Morey et al. 2012	Induction	Verbal scripts	Positive correlation of guilt	6	16(0)
	Peth et al., 2015	Recollection	Verbal	Guilty action > neutral	10	20(6)
	Shin et al. 2000	Recollection	Verbal scripts	Guilt > neutral	8	8(0)
	Takahashi et al. 2004	Induction	Verbal scripts	Guilt > neutral	5	19(9)
	Ty et al. 2017	Induction	Verbal and pictorial stimuli	Restitution > harm	1	18(9)
	Wagner et al. 2011	Recollection	Verbal scripts	Guilt > neutral	24	15(15)
	Yu et al. 2014	Interpersonal game	Pictorial stimuli (dots)	Self-incorrect > both incorrect	1	24(11)
	Zhu et al., 2018	Interpersonal game	Pictorial stimuli (dots)	Guilt > happiness	5	30(17)

2.1. Statistical Analysis

Analyses were conducted using the software GingerALE v3.0.2 (http://brainmap.org/). The activation likelihood estimation method, implemented in the software (Eickhoff et al., 2009; 2012; Turkeltaub et al., 2012), uses probability theory to define the spatial convergence of foci reported in the selected studies. Specifically, a Gaussian blur with an empirically-derived full-width half maximum (dependent on the number of participants included in the study) is applied to each focus from a single study. Then, all the foci from a single study are represented in a modelled activation map and voxel-wise ALE scores are computed combining all the individual maps. To distinguish between true convergence of foci from random noise a permutation test is applied. We adopted the method described by Turkeltaub et al. (2012) that minimizes within-study effects, preventing the summation of foci of the same experiment that are placed close to each other. For studies reporting between-subjects contrasts, we used the number of participants included in the smallest group as the total number of study participants.

The analyses were performed on studies' coordinate in Talaraich space. So, in case coordinate were reported in MNI space we converted them to Talaraich space, using the coordinate converter of the GingerALE software, while we kept the same coordinates in studies reporting results in Talaraich space. For each set of studies, we performed the meta-analysis applying a cluster-level family-wise error correction using an uncorrected p-value < .001 for individual voxels, 1000 permutations and a cluster-level threshold of p < .05, as suggested by Eickhoff and collaborators (2016).

Finally, we performed further analyses. We run 1) a conjunction analysis aiming to elucidate common neural activations of shame/embarrassment and guilt; 2) a subtraction analysis in order to highlight specific neural activations of either shame/embarrassment or guilt.

Subtraction analyses were performed subtracting one of the outputs of the previous analyses (ALE images) to the other (i.e., Shame/Embarrassment vs. Guilt, Guilt vs. Shame/Embarrassment). Since the two sets of studies differ in the sample size, GingerALE software computes a simulation of data randomly pooling the original data and then creating two new sets of the same size of the original datasets. For each new dataset, an ALE image is created and then subtracted to the other. These simulated images are compared with the real observed data. After 104 permutations, a voxelwise P-value image reveals for each voxel, where the real data is located in the distribution of all the possible values (for that specific voxel). Values are converted into z-scores. Subtraction analyses results are presented with a threshold of p < .05 uncorrected and a cluster size > 200 mm3, since input data for these contast analyses were already corrected for multiple comparisons, as in previous studies (Eickoff et al., 2012, Laird et al., 2005; Zmigrod et al., 2016). Results are visualized using MricoGL (https://www.mccauslandcenter.sc.edu/mricrogl).

3. Results

3.1. Shame/Embarrassment

The meta-analysis on shame/embarrassment revealed 6 significant clusters (see Figure 1 and Table 3). One cluster included the left anterior insula and the pars orbitalis of the left inferior frontal gyrus (cluster 1), while 3 clusters were located within the frontal lobes and included left medial prefrontal cortex (cluster 2), right dorsolateral prefrontal cortex (dlPFC) (cluster 3), and right precentral gyrus (cluster 4). The other clusters were located within the medial portion of the left thalamus (cluster 5) and the right fusiform gyrus (cluster 6)

The same analysis on studies contrasting shame/embarrassment with a neutral baseline revealed only a cluster located on bilateral lingual gyri, corresponding to cluster 4 in the previous analysis.

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Table 3. Results of the meta-analysis on shame/embarrassment processing.

Cluster #	Volume (mm^3)	Extrema Value	Coordinate x	y	z	Side	Anatomical Label	BA
1	3896	27.37	-28	22	8	Left	Anterior Insula	
		17.81	-36	20	-8		IFGorb	47
2	2064	21.19	-10	44	26	Left	Medial frontal gyrus	9
		19.53	-20	36	36		Superior frontal gyrus	9
		17.05	-6	38	42		Medial frontal gyrus	8
3	1976	29.51	-6	-10	10	Left	Thalamus	
		18.24	-14	4	14	Left	Caudate	
		15.41	6	-20	6	Right	Thalamus	
4	1688	22.70	-6	14	44	Left	Pre-SMA	6
		22.57	-6	14	48		Pre-SMA	8
		20.21	-8	18	32		dACC	32
5†	1016	16.64	4	-2	34	Right	dACC	24
		16.45	4	16	36		dACC	32
6†	976	17.42	-42	28	16	Left	Middle frontal gyrus	46
		13.98	-52	20	12		IFGtri	45
7†	960	25.41	42	30	14	Right	Middle frontal gyrus	46
8†	832	21.25	44	2	30	Right	Precentral gyrus/IFGop	9

Note. The table shows results on the meta-analysis on shame/embarrassment neural correlates. BA = Brodmann's area, IFGorb = Inferior frontal gyrus *pars orbitalis*, IFGtri = Inferior Frontal gyrus *pars triangularis*, IFGop = Inferior frontal gyrus *pars opercularis*, † = not reach the significance level when studies using facial stimuli are excluded from the analysis. Results are corrected with cluster-wise correction, using $p < .001$ at the voxel level and $p < .05$ at the cluster level. Coordinates are in Talaraich space.

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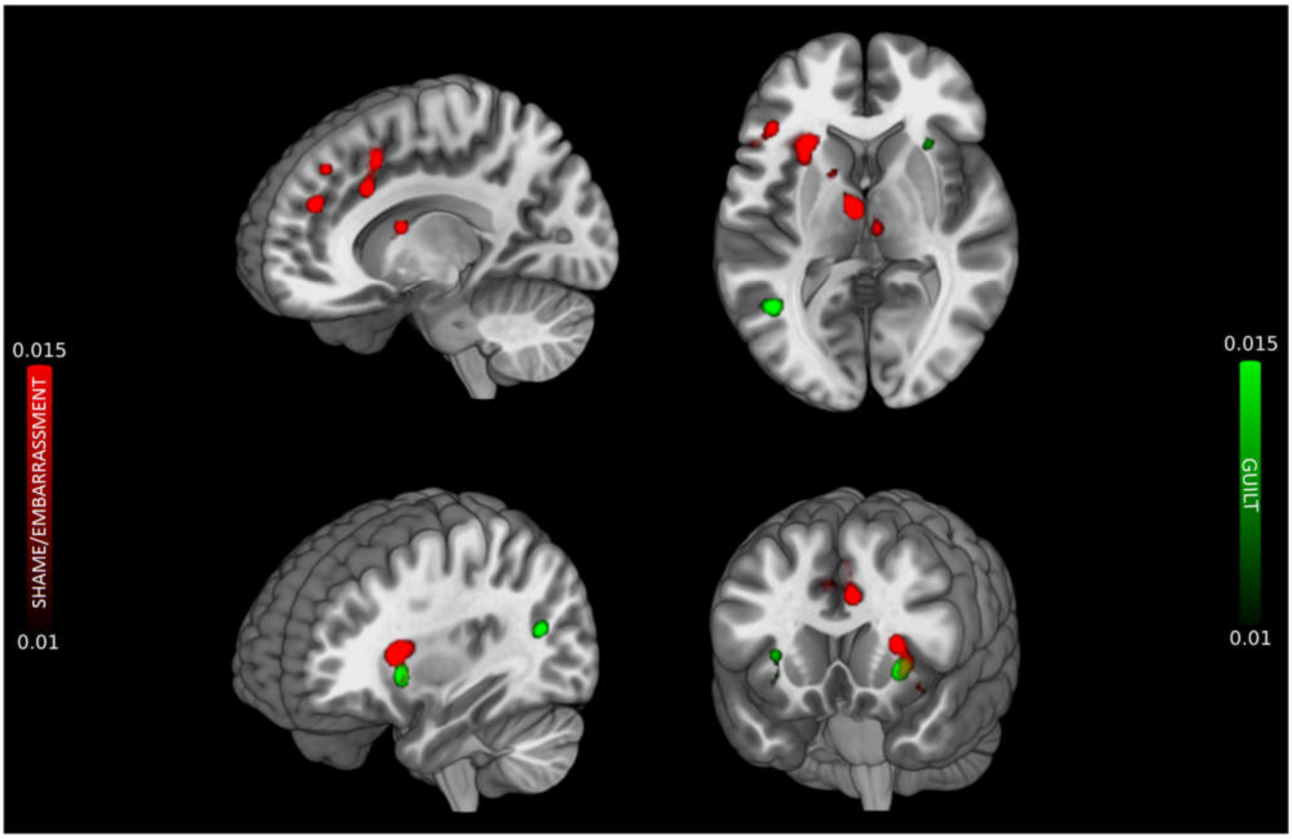

Figure 1. Results on the meta-analysis on shame/embarrassment (in red) and guilt (in green) neural correlates.

3.2. Guilt

The meta-analysis on guilt revealed four significant clusters (See Figure 1 and Table 4). Two clusters were located at the level of insula, with a bigger cluster on the left hemisphere (cluster 1), and a smaller one on the right hemisphere (cluster 3). Another cluster was located on the posterior part of the left superior and middle temporal gyri, at the border with the parietal lobe (cluster 2). The other cluster was located within the occipital lobes, on the midline, at the level of lingual gyri (cluster 4).

Table 4. Results of the meta-analysis on guilt processing.

Cluster #	Volume (mm3)	ALE value (*103)	Coordinates			Side	Anatomical label	BA
			x	y	z			
1	1528	23.42	-32	18	-2	Left	Anterior insula/IFGorb	47
2	1080	20.34	-44	-58	16	Left	Superior temporal gyrus	22
3†	848	14.65	30	20	4	Right	Anterior insula	
		11.04	32	16	-10			
		10.81	28	16	-6			

Note. The table shows results on the meta-analysis on guilt neural correlates. BA = Brodmann's area, IFGorb = Inferior frontal Gyrus pars orbitalis, † = not reach the significance level when studies using autobiographical memory recall tasks are excluded from the analysis. Results are corrected with cluster-wise correction, using $p < .001$ at the voxel level and $p < .05$ at the cluster level. Coordinates are in Talaraich space.

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3.3. Conjunction and subtraction analyses

Conjunction analyses (see Figure 2 and Table 5) showed that both shame/embarrassment and guilt shared the activation of one cluster located within left dorsal anterior insula and the pars orbitalis of the left inferior frontal gyrus. Subtraction analyses revealed one significant cluster for the subtraction 'guilt vs. shame/embarrassment', which was located on the right anterior insula, and eight clusters for the contrast 'shame/embarrassment vs. guilt'. While 6 of these clusters corresponded to clusters from 2 to 4 of the shame/embarrassment meta-analysis, the other clusters included only the dorsal portion of the left anterior insula, being located superiorly to the one emerging from conjunction analysis.

Table 5. Contrast analyses results.

Shame/embarrassment and Guilt								
Cluster #	Volume (mm3)	ALE value (*103)	Coordinates			Side	Anatomical label	BA
			x	y	z			
1	1160	18.76	-34	18	0	Left	Anterior insula/IFGorb	47
Shame/embarrassment vs. Guilt								
Cluster #	Volume (mm3)	Z-scores	Coordinates			Side	Anatomical label	BA
			x	y	z			
1	1280	2.56	0	-10	12	Left	Thalamus	
		2.14	-10	2	14		Caudate	
2	1280	3.06	-30	20	14	Left	Anterior insula	
3	1200	2.56	-8	17	43	Left	dACC	32
		1.98	-10	14	48		Pre-SMA	6
4	1000	3.06	0	4	36	Right	dACC	24
5	960	2.36	40	28	18	Right	Middle frontal gyrus	46
		2.07	44	32	8		IFGorb	46
6	688	3.24	-39	28	17	Left	Middle frontal gyrus	46
7	672	2.44	-18	32	36	Left	Middle frontal gyrus	8
		2.18	-14	38	34		Superior frontal gyrus	9
		2.13	-20	40	36		Superior frontal gyrus	9
8	536	2.12	48	1	29	Right	Precentral gyrus	6
		1.89	46	3	36		Precentral gyrus	6

Note. The table shows results on the meta-analysis on guilt neural correlates. BA = Brodmann's area, dACC = dorsal anterior cingulate cortex, pre-SMA = pre-supplementary motor area, IFGorb = Inferior frontal gyrus pars orbitalis. Results are uncorrected with $p < .05$. Coordinates are in Talaraich space

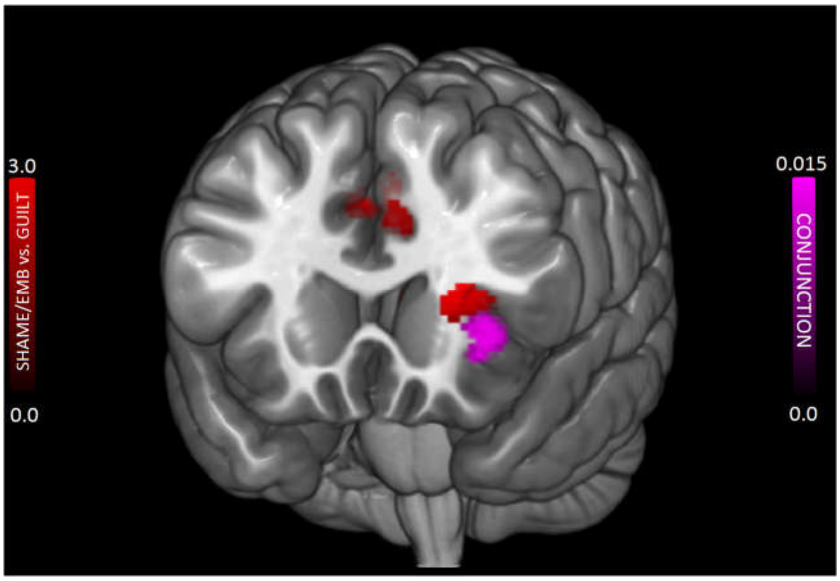

Figure 2. Contrast analysis results. In red, specific activations of shame/embarrassment vs guilt; in purple, conjunction analysis (Shame/embarrassment & guilt).

4. Discussion

In the current meta-analysis we analyzed the functional neuroimaging literature on shame/embarrassment and guilt with the aim to identify the brain areas consistently associated with the processing either emotions. The results show that either emotions to be associated with left anterior insula, but they also show specific sets of areas involved in the processing of shame/embarrassment and guilt.

4.1. Common areas

The anterior insula was found in association of a wide variety of tasks (see Craig 2009). Among the cognitive functions associated with anterior insula that include also interoception, pain perception and body awareness, it is worth mentioning its role in emotional awareness (Craig, 2009), arousal and self-reflection (e.g., Johnson et al., 2005; Modinos et al., 2009). In addition, the lesion of this area is associated with pain asymbolia (Berthier et al., 1988), a condition in which patients are still able to localize a painful stimulation and to identify it as pain but they lose all the unpleasant aspects (e.g. bodily, emotional and behavioral signs) of pain (Aydede, 2005, chapter I section 4.2). The same type of patients showed reduced arousal ratings, and attenuated valence rating to emotional stimuli than both pathological and healthy controls (Berntson et al., 2011). The interpretation of these findings is not univocal. If on the one hand, they might reflect the impairment in arousal processing, on the other they might be caused also by a deficit in emotional awareness. In addition, functional neuroimaging studies on healthy individuals investigating self-referential processing found anterior insula activation (e.g., Johnson et al., 2005; Modinos et al., 2009). Hence, the association between negative self-conscious emotion processing and the activation of left anterior insula in functional neuroimaging studies might reflect the awareness of the subjective experience of shame/embarrassment and guilt, its intensity, or self-directed evaluation processes that are necessary in order to generate both guilt and shame experiences.

Our conjunction analysis did not show the involvement of mPFC in representing both shame and guilt, contrary to our predictions. Although our meta-analysis on shame/embarrassment revealed the activation of left mPFC (cluster 2), the same analysis on guilt did not show this cluster of activation. However, the activation of the very same area in association with guilt processing was evident using a more liberal threshold ($p < .001$ uncorrected, minimum cluster size = 250), possibly reflecting the heterogeneity of the paradigm and stimuli included in the guilt dataset. It is worth noting that these clusters of activations overlap with the results of a previous meta-analysis on guilt processing (Gifuni et al., 2017). The mPFC represents a high-level integration area and is thought to support different aspects of social and affective processing (Amodio and Frith, 2006; Roy et al., 2012), ranging from self-reflection (van der Meer et al., 2010), person perception (Mitchell et al., 2002), affective appraisal (Scherer, 2001; Grecucci et al., 2017), theory of mind (Frith and Frith 2006), learning and predicting actions outcome (Alexander and Brown, 2011). Moreover, the same area was found to be active in functional neuroimaging studies investigating moral judgment, when moral evaluations were contrasted with non-moral or neutral baselines (Garrigan et al., 2016). If on the one hand, it has been proposed that mPFC associate external stimuli (e.g., context–based information) with their socio-emotional value, through a connection with anterior temporal lobes (Moll et al., 2008), on the other it might be involved in self-referential processing (e.g., representation of traits, abilities, attitudes and behaviours regarding the self), which is necessary in order to generate self-conscious emotions. This latter hypothesis seems to be confirmed by neuropsychological studies showing that patients with damage at mPFC were impaired in self-referential memory (Philippi et al., 2011), self-evaluation (Schmitz et al., 2006) and self-referential verbal production (Kurczek et al., 2015).

4.2. The Shame network

The occurrence of self-emotional distress in association with shame/embarrassment (Tangney et al., 2007; Grecucci et al., 2021; Piretti et al., 2020) might explain the association of the processing of these emotions with dorsal ACC (cluster 4 and 5), left anterior insula (cluster 1) and the medial nuclei of the thalami (cluster 3). Neuropsychological studies highlighted that patients with dorsal ACC lesions, typically made in order to treat drug-resistant pain (Yen et al., 2005), are still able to perceive and correctly localize painful sensations, but such sensations are not distressing anymore (Foltz and White, 1962). Moreover, it is worth noting that the surgical lesion of the dorsal ACC also leads to a reduced concern about the opinions or the social judgment of other people (Tow and Whitty, 1953), and can be used in the treatment of drug-resistant obsessive-compulsive disorder, a psychiatric syndrome which is often associated with extremely intense shame experiences (Weingarden et al., 2015). Medial thalamic nuclei are thought to be involved in affective aspects of physical pain perception and attachment-related processes (Price, 2000). This set of areas is highly overlapping with those involved in the processing of both physical and social pain (Eisenberger, 2012). Social pain is the unpleasant experience associated with damage to social bonds or to social values (e.g., rejection, negative social evaluations, bereavement), and is thought to be processed by part of the neural circuit involved in processing physical pain (MacDonald and Leary, 2005). Shame and embarrassment are thought to be important aspects of social pain, since they might signal that the social standards of others are not met (MacDonald and Leary, 2005).

The meta-analysis on shame/embarrassment also revealed a right premotor area (cluster 8) and the left pre-SMA (cluster 4), that have been associated with motor and speech inhibition (Simmonds et al., 2008; Xue et al., 2008), but also with emotional processing (Piretti et al., 2021). Differently from guilt, which is often associated with pro-social behaviour aiming to repair the transgression that has occurred (Tangney et al., 2007), shame and embarrassment lead to a reduction of social presence, speech and movements (Asendorpf, 1990, Keltner and Buswell, 1997), which could explain the activation of areas involved in motor and speech inhibition in shame/embarrassment processing. Hence, the presentation of shameful or embarrassing stimuli might automatically activate behavioral motor scripts aiming to reduce social presence.

The involvement of the bilateral dlPFC (cluster 7) might represent top-down regulatory processes that prevent exaggerated shameful responses. Indeed, it has been proposed that, besides its role in cognitive control (MacDonald et al., 2000), dlPFC might be also involved in regulating emotions (Etkin et al, 2015). Different psychopathological conditions characterised by exaggerated shameful experiences, including obsessive-compulsive disorder (Rotge et al., 2010), borderline personality (De Panfilis et al., 2019; Dadomo et al., 2022; Grecucci et al., 2022), depression (Grieve et al., 2013), schizophrenia (Glahn et al., 2008), bulimia nervosa (Schäfer et al., 2010) and PTSD (Li et al., 2014), showed reduced dlPFC volume with respect to healthy controls. These findings might suggest that dlPFC has a role in regulating shame, inhibiting the occurrence of exaggerated shameful experiences.

4.3. The Guilt network

Differently from shame/embarrassment, guilt is thought to be associated with social abilities, as empathy and theory of mind, might be specifically related to guilt generation (Bastin et al., 2016). Indeed, guilt and theory of mind abilities were found to be correlated (Leith and Baumeister, 1998). In our meta-analysis we found the association between guilt processing and TPJ, which was reliably found as a crucial area for distinguishing self- and other-actions and representing other individuals' mental and affective states (See Decety and Lamm, 2007 for a meta-analysis). Although the association between guilt and TPJ did not reach significance level in the contrast analyses (i.e., guilt vs. shame/embarrassment), considering the convergence with a previous meta-analisis on guilt processing (Gifuni et al., 2017) and the associations between guilt processing and theory of mind, and theory of mind and TPJ, we believe that TPJ should be taken in consideration as a crucial area in the processing of guilt. However, the association between guilt and empathy and theory of mind is not univocal. On the one hand guilt is thought to increase the understanding of others' affective and mental states (Tangney et al., 2007), on the other, taking others' perspective and empathising with others seem to be crucial in order to experience guilt (Giammarco et al., 2015). Hence, our results might refer to functions that are cause or consequence of the emotional experience.

Further analyses obtained excluding autobiographical memory recall paradigms from the dataset confirmed the association between guilt processing and left anterior insula and TPJ. However, this analysis showed also that the cluster located over the right insular cortex did not reach the significance level, suggesting that guilt induction tend to activate less consistently right than left insula.

5. Conclusions

Our meta-analysis revealed common and distinct neural substrates for the processing of shame/embarrassment and guilt. While the activation of left anterior insula was associated with both shame/embarrassment and guilt processing, the pain network, including medial thalami, dorsal ACC and inferior anterior insula, and premotor areas were specifically associated with shame/embarrassment processing and left TPJ and right anterior insula were associated with specific guilt processing.

6. Limitations

The main limitation of our study is the small amount of studies investigating shame, embarrassment and guilt, and the relative small number of participants included in most of the studies. The wide variety of paradigm investigating self-conscious emotions, including reading scripts, viewing vignettes and recalling autobiographical memories, might affect the reliability of the results. Further studies investigating self-conscious emotions are necessary to better characterize common and specific brain networks involved in their processing.

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