Common and distinct neurofunctional representations of core and social disgust in the brain: Coordinate-based and network meta-analyses

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ABSTRACT
Disgust represents a multifaceted defensive-avoidance response. On the behavioral level, the response includes withdrawal and a disgust-specific facial expression. While both serve the avoidance of pathogens, the latter additionally transmits social-communicative information. Given that common and distinct brain representation of the primary defensive-avoidance response (core disgust) and encoding of the social-communicative signal (social disgust) remain debated, we employed neuroimaging meta-analyses to (1) determine brain systems generally engaged in disgust processing, and (2) segregate common and distinct brain systems for core and social disgust. Disgust processing, in general, engaged a bilateral network encompassing the insula, amygdala, occipital and prefrontal regions. Core disgust evoked stronger reactivity in left-lateralized threat detection and defensive response network including amygdala, occipital and frontal regions while social disgust engaged a right-lateralized superior temporal-frontal network engaged in social cognition. Anterior insula, inferior frontal and fusiform regions were commonly engaged during core and social disgust, suggesting a common neural basis. We demonstrate a common and separable neural basis of primary disgust responses and encoding of associated social-communicative signals.

Keywords: disgust, fMRI, meta-analysis, activation likelihood estimation (ALE), meta-analytic connectivity modeling (MACM), defensive-avoidance response, social cognition, face, insula, amygdala

1. Introduction

Disgust represents a basic emotion and has been conceptualized as a multifaceted and evolutionary adaptive defensive-avoidance response. The disgust response may have initially evolved in the context of rejection of potential poisonous food (Darwin, 1965; Rozin and Fallon, 1987; Rozin et al., 2009) but the same underlying mechanism may have subsequently been adapted to facilitate avoidance of contaminations by pathogens and may even serve the avoidance of harmful social interactions (Curtis et al., 2011; Davey, 2011; Haidt et al., 1994; Kupfer and Fessler, 2018; Rozin and Fallon, 1987; Rozin et al., 2016; Vicario et al., 2017). In line with its evolutionary function, disgust is primarily elicited by exposure to potentially poisonous or infectious stimuli such as rotten food, cockroaches or individuals with poor personal hygiene as well as injury- and mutilation-related stimuli (Haidt et al., 1994; Olatunji and Sawchuk, 2005; Rozin and Fallon, 1987; Vicario et al., 2017). Exposure to these stimuli induces a distinct disgust reaction on different levels encompassing subjective experience of revulsion, as well as physiological and behavioral responses. The behavioral response includes rapid withdrawal from the eliciting stimulus as well as a distinct facial expression characterized by a wrinkled nose (Rozin et al., 1994) and raised upper lip (Rozin et al., 1994), reflecting the primary purpose of the disgust reaction in terms of avoiding or rejecting pathogens (Chapman et al., 2009; Oaten et al., 2009; Olatunji and Sawchuk, 2005; Rozin and Fallon, 1987; Rozin et al., 2009; Rozin et al., 1994; Schienle and Wabnegger, 2021) (in line with Vicario et al., (2017) henceforward referred to as *core disgust* processing). The highly distinct facial expression for disgust additionally serves social-communicative purposes (Chapman and Anderson, 2012; Chapman et al., 2009; Vicario et al., 2017; von dem Hagen et al., 2009) such that a disgusted facial expression signals to conspecifics a danger of being exposed to potential pathogens (Burklund et al., 2007; Darwin, 1965; Rozin et al., 1994; Surguladze et al., 2003; von dem Hagen et al., 2009) or an attitude of social rejection (Burklund et al., 2007; Surguladze et al., 2010; von dem Hagen et al., 2009). Accurate decoding of these signals is essential for survival and adaptive social interactions (Darwin, 1965; Ekman, 1993; Fusar-Poli et al., 2009b; Malhi et al., 2007; Phillips et al., 1999). In line with Vicario et al. (2017) who refer to the perception or appraisal of a disgusted facial expression in others as a social-communicative signal we henceforward refer to perception/appraisal of disgusted faces as *social disgust* processing. Of note, we thus specifically consider the perception of disgusted faces in others as *social disgust*, while a broader definition may also encompass other social signals of disgust, such as words, or the production of a disgusted facial expression. Although both, core and social disgust, share the essential function of a defensive-avoidance reaction towards potential pathogen exposure, the facial expression of disgust as social signal represents a more indirect and context depended signal which requires further interpretation by the observer (for similar reasoning with respect to other facial expression domains see e.g., Hadjistavropoulos et al., 2011; Zhou et al., 2020).

Initial evidence for common and separable neurobiological systems underlying core and social disgust responses additionally comes from human lesion models reporting that a patient with focal anterior insula and putamen lesions exhibited intact core disgust reactivity but exhibited selective impairments in recognizing disgust from facial signals (Calder et al., 2000) while a patient with selective lesions of the anterior insula exhibited both, dysregulated core disgust reactivity as well as altered production of disgust expressions (Cantone et al., 2019). A recent study in a larger sample of lesion patients confirmed core as well as social disgust processing

impairments in patients with insula-basal ganglia lesions and additionally reported that patients with left hemispheric lesions exhibited pronounced impairments, suggesting a lateralization of disgust processes (Holtmann et al., 2020).

Indirect evidence for common and separable neurobiological systems comes from numerous functional imaging, particularly functional MRI, studies that examined the neural substrates of disgust processing in healthy subjects (the first functional MRI study on disgust was published in 1997) (Phillips et al., 1997). These studies demonstrated that visual, gustatory (Corradi-Dell'Acqua et al., 2016; Jabbi et al., 2008), olfactory (Berlin et al., 2017; Heining et al., 2004; Meier et al., 2015; Wicker et al., 2003), and auditory (Phillips et al., 1998; Zimmer et al., 2016) stimuli can induce the subjective experience of disgust and neural reactivity in the domains of core and social disgust reactivity.

Visual stimuli, such as pictures and film clips depicting core disgust elicitors (e.g., rotten food) or social disgust stimuli (i.e., disgusted faces) in combination with corresponding non-disgust related stimuli have been widely used in separate studies on core or social disgust. However, despite the large number of original studies the key regions involved in disgust in general, as well as core and social disgust in particular, remain strongly debated. For instance, while the insula has been considered and often reported as a key region for general disgust processing (Calder et al., 2001; Kirby and Robinson, 2017; Murphy et al., 2003; Phan et al., 2002; Vytal and Hamann, 2010) and insula activity has been reported during core (Schäfer et al., 2009; Schäfer et al., 2005; Schienle et al., 2020; Schienle et al., 2002; Shapira et al., 2003; Stark et al., 2007) as well as social disgust processing paradigms (Ashworth et al., 2011; Phillips et al., 1997; Wicker et al., 2003), several studies examining disgust processes did not observe insula activity (Deeley et al., 2008; Gorno-Tempini et al., 2001; Schienle et al., 2006; Schienle et al., 2005b; Stark et al., 2005; Stark et al., 2004; Stark et al., 2003; Trautmann et al., 2009), which may reflect a general involvement of the insula in interoceptive processes rather than a disgust specific engagement (Li et al., 2019; Stark et al., 2005; Yao et al., 2018a).

Moreover, several studies suggest a role of the amygdala in disgust processing, probably related to its role in early detection of threat and initiation of defensive responses (e.g., Becker et al., 2012; Zhou et al., 2021). Amygdala activity in response to core disgust stimuli (Pujol et al., 2018; Schienle et al., 2009; Schienle et al., 2006; Schienle et al., 2002; Schienle et al., 2014; Stark et al., 2005; Stark et al., 2003; Stark et al., 2007) as well as social disgust stimuli (Burklund et al., 2007; Fitzgerald et al., 2006; Phillips et al., 1998; Winston et al., 2003) has been reported in several studies, yet a considerable number of studies on the neural basis of disgust failed to find an engagement of the amygdala (Caseras et al., 2007; Deeley et al., 2007; Phillips et al., 2000; Phillips et al., 2004; Phillips et al., 1999; Phillips et al., 1997; Schienle and Scharmüller, 2013; Schroeder et al., 2005; Sprengelmeyer et al., 1998; Surguladze et al., 2010; Wicker et al., 2003). Finally, two studies included different visual disgust stimuli (i.e., core disgust and social disgust stimuli), yet surprisingly did not find robust social disgust related activity or common neural activity during social and core disgust processing, respectively (Schäfer et al., 2005; Schienle et al., 2020).

The ongoing debates about the brain systems generally engaged in disgust processing as well as during core or social disgust processing separately might be partly rooted in the limitations of single fMRI studies and particularly factors such as low and underpowered sample sizes, variations in processing depths (i.e., implicit vs explicit processing), stimuli sets, experimental

designs (e.g., block design vs event-related design), study-specific samples with variations in cultural background or disgust propensity, field strength (e.g., 1T vs 3T) and methods of data analysis may have considerably contributed to the lack of robustly identified neural systems for disgust. The development and application of neuroimaging based meta-analyses have allowed to overcome these limitations by capitalizing on the results from previously published studies (Eickhoff et al., 2012; Laird et al., 2005; Wager et al., 2007), thus allowing to determine the convergent and robust neurofunctional basis of emotional and cognitive processes as well as to determine common and distinct neurofunctional underpinnings between processes (e.g., Chen et al., 2018; Feng et al., 2018). Previous studies have capitalized on neuroimaging meta-analyses to successfully determine common and separable brain representations of core emotions or emotional face expressions (Fusar-Poli et al., 2009b; Kirby and Robinson, 2017; Murphy et al., 2003; Phan et al., 2002; Vytal and Hamann, 2010).

By capitalizing on neuroimaging meta-analyses, we aimed at determining brain systems that are robustly engaged in general disgust processing, as well as core and social disgust processing in healthy subjects. Moreover, we aimed for the first time to systematically determine common and separable systems involved in core and social disgust processing which – in a conceptual context – may allow to (1) determine embodied simulation processes in the domain of disgust, with the embodied simulation theories proposing that overlapping cognitive and brain mechanisms are key to embodied simulation (Gallese and Sinigaglia, 2011, 2012) which in turn critically supports understanding of emotions, cognitions and intentions of other persons, and (2) may help to further segregate regions which facilitate survival relevant rapid evaluation of disgust-related features from regions that are involved in other domains such as e.g., face processing. Moreover, disgust has received increasing attention as a behavioral domain involved in the pathogenesis and maintenance of a number of psychiatric and neurological disorders with increasing evidence for common as well as core and social disgust-specific dysregulations in specific diagnostic entities (Vicario et al., 2017). A clearer understanding of the common and separable neural systems of disgust processing in healthy populations could thus provide a basis for further delineating transdiagnostic and disorder-specific dysregulations in these domains.

Based on overarching disgust frameworks, we hypothesized that disgust-related processing will generally recruit regions engaged in motivational aspects, defensive responses and interoception such as the insula and amygdala, and - considering the role of prefrontal cortex as an integration hub for affective and cognitive functions (Kirby and Robinson, 2017) and its activation during disgust processing (Baumann and Mattingley, 2012; Phillips et al., 1997; Tettamanti et al., 2012; Wicker et al., 2003) - we expected this region to be involved during general disgust processing. Given that previous studies reported that occipital regions showed a strong engagement during the processing of negatively valenced emotional visual stimuli (Paradiso et al., 1997; Radua et al., 2014; Stark et al., 2007; Tao et al., 2021) we expected that these regions would be activated during general disgust processing. Based on the previous literature, we further expected that common and separable (domain-specific) networks would underlie core and social disgust processes, such that the insula, together with orbitofrontal/inferior frontal regions - proposed to serve as a common endpoint of distributed networks engaged in emotion processing (Sprengelmeyer et al., 1998) and repeatedly observed during core (Pujol et al., 2018; Schienle and Scharmüller, 2013; Stark et al., 2007; Tettamanti et al., 2012) as well as social disgust processing (Chakrabarti et al., 2006; Reidy et al., 2016; Sprengelmeyer et al., 1998; von dem Hagen et al.,

2009) - would be recruited across domains; while regions involved in social processing, such as the face processing network and social cognition network including e.g., superior temporal and dorsomedial prefrontal regions (Fusar-Poli et al., 2009b; Liu et al., 2021; Sabatinelli et al., 2011), would be differentially engaged.

2. Methods

2.1. Literature search

The present meta-analytic review was conducted in line with the PRISMA guidelines for systematic reviews (Page et al., 2021) and the meta-analytic protocols were preregistered on the Open Science Framework (https://osf.io/pu59t).

Articles published prior to May 2021 were identified using the following keywords: ("functional magnetic resonance imaging" OR "fMRI") AND ("disgust facial expression" OR "disgusted facial expression" OR "disgust face" OR "disgusted face" OR "facial motion, disgust" OR "disgust elicitors" OR "disgusting elicitors" OR "disgust stimuli" OR "disgusting stimuli" OR "disgust visual scenes" OR "disgusting visual scenes" OR "disgust") on the PubMed and Web of Science databases. The search was complemented by a corresponding search on the BrainMap functional database (May 2021; containing 3406 papers and 16901 experiments) using the Sleuth software (version 3.0.4, https://www.brainmap.org/sleuth/) with the following search terms: "Experiments: Context, Normal Mapping", "Experiments: Activations, Activations only", "Experiments: Imaging Modality, fMRI" and "Experiments: Behavioral Domain, Emotion, Negative-Disgust". Finally, reference lists of included articles were searched for relevant articles not identified during the initial database search. Noteworthy, in line with our working definition of social disgust, studies for the social disgust analyses were limited to studies examining the perception/appraisal of disgusted facial expressions in others. Following removal of duplicates, 419 neuroimaging papers on disgust processing were retained.

2.2. Inclusion and exclusion criteria

To identify suitable publications according to our criteria, titles and abstracts of identified papers were initially examined by two independent reviewers (X. G. and X. Z.). Full texts of eligible papers were downloaded for detailed examination. Any disagreement between these two reviewers was resolved by discussion and a final decision by a third independent reviewer (J. L.). Papers that passed the screening process underwent a thorough and detailed evaluation of eligibility (B. B. and X. G.), studies with ambiguous experimental contrasts were removed at this stage and disagreements were further resolved by another reviewer (B. K-B.). A flowchart illustrating the detailed article screening and exclusion process is shown in **Fig. 1**. The following inclusion criteria were applied: (1) studies reporting neuroimaging experiments on disgust processing which presented static pictures or film clips displaying clearly disgust-related contents (e.g., disgusted facial expressions and disgusting visual scenes; we limited the stimuli only to the visual modality for two reasons: one is to control for modality when comparing core and social disgust, the other reason is that the number of studies using olfactory, gustatory and auditory stimuli or script-induced imagination was too low to warrant a robust modality-specific meta-analyses); (2) results were published as original papers in peer-reviewed English-language journals; (3) contrasts for healthy subjects were reported (i.e., healthy volunteers only). Studies reporting only spatial coordinates across or between healthy controls and clinical groups were

excluded, but included if data was separately reported for the healthy control group; (4) task-related fMRI was employed; (5) activation contrasts generated by the subtraction approach represent main effects of disgust relative to a baseline or control condition (e.g., disgust faces > neutral faces, disgust elicitors > fixation); (6) activation in terms of higher activity for the disgust-related stimuli reported (deactivations were not included because the underlying functional process remains difficult to interpret in fMRI studies and because the current version of the ALE software can't differentiate activations from deactivations, similar approach see e.g., Vytal and Hamann, 2010); (7) results reported in standard stereotactic coordinates (either Talairach or Montreal Neurological Institute [MNI] space); (8) results describing associations between disgust-related neural activity and behavioral ratings of disgust, psychophysiological responses or personality and symptom dimensions were not included; (9) other types of emotional faces including schematic faces were excluded; (10) whole-brain results were reported (we excluded studies reporting only region-of-interest, ROI, analyses); (11) for studies reporting multiple but not independent contrasts, only the contrast that substantially reflected the process of interest was included. For instance, if one study reported two contrasts employed disgust stimuli with different intensity levels, only the results corresponding to higher disgust intensity were included (similar approach see Tao et al., 2021); (12) for studies that included multiple relevant and independent contrasts, all such contrasts were included (similar approach see Tao et al., 2021).

To reduce the possibility of biased study sampling, we contacted the corresponding authors of 11 studies for which Talairach or MNI coordinates for the appropriate contrast were not reported (e.g., for healthy controls in a case-control neuroimaging study).

After the in-depth screening procedure, a total of 69 papers (**Supplementary Table 1**) were included in the meta-analyses, and according to the aims of the analyses organized as follows: (1) general disgust processing: 69 papers, 71 experiments, 717 foci, 78 contrasts, 1409 subjects; (2) core disgust processing: 39 papers, 41experiments, 402 foci, 46 contrasts, 897 subjects; (3) social disgust processing: 30 papers, 30 experiments, 315 foci, 32 contrasts, 512 subjects. Based on recent recommendations for activation likelihood estimation (ALE) meta-analyses suggesting that at least 20 (and 17 in worst case) experiments are sufficient to determine moderate effects with sufficient statistical power (80%) (Eickhoff et al., 2016), this database allowed us to draw robust inferences.

2.3. Activation likelihood estimation

We performed a series of coordinate-based meta-analyses using the current version of GingerALE 3.0.2 (Eickhoff et al., 2012; Eickhoff et al., 2011; Eickhoff et al., 2009) available via http://www.brainmap.org/ale/. All coordinates (either in Talairach or MNI space) and sample size were manually extracted from the original articles. The coordinates in Talairach space were converted to MNI space using the Lancaster transform algorithm, while Talairach space coordinates transformed from MNI space using the Brett transformation were converted back to MNI space using the Brett transformation (Laird et al., 2010; Lancaster et al., 2007). Briefly, the ALE method estimates the likelihood of each voxel being activated under multiple independent experiments with consideration of participants in each experiment. In other words, ALE aims to find the most robust convergent foci between a number of included experiments. To address spatial uncertainty, ALE treats activation foci from single studies as 3D Gaussian probability

distributions. Modeled activation (MA) maps for each study were generated by combining the probabilities of all activation foci for each voxel (Eickhoff et al., 2009; Turkeltaub et al., 2012). The union of these generated MA maps was computed while taking into account the disparities between true activation and noise to determine a voxel-wise ALE score (Klugah-Brown et al., 2020). These ALE scores use the convergence of whole-brain coordinates from experiments under a non-random spatial distribution to create clusters formed by equal probabilities of voxels (Eickhoff et al., 2012; Müller et al., 2018). The ALE map reflects clusters corresponding to the location of convergence. And the resulting non-parametric p values account for the proportion of the random spatial relation between the various experiments under the null distribution (Klugah-Brown et al., 2021; Kohn et al., 2014).

For single dataset analyses (i.e., general disgust processing, core disgust processing, and social disgust, respectively), the ALE statistics were calculated at each voxel, and cluster-level family-wise error correction (cluster-FWE) (Eickhoff et al., 2016) was applied to the ALE results to control for multiple comparisons. The voxel-level threshold was set at $p < 0.001$ (uncorrected cluster forming), and the cluster-level threshold was set at $p < 0.05$ (Eickhoff et al., 2017; Eickhoff et al., 2016; Müller et al., 2018), p values in our analyses were generated by 5,000 permutations (Laird et al., 2010; Tao et al., 2021).

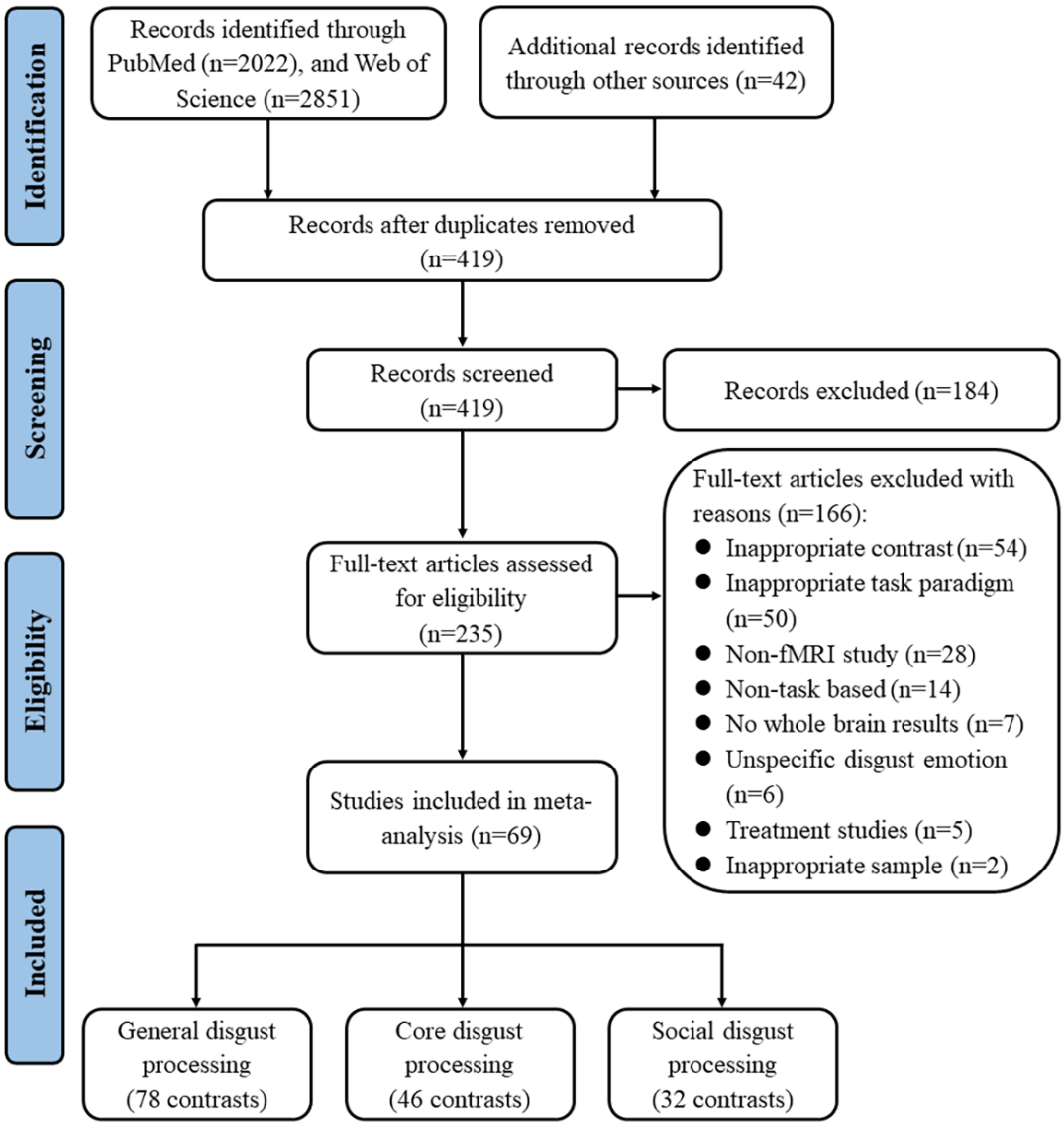

Fig. 1. Flowchart illustrating the article screening, exclusion and inclusion process according to PRISMA procedure.

2.4. Contrast and conjunction analyses

The present meta-analysis aimed at determining regions robustly involved in disgust processing across domains as well as to differentiate regions that are convergent and divergent between core and social disgust processing in healthy subjects. To this end we employed a series of contrast and conjunction analyses (comparing the meta-analytic maps for core and social disgust processing) according to the following steps: (1) single dataset analyses were performed separately for core disgust processing and social disgust processing; (2) the two single datasets to be compared were pooled together using the "Merge & Save Foci" function; (3) a single dataset analysis was conducted on the pooled foci file employing identical statistical criteria as for the preceding single dataset analyses; (4) via the separate single dataset analysis three corrected ALE images were obtained for general disgust processing, core disgust processing, and social disgust

processing, respectively. Then, we further determined common and distinct brain regions by conducting contrast and conjunction analyses by subjecting these images into GingerALE toolbox to obtain the similarities as well as differences in the neurobiological basis of core and social disgust processing. Conjunction analyses were performed to determine common regions across core and social disgust processing which were considered as brain systems involved in disgust across processing domains (domain-general). While contrast analyses were implemented to determine brain regions differentially activated for core and social disgust processing (domain-specific) (See **Supplementary Materials** for detailed methodology of conjunction and contrast analyses).

In accordance with previous studies employing contrast and conjunction analyses (Alain et al., 2018; Papitto et al., 2020), the ALE images were thresholded at $p < 0.05$ (uncorrected), with minimum cluster size of 100 mm^3 and 10,000 permutations, thereby resulting in a larger number of permutations as compared to single dataset analyses (Alain et al., 2018; Papitto et al., 2020; Wertheim and Ragni, 2018; Yu et al., 2018). In general, the rationale was to combine a strict threshold for the determination of the general networks examined in the single dataset analyses with a more sensitive threshold for examining common and separable neural bases in the conjunction and contrast analyses. Moreover, we applied a higher number of permutations to the conjunction and contrast analyses to determine a more accurate number of voxels reflecting the overlapping neural basis of the different disgust processes (i.e., social and core disgust). Results based on an identical number of permutations revealed similar results and are additionally presented in the supplements.

2.5. Meta-analytic connectivity modeling (MACM) analyses

To further functionally characterize the domain-general disgust regions on the network level MACM was employed. Briefly, MACM examines whole-brain functional connectivity patterns by identifying the above-chance covariance between two or more brain regions (Laird et al., 2009; Robinson et al., 2012; Robinson et al., 2010). This approach is similar to the functional connectivity patterns observed in resting-state fMRI (Kotkowski et al., 2018; Reid et al., 2017; Smith et al., 2009), yet further complements the resting-state functional connectivity approach as it provides a measure of functional connectivity during a range of task-associated mental states (Langner et al., 2014). Coordinates of the peak activation clusters (i.e., right inferior frontal gyrus and left fusiform gyrus) from the conjunction analyses were selected, with the right inferior frontal gyrus located at (44, 26, -8) and the left fusiform gyrus located at (-42, -50, -14). For the fusiform gyrus clusters, we focused on the peak with the higher ALE value. For the MACM analyses, the regions were defined in MNI space using a 10 mm sphere centered at the peak coordinates using the SPM toolbox MarsBaR (http://marsbar.sourceforge.net). A standard MNI brain template (Colin27_T1_seg_MNI.nii; https://www.brainmap.org/ale/Colin27_T1_seg_MNI.nii.gz) was used to visualize both ROI masks. Next region-specific functional connectivity was employed using the functional database of BrainMap's Sleuth 3.0.4 software. To increase the robustness, we employed

two convergent approaches (labeled as MACM-A and MACM-B, respectively) which enable us to determine the functional network characterization by determining co-activated regions in previous experiments. Specifically, we used two different search terms when conducting these two separate MACM analyses in Sleuth database. The search terms for "MACM-A" incorporating (1) "Locations: MNI Image" used to upload the corresponding 10 mm spherical ROI in MNI space, (2) "Experiments: Behavioral Domain, Emotion, Negative-Disgust". In this way, we can get the co-activation patterns engaged in disgust processing, and this approach has been adopted by one recent published paper (Tao et al., 2021). The search terms for "MACM-B" are: (1) "Locations: MNI Image" used to upload the corresponding 10 mm spherical ROI in MNI space, (2) "Experiments: Activations, Activations only", (3) "Experiments: Context, Normal Mapping", (4) "Subjects: Diagnosis, Normals". This approach has been recommended by many researchers (Meier et al., 2021; Papitto et al., 2020), including the user manual for GingerALE (https://www.brainmap.org/ale/manual.pdf). This approach enables the investigation of brain region covariance above chance within a given seed ROI across a large and different pool of neuroimaging experiments from the functional database. After each of these separate searching approaches, coordinates from downloaded experiments meeting the criteria were automatically exported as a text file and converted into MNI space.

The composition of the two datasets for MACM-A is as follows: (1) the ROI in right inferior frontal gyrus (73 experiments, 891 subjects, 719 foci), (2) the ROI in left fusiform gyrus (28 experiments, 414 subjects, 163 foci). And the composition of the two datasets for MACM-B is the following: (1) the ROI in right inferior frontal gyrus (473 experiments, 7,768 subjects, 7,195 foci), (2) the ROI in left fusiform gyrus (366 experiments, 5,439 subjects, 5,801 foci). Finally, these new datasets were analyzed separately using GingerALE 3.0.2 with the same statistical criteria previously applied in the single dataset analyses (voxel-level of $p < 0.001$ (uncorrected), cluster-FWE of $p < 0.05$, 5,000 permutations).

2.6. Functional characterization of ALE activations on the behavioral level

To facilitate a robust characterization of the identified regions on the behavioral level a meta-analytic decoding approach was employed. To this end, we capitalized on the Brain Annotation Toolbox (BAT, available at https://istbi.fudan.edu.cn/lnen/info/1173/1788.htm) (Liu et al., 2019), which is based on the activation maps in MNI space for the 217 functional terms from the Neurosynth database (http://neurosynth.org/) (Yarkoni et al., 2011). The corresponding functional annotation analysis hypothesizes that voxels within a given cluster/region are more likely to be co-activated by the same terms that are functionally connected with the cluster/region, compared with voxels selected randomly, this way BAT enables the functional characterization of a given region based on the meta-analytically associated terms (Liu et al., 2019). In the present study, we employed this approach to characterize the domain-general disgust (core $\cap$ social; where $\cap$ represents intersection) as well as core disgust and social disgust regions. $P < 0.05$ was considered statistically significant based on 10,000 permutations. For further details, please turn to the BAT

website (https://istbi.fudan.edu.cn/lnen/softwares/BAT_User_Manual_V1.1.docx).

2.7. Report and visualization of results

For the results presented in tabular overview, the following indices were reported: volume of clusters, lateralization of brain regions, labels of brain regions, peak coordinates from voxels, ALE/Z value (Tao et al., 2021). For the conjunction and contrast results, information of percentage of overlap was further reported. With respect to the statistical indices ALE and Z values are provided for single dataset analyses; while ALE values are provided for conjunction and Z values are provided for contrast analyses (see Papitto et al., (2020) for details regarding the underlying inferential statistic approach). For visualization, the ALE results were displayed using the current version of Mango 4.1 (https://rii.uthscsa.edu/mango/), overlaid onto a standard MNI brain template (Colin27_T1_seg_MNI.nii).

3. Results

3.1. General disgust processing

The ALE meta-analysis encompassing all disgust processing studies revealed twelve significant clusters (**Table 1, Fig. 2a**) that were robustly engaged in general disgust processing. The clusters were located in the bilateral insula, amygdala spreading into the right globus pallidus, fusiform gyrus spreading into the declive, middle occipital gyrus, right inferior occipital gyrus, right lingual gyrus, left inferior temporal gyrus, left inferior parietal lobule, right inferior frontal gyrus, and left superior frontal gyrus. See **Supplementary Materials** for a detailed presentation of percentage of overlap with atlas-based brain regions.

3.2. Core disgust processing

Core disgust robustly engaged ten clusters of significant activation, primarily encompassing the bilateral amygdala (spreading into the right globus pallidus) and insula, left inferior frontal gyrus, left declive, left fusiform gyrus, left inferior parietal lobule, left middle occipital gyrus, left inferior temporal gyrus, left superior frontal gyrus, bilateral inferior occipital gyrus spreading into the adjacent lingual gyrus (**Table 2, Fig. 2b**). See **Supplementary Materials** for a detailed presentation of percentage of overlap with atlas-based brain regions.

3.3. Social disgust processing

Examining social disgust processing studies revealed six significant clusters of robust activation located in the right insula and adjacent inferior frontal gyrus, bilateral fusiform gyrus spreading into the right declive, left superior frontal gyrus, right cingulate gyrus, right middle occipital gyrus, and right superior temporal gyrus (**Table 3, Fig. 2c**). See **Supplementary Materials** for a detailed presentation of percentage of overlap with atlas-based brain regions.

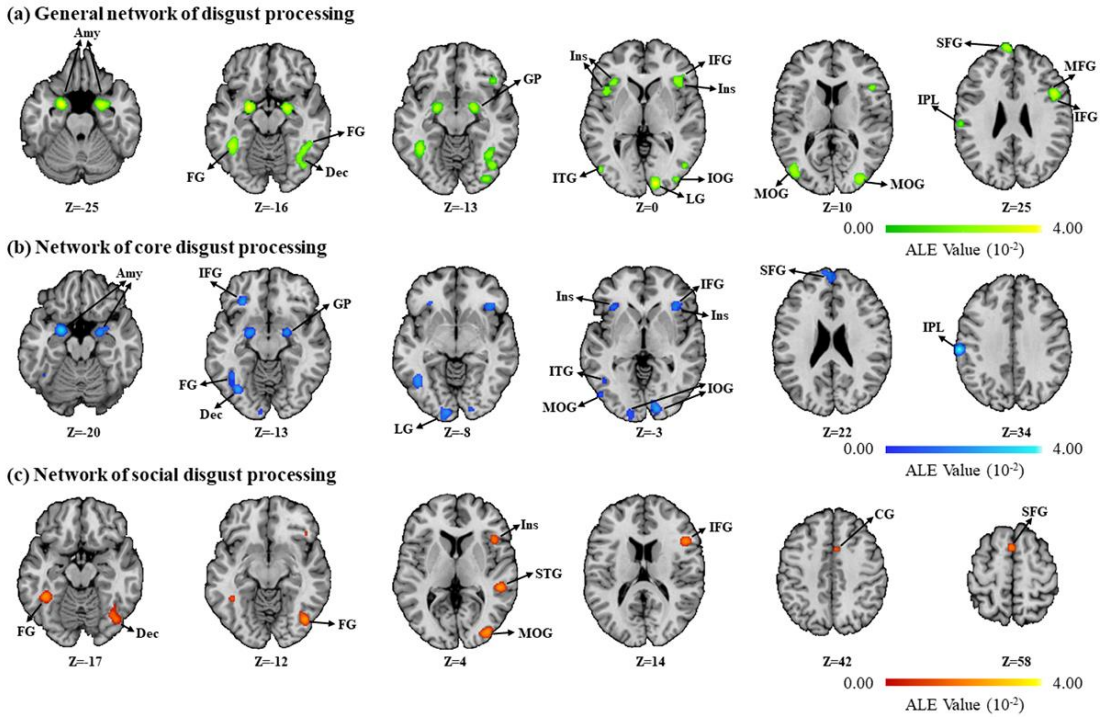

Fig. 2. Overview of significant clusters from the single dataset analyses. **(a)** General network of disgust processing in healthy subjects. **(b)** Network of core disgust processing in healthy subjects. **(c)** Network of social disgust processing in healthy subjects. Coordinates are in the MNI space. Abbreviations: Amy = Amygdala, CG = Cingulate Gyrus, Dec = Declive, FG = Fusiform Gyrus, GP = Globus Pallidus, IFG = Inferior Frontal Gyrus, Ins = Insula, IOG = Inferior Occipital Gyrus, IPL = Inferior Parietal Lobule, ITG = Inferior Temporal Gyrus, LG = Lingual Gyrus, MFG = Middle Frontal Gyrus, MOG = Middle Occipital Gyrus, SFG = Superior Frontal Gyrus, STG = Superior Temporal Gyrus.

3.4. Common and differential brain regions for core and social disgust processing

Examining the common brain systems by means of conjunction analyses revealed that the right inferior frontal gyrus (extending into the anterior insula) and left fusiform gyrus were robustly activated during core and social disgust processing (domain-general disgust processing) (**Table 4, Fig. 3a**).

The contrast analyses revealed stronger recruitment of the left inferior parietal lobule, left postcentral gyrus, left middle occipital gyrus, left inferior temporal gyrus, left limbic-striatal cluster (encompassing the amygdala, hippocampus and globus pallidus), right superior frontal gyrus, left medial frontal gyrus, left inferior frontal gyrus, left declive, left fusiform gyrus and left lingual gyrus for core disgust compared with social disgust (domain-specific core disgust processing), suggesting a left hemisphere predominance (**Table 5, Fig. 3b**). In contrast social disgust processing was characterized by a stronger engagement of the right inferior frontal gyrus (extending to the insula), left medial frontal gyrus, right cingulate gyrus, right middle occipital gyrus, right declive, right superior temporal gyrus, right middle temporal gyrus, and bilateral fusiform gyrus as compared to core disgust processing (domain-specific social disgust

processing), reflecting a right hemispheric predominance (**Table 5, Fig. 3c**). We additionally repeated the contrast and conjunction analyses with the same number of permutations as employed in the single dataset analyses (5,000 permutations, $p < 0.05$, uncorrected, minimum cluster size of 100 mm^3) which generated a highly similar pattern of results as the initial analyses (details are reported in **Supplementary Table 2** and **Supplementary Table 3**).

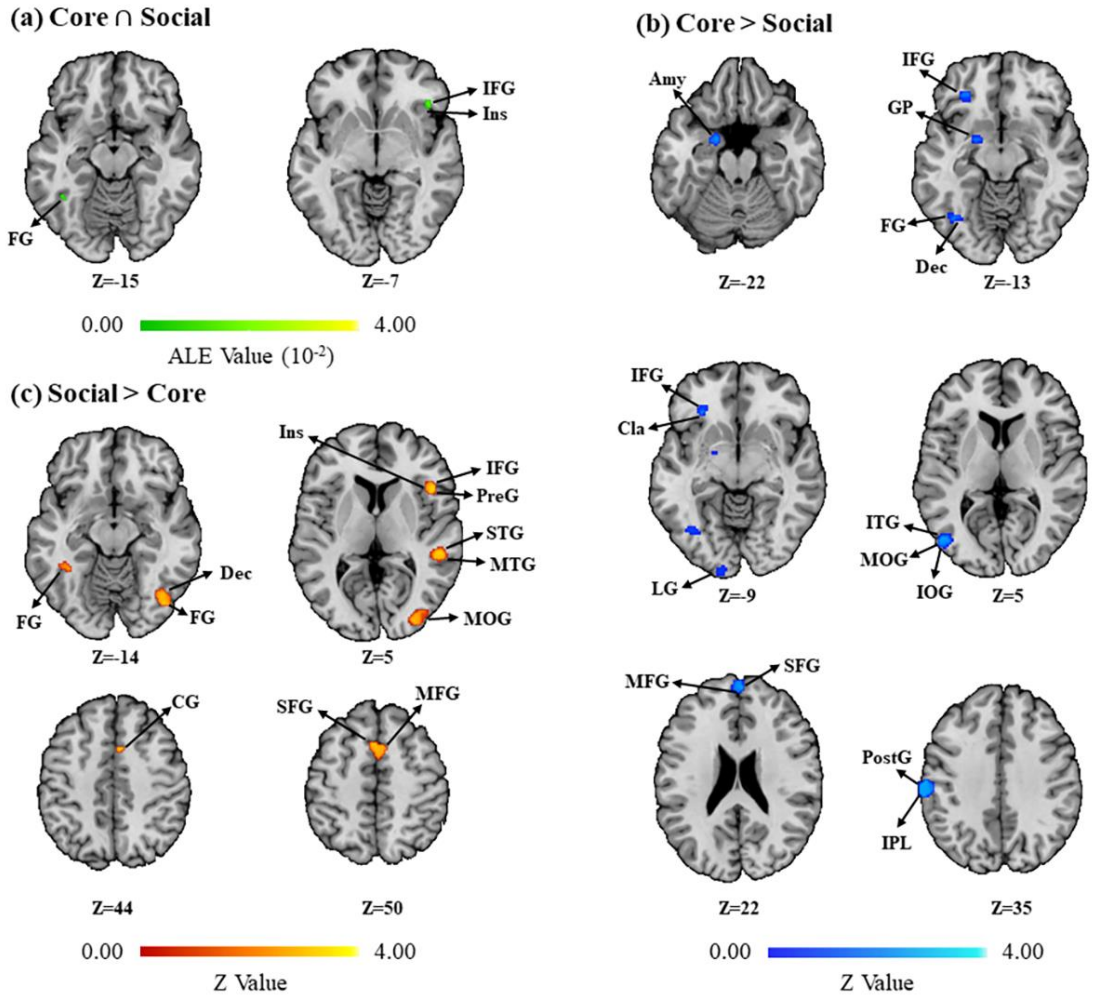

Fig. 3. Overview of significant clusters from the conjunction and contrast analyses. **(a)** Common activations for core and social disgust processing in healthy subjects (domain-general disgust processing). **(b)** Greater activations for Core disgust processing (Core > Social) in healthy subjects (domain-specific regions for core disgust). **(c)** Greater activations for social disgust processing (Social > Core) in healthy subjects (domain-specific regions for social disgust). Coordinates are in the MNI space. Abbreviations: Amy = Amygdala, CG = Cingulate Gyrus, Cla = Claustrum, Dec = Declive, FG = Fusiform Gyrus, GP = Globus Pallidus, IFG = Inferior Frontal Gyrus, Ins = Insula, IOG = Inferior Occipital Gyrus, IPL = Inferior Parietal Lobule, ITG = Inferior Temporal Gyrus, LG = Lingual Gyrus, MFG = Medial Frontal Gyrus, MOG = Middle Occipital Gyrus, MTG = Middle Temporal Gyrus, PostG = Postcentral Gyrus, PreG = Precentral Cyrus, SFG = Superior Frontal Gyrus, STG = Superior Temporal Gyrus.

3.5. Network level functional characterization via MACM analyses

We adopted two different approaches (labeled as MACM A as well as MACM B) aiming to unveil the functional network of right inferior frontal gyrus and left fusiform gyrus from conjunction analyses across core and social disgust processing.

From MACM-A, co-activation maps for the right inferior frontal gyrus included bilateral insula, bilateral inferior frontal gyrus, right anterior cingulate, bilateral medial frontal gyrus and left cingulate gyrus (**Table 6, Fig. 4a**). Co-activation maps for the left fusiform gyrus were significant for bilateral fusiform gyrus, bilateral parahippocampal gyrus, bilateral amygdala, right putamen and right inferior occipital gyrus (**Table 7, Fig. 4a**).

The additional functional network analyses (MACM-B) of right inferior frontal gyrus showed converging results as with MACM-A analyses, including bilateral inferior frontal gyrus, bilateral insula, bilateral medial frontal gyrus, left cingulate gyrus, and right anterior cingulate. MACM-B analyses of left fusiform gyrus also showed highly overlapping regions with MACM-A analyses, including bilateral fusiform gyrus, bilateral amygdala, right putamen and right inferior occipital gyrus (**Fig. 4b**, see **Supplementary Table 4** and **Supplementary Table 5** for detailed activated regions). In other words, both functional network characterization analyses confirmed each other.

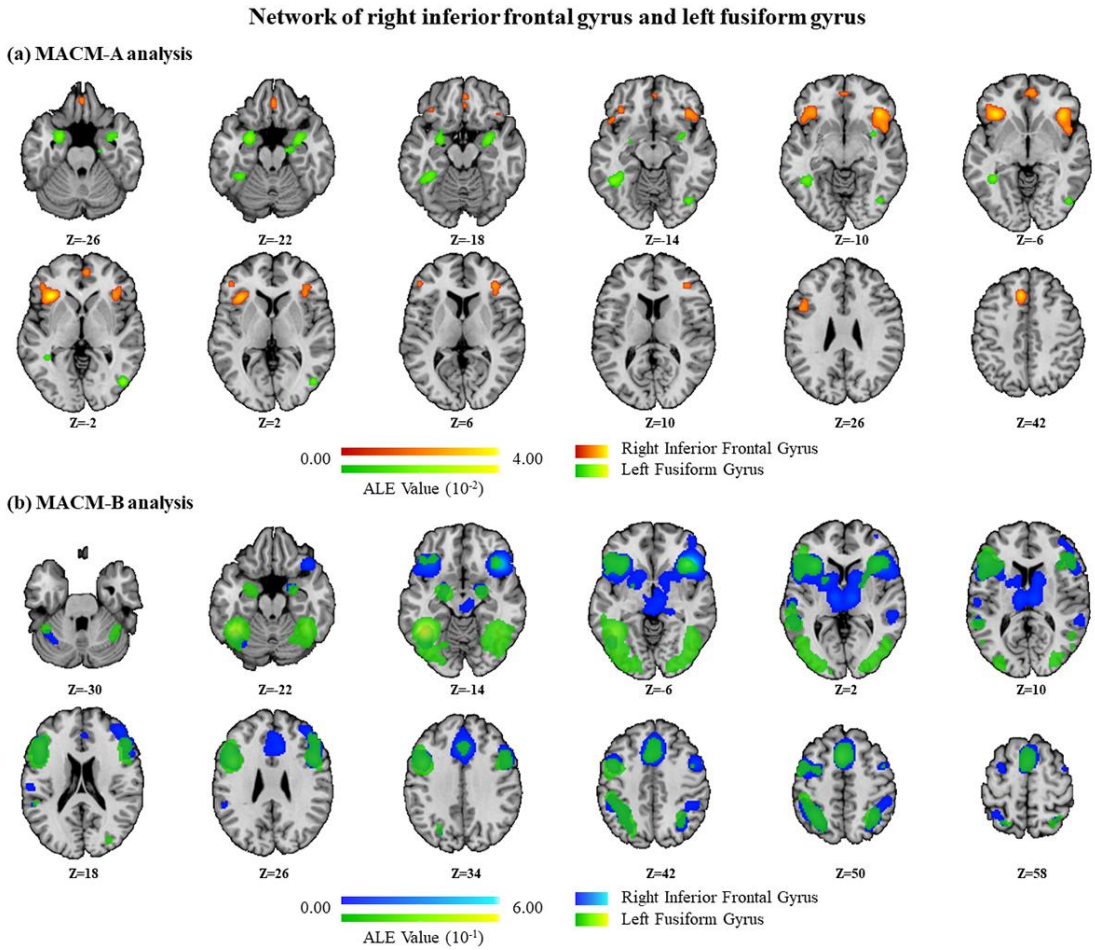

Fig. 4. Overview of the functional networks of right inferior frontal gyrus and left fusiform gyrus by MACM analyses. **(a)** Network of right inferior frontal gyrus and left fusiform gyrus by MACM-A analyses. **(b)** Network of right inferior frontal gyrus and left fusiform gyrus by MACM-B analyses. Coordinates are in the MNI space.

3.6. Functional characterization of the ALE maps on the behavioral level

We conducted three separate quantitative functional annotation analyses by testing the associations of functional terms provided by the Neurosynth database with the brain regions robustly engaged during domain-general disgust processing generated from conjunction analyses as well as core disgust processing and social disgust processing obtained from single dataset analyses. The top 20 terms were visualized with a larger font size reflecting a smaller p-value (see **Fig. 5**). Whereas the domain-general network was mainly characterized by general attention and emotional processes (**Fig. 5a**), core disgust processing regions primarily associated with threat- and avoidance-related processes (**Fig. 5b**), while social disgust processing revealed social- and adaptation-related terms (**Fig. 5c**).

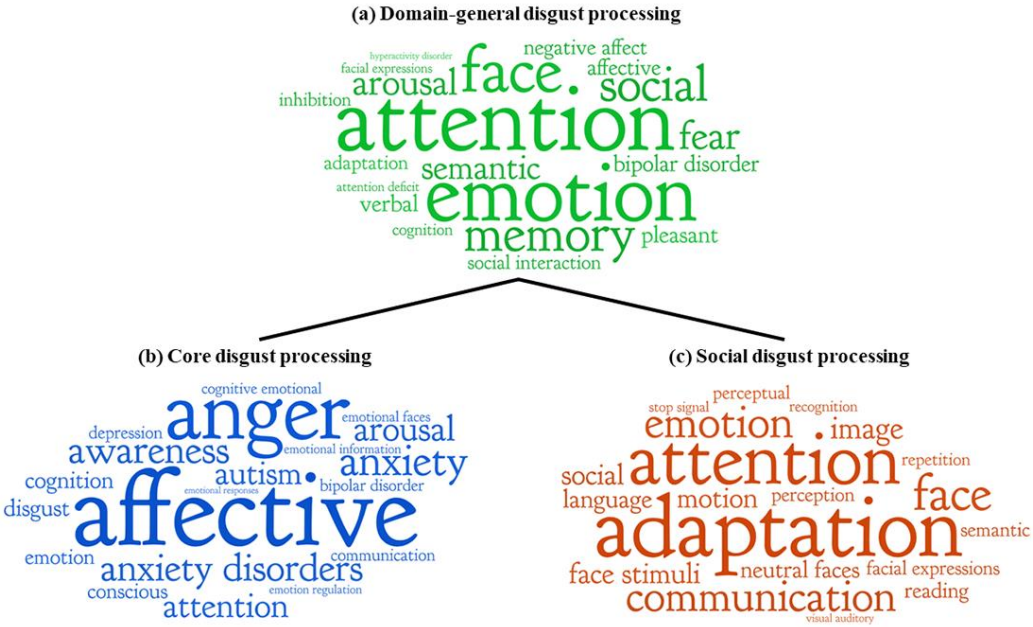

Fig. 5. Functional characterization of the neural correlates from three categories. **(a)** Neural substrates for domain-general disgust processing (Core ∩ Social). **(b)** Neural substrates for core disgust processing. **(c)** Neural substrates for social disgust processing. Only the top 20 terms are displayed. The font size of words is proportional to the permutation p value for association between user-provided cluster of regions and each functional term provided by Neurosynth, with smaller p value indicating bigger term size.

4. Discussion

Previous studies on the brain systems that mediate disgust-related processes and initial studies that examined common and separable neural representations of direct exposure to disgust elicitors (core disgust) and social-communicative signals of disgust (social disgust) revealed inconsistent results. Against this background, we employed neuroimaging meta-analyses that capitalized on a large number of previous fMRI studies to determine the neural substrates robustly engaged in general, core as well as social disgust processing, respectively. Next, by employing meta-analytic conjunction and contrast analyses, we further segregated common (domain-general) and distinct (domain-specific) neural correlates of core and social disgust processing and utilized meta-analytic behavioral and network level decoding to functionally characterize the identified brain regions.

4.1. Brain systems mediating general, core and social disgust processing

The overarching meta-analysis pooling the data from the 69 qualified studies, comprising 78 eligible contrasts (general disgust processing) yielded robust engagement of a bilateral network encompassing primarily the bilateral anterior insular cortex, bilateral amygdala and adjacent globus pallidus, inferior and superior frontal, visual occipital (fusiform gyrus, inferior and middle occipital gyri, lingual gyrus) and cerebellar regions. Separate analyses of the subdomains of core and social disgust processing revealed that the core disgust network largely overlapped with the general disgust network while the social disgust processing network additionally engaged superior temporal regions involved in social processing and face processing regions such as fusiform-extrastriate and frontal cortices, mainly in the right hemisphere.

The identified network for general disgust processing largely resembles regions that have been consistently engaged in disgust-related processes (Fusar-Poli et al., 2009b; Kirby and Robinson, 2017; Vytal and Hamann, 2010; Wager et al., 2015) and may reflect the multifaceted nature of the disgust response. The identified regions may support the engagement of different simultaneous processes which allow a concerted disgust reaction, ranging from initial detection of biologically salient stimuli in occipital visual regions (Tao et al., 2021), early threat detection and implementation of the defensive motor response by the amygdala, globus pallidus, fusiform and cerebellar regions (e.g., Phelps and LeDoux, 2005; Surguladze et al., 2003; Yao et al., 2018b), as well as salience allocation and interoceptive awareness of the emotional state in the insula cortex (Craig, 2009; Li et al., 2019; Uddin, 2015), and the subjective experience and interpretation of the emotional state in prefrontal regions (LeDoux and Pine, 2016).

Examining the core disgust network, i.e., regions robustly activated by disgust eliciting visual stimuli, revealed a similar network primarily encompassing the bilateral insula and adjacent inferior frontal regions, the bilateral amygdala and adjacent globus pallidus as well as temporo-occipital regions. The overlap may reflect that the direct exposure to potential infectious and harmful stimuli triggers the evolutionary defensive-avoidance circuits engaged in early salience and threat detection and the initiation of the physiological and behavioral defensive response, thus facilitating rapid withdrawal. Previous studies have for instance extensively documented reactivity of the amygdala towards aversive stimuli (Zald, 2003) with meta-analytic data demonstrating a higher probability of amygdala activation for stimuli signaling a potential danger, including fear and disgust inducing stimuli, as compared to non-threatening stimuli (Costafreda et al., 2008), indicating a critical role in threat detection and initiation of protective responses (Mihov et al.,

2013; Schienle et al., 2016). The amygdala receives dense projections from the visual cortex and via projections with cerebellar regions and the globus pallidus initiates motor and physiological defensive responses towards aversive stimuli (Giovanniello et al., 2020; Lindquist, 2020; Salih et al., 2009; Sambataro et al., 2006), while bilateral projections to the orbitofrontal cortex further mediate withdrawal or avoidance behavior (Rolls, 1999, 2000b). In support of this interpretation, the meta-analytic functional characterization of the identified core disgust network revealed primarily terms associated with negative affective responses, including e.g., anxiety, arousal as well as disgust.

Separately examining the social disgust studies revealed a right lateralized network encompassing the right anterior insula and inferior frontal gyrus, middle occipital cortex, fusiform gyrus, superior temporal gyrus and cingulate regions. The corresponding meta-analytic functional decoding of the regions revealed primarily terms associated with salience and social communication, including attention as well as face and communication. In line with the functional decoding, the identified regions have been previously associated with emotional face processing (Fusar-Poli et al., 2009b), with the middle occipital cortex involved in early face processing stages (Tu et al., 2013) and the fusiform gyrus being involved in visual attention and higher level face perception processing (Weiner and Zilles, 2016), while superior temporal regions have been strongly involved in social cognitive processes including theory of mind and mentalizing (Frith, 2007; Zilbovicius et al., 2006).

In contrast to several previous original studies, the present meta-analysis did not reveal a robust engagement of the amygdala or main basal ganglia regions (i.e., caudate and putamen) during social or general disgust processing, respectively. However, despite a number of previous studies reporting amygdala engagement during the perception of disgusted faces, a previous meta-analysis failed to corroborate amygdala engagement during disgust faces processing (Fusar-Poli et al., 2009b) and previous studies found either strongest amygdala responses to fear (Mattavelli et al., 2014) or comparable responses to emotional and neutral faces (Derntl et al., 2009; Fitzgerald et al., 2006; Winston et al., 2003) while amygdala lesion patients exhibited intact disgusted face decoding (Becker et al., 2012). With respect to the role of the basal ganglia in disgust, previous imaging (Ahn et al., 2014; Benuzzi et al., 2008; Lassalle et al., 2019; Phillips et al., 2000; Phillips et al., 2004; Phillips et al., 1998; Phillips et al., 1997; Pujol et al., 2018; Shapira et al., 2003; Sprengelmeyer et al., 1998; Tettamanti et al., 2012; Ziegler et al., 2018) and lesion studies (Calder et al., 2000; Sprengelmeyer et al., 1996; Straube et al., 2010) revealed inconsistent results and the present meta-analysis did not confirm a robust engagement.

4.2. Common and distinct neural correlates of core and social disgust processing

Notably the right anterior insula was consistently and specifically identified across both, the separate analyses for core disgust and social disgust. Although the consistent involvement of the insula in disgust processing has long been debated in the original disgust literature (Deeley et al., 2008; Gorno-Tempini et al., 2001; Schienle et al., 2006; Schienle et al., 2005b; Stark et al., 2005; Stark et al., 2004; Stark et al., 2003; Trautmann et al., 2009), several previous studies reported engagement of this region during core disgust as well as social disgust processing (Chapman and Anderson, 2012; Fusar-Poli et al., 2009b; Vytal and Hamann, 2010). Further support for a role of the insula in disgust processing comes from lesion (Adolphs et al., 2003; Calder et al., 2000; Kipps et al., 2007) and intracerebral recording studies (Krolak-Salmon et al., 2003), and studies in

healthy subjects reporting a convergent engagement of the insula across disgust paradigms employing not only visual but also olfactory (Heining et al., 2004; Wicker et al., 2003), gustatory (Corradi-Dell'Acqua et al., 2016; Jabbi et al., 2008) and imagination (Jabbi et al., 2008) procedures. The insula is a functionally heterogenous region and has been involved not only in general salience and interoceptive processes but also in the awareness and experience of emotional states (e.g., Craig, 2009; Uddin, 2015; Zhou et al., 2020). Previous studies have demonstrated that negative affective experience induced by visual stimuli (Viinikainen et al., 2010), subjective experienced unpleasantness (Benuzzi et al., 2008), as well as aversive electrical stimulations and unfair offers in social interactions (Corradi-Dell'Acqua et al., 2016) consistently engage the anterior insula, confirming its potential role in the representation of negative emotional experiences.

Using a conjunction and contrast meta-analytic approach, we aimed to further segregate common and domain-specific neural correlates for core and social disgust processing. In line with the observations from the separate analyses, the right anterior insula extending into the adjacent inferior frontal gyrus and the left fusiform gyrus specifically exhibited convergent engagement during core and social disgust processing. Together with the anterior insula, the inferior frontal cortex plays an important role in general emotional processes such as evaluation of biological significant stimuli (Rolls, 2000a, 2004), interoception (Critchley et al., 2004), multimodal representation emotion salient stimuli (Yamasaki et al., 2002), and emotion recognition (Sprengelmeyer et al., 1998) while the fusiform gyrus plays a role in higher order visual processing (Fusar-Poli et al., 2009b) and emotional reactivity towards negative and threatening stimuli (Kirby and Robinson, 2017; Tao et al., 2021). Initial original studies have begun to examine the shared neural substrates for core and social disgust. For example, Wicker et al. (2003) found that observing disgusted faces activated the anterior insula which was also implicated in first-person disgust experience evoked by unpleasant odorants (Wicker et al., 2003). Similarly, Jabbi et al. (2008) observed that the anterior insula was activated both during the observation of another person's disgusted facial expressions and during the taste of disgusting liquids (Jabbi et al., 2008). A subsequent model from Vicario et al. that was based on data from clinical populations proposed that the insula mediates disgust processing in both core and social disgust domains (Vicario et al., 2017) and explained the common activity between core and social disgust in the context of embodied simulation theories of emotion perception (Gallese and Goldman, 1998; Gallese and Sinigaglia, 2011; Vicario et al., 2017; Wicker et al., 2003). These theories propose that observing a facial emotional expression (i.e., a disgusted face, in the present work referred to as *social disgust*) triggers activation in some of the neural systems engaged in the actual (first-person) experience of the same emotion (core disgust). The present findings extend the previous literature and suggest that the right anterior insula and left fusiform gyrus may support this emotion perception mechanism for disgust. A number of previous studies reported an involvement of the insula in the first-hand experience of pain and vicarious pain induced by observing another person in a painful situation or expressing a painful facial expression (Bzdok et al., 2012; Corradi-Dell'Acqua et al., 2016; Fan et al., 2011; Singer et al., 2004). In the context of the present findings this may indicate a rather general role of the insula in mirroring during different aversive emotional states such as pain and disgust. In contrast the fusiform gyrus has not been consistently reported in emotional empathy or mirroring studies and thus may represent a rather process-specific common neural substrate in the domain of observed and self-experienced disgust. Given

the role of the fusiform gyrus in visual processing and its dense projections with the amygdala (Ardila et al., 2015; Fusar-Poli et al., 2009b; Weiner and Zilles, 2016), this region may support an early discrimination of salient visual stimuli across disgust-related processes (for a potential role of the fusiform gyrus in not face-related fear and threat detection see e.g., Larson et al., 2009; Mueller and Pizzagalli, 2016).

Further meta-analytic network decoding via MACM demonstrated that the identified anterior insula cortex region coupled with a bilateral network encompassing the insula and ventrolateral prefrontal regions as well as anterior cingulate and medial frontal regions. The lateral prefrontal cortex, insula and anterior cingulate exhibit strong anatomical and functional connections (Craig, 2009; Mesulam and Mufson, 1982b) and represent key hubs within the salience network, the fronto-parietal executive control network and the sensorimotor networks (Belyk et al., 2017; Cloutman et al., 2012; Cox et al., 2010). Functional interactions between these regions have been involved in attentional processes (Wang et al., 2019), emotion regulation (Morawetz et al., 2017) and goal-directed behavior (Dosenbach et al., 2006), which may support disgust processing across core and social domains. The identified left fusiform gyrus network comprised a limbic-occipital network encompassing the amygdala, parahippocampal gyrus, putamen and inferior occipital regions. The functional interplay between these regions has been demonstrated in several previous studies (Amting et al., 2010; Fairhall and Ishai, 2007; Herrington et al., 2011; Molapour et al., 2015; Turk-Browne et al., 2010) and plays an important role in early threat detection (Tao et al., 2021), suggesting that this network may facilitate detection of potential threats across core and social disgust processes.

Examining regions specifically engaged during the two disgust processing domains revealed stronger activity of several regions in the left hemispheric disgust network during core disgust processing, including e.g., occipito-temporal visual, limbic, inferior frontal and parietal regions. These regions mainly mirror the results of the core disgust processing network and may suggest a neurobiological model for domain-specific core disgust processing in which visual disgust stimuli undergo an early screening in occipito-temporal, which – due to the salience of the stimuli – encompass both, primary and secondary visual cortex processing (Bradley et al., 2003). Next the information is transmitted via inferior temporal pathways to the amygdala and orbitofrontal cortex regions strongly engaged in emotional evaluation (Rolls, 2000b), while the parahippocampal gyrus may further qualify the contextual relevance of the stimuli (Tao et al., 2021). The survival relevant reactivity moreover requires rapid withdrawal behavior (Rolls, 1999, 2000b), which are potentially mediated by prefrontal, inferior parietal and pallidal regions. In particular prefrontal regions (e.g., superior and medial frontal gyrus) exhibit dense connections with parietal, temporal, and occipital regions (Cechetto and Topolovec, 2002) and play a key role in both, emotional awareness and executive control, including attention and initiation of appropriate responses (LeDoux, 2014; LeDoux and Pine, 2016; Rozzi and Fogassi, 2017) while the inferior parietal lobule is an important locus for motor planning (Buxbaum and Randerath, 2018) and receives input from both, visual as well as somatosensory regions thus being optimal positioned to integrate these modalities (Andersen, 2011). The globus pallidus finally has been implicated in implementing rapid motor reactions in response to emotional stimuli (Sambataro et al., 2006) and via connections with the amygdala regulates responses to (unconditioned) threat stimuli (Giovanniello et al., 2020). Together these findings indicate that – compared to social disgust stimuli - exposure to disgusting and thus potentially dangerous stimuli engages the core defensive-

avoidance circuits.

In contrast, for domain-specific social disgust processing, a right lateralized network encompassing anterior insula (extending into the inferior frontal gyrus), middle occipital gyrus (occipital face area), superior temporal gyrus and anterior cingulate regions as well as the left fusiform face area exhibited stronger activation. In the context of previous face processing models (Haxby et al., 2000; Liu et al., 2021), the present findings may suggest a model of social disgust processing that aligns with the ventral and dorsal face processing streams. The dorsal pathway includes superior temporal and middle temporal regions, while the ventral pathway comprises of occipital face area, fusiform face area, and inferior frontal regions. The dorsal pathway has been implicated in emotional face processing (Britton et al., 2006; Fusar-Poli et al., 2009b) and may facilitate subsequent social cognitive processes including theory of mind and mentalizing (Frith, 2007; Zilbovicius et al., 2006), while the ventral stream is strongly engaged in determining dynamic processes of facial emotion processing, such that the right middle occipital gyrus may relay the information of disgusted faces to the left fusiform face area, and the right inferior frontal gyrus may play a key role in maintaining attention to the social information in the perception of disgusted facial expressions (Liu et al., 2021). In addition to core regions of these pathways the social disgust systems encompassed the right insula, right anterior cingulate gyrus, left prefrontal regions and right declive, which all have been involved in face and particular emotional face processing (Britton et al., 2006; Fusar-Poli et al., 2009a; Fusar-Poli et al., 2009b; Liu et al., 2021; Sabatinelli et al., 2011) and accumulating evidence from human and non-human primate models suggests a role of the insula in decoding the emotional content of faces (Desimone et al., 1984; Haxby et al., 2000; Mesulam and Mufson, 1982a; Perrett et al., 1982) as well as emotional awareness and interoception (Craig, 2009) and disgust processing it is conceivable that activation in this region may support the emotional and cognitive decoding of the facial disgust signals.

Notably, a strong lateralization effect was observed such that core disgust processing primarily engaged a left-lateralized, while social disgust processing primarily engaged a right-lateralized network. Although we did not have a priori lateralization hypothesis, the findings resonate with some previous studies suggesting a left lateralization of withdrawal-related activity (Tucker et al., 1995; Wager et al., 2003) while conscious emotional perception is represented in a right lateralized network (Adolphs, 2002; Adolphs et al., 1996; Davidson and Irwin, 1999; Oliveri et al., 2003). However, the explanation of a left-lateralized withdrawal-network stands in contrast with overarching approach/avoidance models (Chen et al., 2021; Güntürkün et al., 2020; Palomero-Gallagher and Amunts, 2021), which assumes that the left hemisphere is relatively specialized in processing approach behavior, while the right hemisphere is relatively specialized in processing avoidance or withdrawal behavior. However, evidence for either of the proposed models is not unequivocal such that for instance several previous meta-analyses reported bilateral networks in response to withdrawal-related stimuli including threat- and disgust-related stimuli (Fusar-Poli et al., 2009a; Fusar-Poli et al., 2009b; Tao et al., 2021; Vytal and Hamann, 2010).

4.3. Specificity of the identified brain systems for disgust-related processes

While several avoidance-related processes such as the processing of threat- and disgust-related stimuli has been associated with increased activity in the defensive networks described above evidence from lesion studies suggests a relative specialization of the underlying systems.

For instance, evidence from previous lesion models showed that insula lesion led to deficits in disgust processing (Adolphs et al., 2003; Calder et al., 2000; Cantone et al., 2019; Holtmann et al., 2020; Kipps et al., 2007) while amygdala lesion led to deficits in fear processing (Adolphs et al., 2005; Becker et al., 2012; Calder et al., 1996; Feinstein et al., 2011; Mihov et al., 2013). However, the conventional fMRI approach is limited with respect to disentangling process-specific neurofunctional correlates (Woo et al., 2017; Zhou et al., 2021). Recent studies thus adopted multivariate pattern analyses which allows a more precise determination of common and separable neurofunctional representations revealed for instance that the anterior insula represents vicarious and self-experienced pain, however, the common local patterns in this regions also represented disgust (Corradi-Dell'Acqua et al., 2016), or that both, empathic pain evolved by the observation of noxious stimulation of body limbs and painful facial expressions share a common representation in the mid-insula (Zhou et al., 2020), while other defensive responses such as fear and conditioned threat exhibit separable neurofunctional representations (Zhou et al., 2021). Within this context the specificity of the determined defensive network for disgust versus other defensive responses needs to be further determined in future studies.

4.4. Limitations

Results of the present study need to be considered in the context of several limitations. First, core disgust in the present study included contamination and envelope violations (Vicario et al., 2017) while some previous disgust conceptualizations differentiate these stimuli (Haidt et al., 1994; Olatunji and Sawchuk, 2005; Olatunji et al., 2007; Rozin and Fallon, 1987; van Overveld et al., 2009). Initial neuroimaging studies revealed inconsistent support of this notion (Borg et al., 2012; Harrison et al., 2010; Schienle et al., 2006; Wright et al., 2004) and an increasing number of neuroimaging studies on disgust may allow a reasonable powered examination of further disgust subprocesses in the future. Second, in line with the conceptualization in Vicario et al. (2017) *social disgust* in the present study specifically referred to experiments that employed disgusted facial expression as social communicative signal. However, a broader definition of *social* forms of disgust could also include social disgusting words and social disgusting scenes. While the common and separable neural bases of these social disgust aspects are of high interest for future research the low number of studies employing these stimuli does currently not allow a robust meta-analytic examination. Third, the included studies on social disgust investigated perception rather than production of disgusted facial expression. Although the number of facial expression production fMRI studies for disgust is currently too small to warrant a meta-analytic examination, determining common and separable neural correlates of production and perception would be of interest for future studies. Fourth, the present study focused on core and social processing in the domain of disgust. Previous original studies have employed experimental designs to compare core and social disgust processing but have been limited due to limitations inherent to original studies (Schäfer et al., 2005; Schienle et al., 2020). Previous meta-analyses have employed a similar strategy in the domain of empathy processing by comparing meta-analytic activity maps for facial pain expressions and stimuli presenting acute pain infliction (Timmers et al., 2018). While future studies may extend this approach to other emotional domains such as fear and encompass emotional domain as additional dimension of common and shared neural representations in neuroimaging meta-analysis, the conventional fMRI and meta-analytic approach is limited with respect to determining fine-grained separable neurofunctional representations and multivariate

representational models may help to further determine separable process-specific neurofunctional representations (see e.g., Zhou et al., 2020; Zhou et al., 2021). Fifth, the present database of original studies did not allow to examine sex-differences in the neural basis of disgust processing. Initial studies reported e.g., stronger disgust-related inferior frontal reactivity in women (Caseras et al., 2007), while other studies did not find sex differences (Baumann and Mattingley, 2012; Schienle et al., 2005a; Stark et al., 2003). Lastly, the present study included task-based fMRI studies focusing on regional analyses, while recent advanced approaches and findings suggest a distributed neural representation (Zhou et al., 2021) or a functional division between gyri and sulci (Jiang et al., 2015; Jiang et al., 2018; Jiang et al., 2021) of cognitive and emotional processes. Future studies may capitalize on these developments to further dissect common and differential neural representation of social and non-social processes or different defensive responses such as disgust and fear.

5. Conclusions

The present study employed a coordinate-based neuroimaging meta-analytic approach to determine the neurobiological basis of disgust processing in humans. Exposure to disgust eliciting stimuli induced robust activity in a network encompassing regions engaged in early visual threat detection, emotional experience and defensive motor responses, while social stimuli of disgust primarily engaged regions engaged in facial and social cognitive processes. Across both disgust domains, the anterior insula/inferior frontal gyrus and the fusiform gyrus were robustly engaged suggesting an involvement of these regions across disgust processing modalities.

Declaration of Competing Interest

We declare no conflict of interest.

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Table 1
Brain regions generally activated by all studies of disgust processing in healthy subjects.

Volume (mm^3)	Side	Brain region	BA	MNI coordinates (x, y, z)			ALE value (10^{-2})	Z
2568	right	Amygdala		22	-6	-16	3.34	5.30
	right	Amygdala		24	-2	-26	3.26	5.21
2560	right	Inferior Frontal Gyrus	47	42	26	-6	3.22	5.16
	right	Middle Frontal Gyrus	46	48	18	14	2.28	3.97
	right	Insula	13	44	20	4	1.89	3.42
2272	left	Fusiform Gyrus	37	-42	-48	-16	2.97	4.86
	left	Fusiform Gyrus	37	-44	-58	-8	2.93	4.81
2176	right	Fusiform Gyrus	19	42	-72	-12	2.48	4.24
	right	Fusiform Gyrus	37	42	-52	-18	2.41	4.14
	right	Fusiform Gyrus	37	42	-46	-20	2.24	3.92
	right	Declive		38	-58	-14	2.23	3.89
	right	Inferior Occipital Gyrus	19	48	-72	-2	1.98	3.55
2104	left	Amygdala		-22	-2	-22	4.48	6.57
2024	right	Middle Occipital Gyrus	18	36	-88	6	3.18	5.12
	right	Inferior Occipital Gyrus	18	36	-88	-10	2.82	4.68
1400	right	Lingual Gyrus	17	14	-92	0	3.89	5.93
1304	left	Middle Occipital Gyrus	19	-44	-78	8	2.77	4.61
	left	Inferior Temporal Gyrus	19	-50	-76	0	2.01	3.60
1256	left	Insula		-36	26	-4	2.29	3.99
	left	Insula	13	-34	24	0	2.28	3.97
	left	Insula	13	-44	14	-2	2.12	3.75
1224	left	Inferior Parietal Lobule	40	-62	-24	34	4.07	6.14
960	right	Inferior Frontal	9	48	10	24	3.27	5.22

		Gyrus						
888	left	Superior Frontal Gyrus	9	-6	64	26	2.76	4.60
	left	Superior Frontal Gyrus	9	2	62	18	2.14	3.78

Abbreviations: ALE = Action Likelihood Estimation, BA = Brodmann Area, MNI = Montreal Neurological Institute.

Table 2

Brain regions activated during core disgust processing in healthy subjects.

Volume (mm^3)	Side	Brain region	BA	MNI coordinates (x, y, z)			ALE value (10^{-2})	Z
2216	left	Amygdala		-22	-2	-22	3.80	6.49
1736	left	Declive		-34	-70	-14	2.53	4.89
	left	Fusiform Gyrus	37	-44	-60	-8	2.09	4.27
	left	Fusiform Gyrus	37	-42	-54	-18	1.69	3.67
1696	right	Amygdala		22	-6	-16	2.85	5.31
	right	Amygdala		26	-2	-24	2.33	4.62
1512	left	Inferior Parietal Lobule	40	-62	-24	34	3.99	6.71
1472	left	Middle Occipital Gyrus	19	-44	-76	8	2.47	4.81
	left	Inferior Temporal Gyrus	19	-50	-76	0	2.01	4.16
1240	left	Superior Frontal Gyrus	9	-6	64	26	2.21	4.44
	left	Superior Frontal Gyrus	9	2	62	18	2.14	4.34
1120	right	Inferior Occipital Gyrus	17	14	-92	-2	2.64	5.04
976	left	Inferior Frontal Gyrus	47	-30	32	-14	2.68	5.09
	left	Insula	13	-34	24	-2	1.73	3.72
896	right	Insula		40	26	-6	2.16	4.37
808	left	Inferior Occipital Gyrus	17	-10	-98	-8	2.14	4.34

Abbreviations: ALE = Action Likelihood Estimation, BA = Brodmann Area, MNI = Montreal Neurological Institute.

Table 3

Brain regions activated during social disgust processing in healthy subjects.

Volume (mm^3)	Side	Brain region	BA	MNI coordinates (x, y, z)			ALE value (10^{-2})	Z
1848	right	insula	13	48	18	12	2.11	4.66
	right	insula	13	44	20	4	1.81	4.19
	right	Inferior Frontal Gyrus	47	46	28	-8	1.50	3.67
1416	left	Superior Frontal Gyrus	6	2	10	54	1.92	4.37
	left	Superior Frontal Gyrus	6	-2	12	56	1.90	4.33
	right	Cingulate Gyrus	24	6	10	42	1.40	3.51
1392	right	Middle Occipital Gyrus	18	36	-88	8	2.93	5.82
1256	right	Fusiform Gyrus	19	42	-72	-14	2.42	5.12
888	left	Fusiform Gyrus	37	-40	-46	-18	2.31	4.97
728	right	Superior Temporal Gyrus	22	52	-34	4	2.31	4.96

Abbreviations: ALE = Action Likelihood Estimation, BA = Brodmann Area, MNI = Montreal Neurological Institute.

Table 4

Brain regions activated by conjunction analysis between core and social disgust processing in healthy subjects.

Volume (mm^3)	Side	Brain region	Percentage of overlap	BA	MNI coordinates (x, y, z)			ALE value (10^{-2})
136	right	Inferior Frontal Gyrus	80% Inferior Frontal Gyrus, 20% Insula.	47	44	26	-8	1.49
16	left	Fusiform Gyrus	100% Fusiform Gyrus.	37	-40	-52	-16	1.21
16	left	Fusiform Gyrus	100% Fusiform Gyrus.	37	-42	-50	-14	1.37

Abbreviations: ALE = Action Likelihood Estimation, BA = Brodmann Area, MNI = Montreal Neurological Institute.

Table 5
Brain regions activated by contrast analysis between core and social disgust processing in healthy subjects.

Volume (mm^3)	Side	Brain region	Percentage of overlap	BA	MNI coordinates (x, y, z)			Z
Hyper-activation (core > social)								
1256	left	Postcentral Gyrus	67.9% Inferior Parietal Lobule, 32.1% Postcentral Gyrus.	2	-66	-20	34	2.64
	left	Postcentral Gyrus		2	-61.3	-21.3	36.7	2.56
	left	Inferior Parietal Lobule		40	-66	-24	32	2.53
	left	Inferior Parietal Lobule		40	-64.7	-27.3	35	2.47
	left	Inferior Parietal Lobule		40	-64	-28	28	2.34
992	left	Inferior Temporal Gyrus	47.8% Middle Occipital Gyrus, 34.8% Inferior Temporal Gyrus, 8.7% Inferior Occipital Gyrus, 8.7% Middle Temporal Gyrus.	37	-50	-74	0	3.29
	left	Middle Occipital Gyrus		37	-44	-72	6	2.58
808	left	Parahippocampal Gyrus	49.1% Brodmann area 34, 45.5% Amygdala, 3.6% Globus Pallidus, 1.8% Brodmann area 28.	34	-16	-2	-22	2.14
	left	Parahippocampal Gyrus		34	-18	0	-14	1.90
688	right	Superior Frontal Gyrus	73.7% Superior Frontal Gyrus, 26.3% Medial	9	4	60	20	2.45
	right	Superior Frontal Gyrus		9	4	64	16	2.34

	left	Medial Frontal Gyrus	Frontal Gyrus.	10	0	64	14	2.33
360	left	Inferior Frontal Gyrus	100% Inferior Frontal Gyrus.	47	-28	34	-10	2.23
	left	Claustrum			-28	30	-8	2.13
240	left	Fusiform Gyrus	69.2% Declive, 30.8% Fusiform Gyrus.	37	-40	-66	-12	2.17
	left	Declive			-32	-70	-10	1.87
224	left	Lingual Gyrus	92.9% Lingual Gyrus, 7.1% Inferior Occipital Gyrus.	17	-8	-100	-6	1.89
Hyper-activation (social > core)								
1344	right	Inferior Frontal Gyrus	70.6% Insula, 20.6% Inferior Frontal Gyrus, 8.8% Precentral Gyrus.	44	49	18	8	3.54
	right	Inferior Frontal Gyrus		45	46	22	8	3.35
1128	left	Medial Frontal Gyrus	57% Medial Frontal Gyrus, 31.6% Superior Frontal Gyrus, 11.4% Cingulate Gyrus.	32	-2	14	48	3.54
	right	Cingulate Gyrus		24	5	10	44	3.09
1040	right	Middle Occipital Gyrus	100% Middle Occipital Gyrus.		30	-90	2	3.09
	right	Middle Occipital Gyrus		19	38	-86	10	3.06
1032	right	Declive	81.3% Declive, 18.7% Fusiform Gyrus.		44	-76	-16	3.16
	right	Declive			42	-70	-18	3.04
728	right	Superior Temporal Gyrus	55.6% Middle Temporal	22	54.8	-33.6	3.2	3.29

	right	Middle Temporal Gyrus	Gyrus, 44.4% Superior Temporal Gyrus.		52	-35	0	3.24
472	left	Fusiform Gyrus	78.9% Fusiform Gyrus, 21.1% Culmen.	37	-36	-46	-16	2.49

Abbreviations: ALE = Action Likelihood Estimation, BA = Brodmann Area, MNI = Montreal Neurological Institute.

Table 6

Network of right inferior frontal gyrus revealed by MACM-A analysis.

Volume (mm^3)	Side	Brain region	BA	MNI coordinates (x, y, z)			ALE value (10^{-2})	Z
5352	right	Inferior Frontal Gyrus	47	40	26	-8	3.54	5.85
	right	Insula	13	46	10	-8	2.47	4.46
	right	Inferior Frontal Gyrus	46	38	36	6	2.42	4.39
	right	Inferior Frontal Gyrus	13	38	28	2	2.14	3.99
4808	left	Insula	13	-34	24	-2	3.88	6.25
	left	Inferior Frontal Gyrus	46	-48	38	4	1.98	3.75
1536	right	Anterior Cingulate	32	6	50	-4	2.43	4.41
	right	Medial Frontal Gyrus	11	2	38	-22	2.13	3.97
	left	Medial Frontal Gyrus	11	0	42	-26	2.08	3.90
	right	Anterior Cingulate	32	4	46	-16	1.94	3.69
1192	left	Cingulate Gyrus	32	-8	26	42	3.24	5.48
1104	left	Inferior Frontal Gyrus	9	-46	12	26	2.27	4.18

Abbreviations: ALE = Action Likelihood Estimation, BA = Brodmann Area, MNI = Montreal Neurological Institute.

Table 7

Network of left fusiform gyrus revealed by MACM-A analysis.

Volume (mm^3)	Side	Brain region	BA	MNI coordinates (x, y, z)			ALE value (10^{-2})	Z
2776	left	Fusiform Gyrus	37	-44	-50	-14	2.04	5.18
	left	Parahippocampal Gyrus	19	-40	-48	-6	1.58	4.39
2240	right	Amygdala		30	-4	-20	1.88	4.90
	right	Parahippocampal Gyrus	28	20	-16	-24	1.18	3.59
	right	Putamen		34	4	-10	1.16	3.55
1872	left	Amygdala		-26	-2	-22	2.27	5.56
1184	right	Inferior Occipital Gyrus	19	48	-74	-2	2.21	5.46
	right	Fusiform Gyrus	19	40	-72	-14	1.43	4.11

Abbreviations: ALE = Action Likelihood Estimation, BA = Brodmann Area, MNI = Montreal Neurological Institute.

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