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Facial Expression Recognition: A Meta-Analytic Review of Theoretical Models and Neuroimaging Evidence

Pengfei Xu[1-3, #, *], Shaoling Peng[4, #], Yuejia Luo[1, 2, 4], Gaolang Gong[4, 5, *]

[1]Faculty of Psychology, Beijing Normal University, Beijing, China
[2]Center for Emotion and Brain, Shenzhen Institute of Neuroscience, Shenzhen, China
[3] Guangdong-Hong Kong-Macao Greater Bay Area Research Institute for Neuroscience and Neurotechnologies, Kwun Tong, Hong Kong, China
[4]State Key Laboratory of Cognitive Neuroscience and Learning & IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing, China
[5]Beijing Key Laboratory of Brain Imaging and Connectomics, Beijing Normal University, Beijing, China

[#] These authors contributed equally to the current work.

[*]Corresponding author:

Pengfei Xu, PhD
Faculty of Psychology
Beijing Normal University, Beijing, China
Email: pengfeixu.px@gmail.com

Gaolang Gong, PhD
State Key Laboratory of Cognitive Neuroscience and Learning
Beijing Normal University, Beijing 100875, China.
Email: gaolang.gong@bnu.edu.cn

Highlights

- Brain organizations of facial expression recognition support the constructionist hypothesis.
- Common brain activation and connectivity distributions are shared by different discrete/dimensional facial expressions.
- The amygdala-centered 'core' affect system are connected distributed networks.
- The brain organizations of facial expression recognition are flexibly asymmetrical.

Abstract

Discrimination of facial expressions is an elementary function of the human brain. While the way emotions are represented in the brain has long been debated, common and specific neural representations in recognition of facial expressions are also complicated. To examine brain organizations and asymmetry on discrete and dimensional facial emotions, we conducted an activation likelihood estimation meta-analysis and meta-analytic connectivity modelling on 141 studies with a total of 3138 participants. We found consistent engagement of the amygdala and a common set of brain networks across discrete and dimensional emotions. The left-hemisphere dominance of the amygdala and AI across categories of facial expression, but category-specific lateralization of the vmPFC, suggesting a flexibly asymmetrical neural representations of facial expression recognition. These results converge to characteristic activation and connectivity patterns across discrete and dimensional emotion categories in recognition of facial expressions. Our findings provide the first quantitatively meta-analytic brain network-based evidence supportive of the psychological constructionist hypothesis in facial expression recognition.

Keywords: Facial expression recognition; constructionist hypothesis; locationist hypothesis; activation likelihood estimation (ALE); meta-analytic connectivity modelling (MACM)

1. Introduction

Facial expressions have been studied in infants (Field et al., 1982) and universally across cultures and races (Ekman and Friesen, 1971; Elfenbein and Ambady, 2002). Given that our basic emotions such as anger, happiness, surprise, fear, disgust and sadness can be signaled by different facial expressions, recognizing facial expressions is a fundamental ability of the brain for social communications (Adolphs, 2002a). A variety of models have been proposed to account for cognitive processes and neural representations of emotions, such as discrete emotion theory (Ekman, 1992, 2008), dimensional emotion theory (Barrett, 1998; Gable and Harmon-Jones, 2010; Hamann, 2012), the locationist account (Barrett, 2006; Ekman and Cordaro, 2011), and the psychological constructionist account (Lindquist and Barrett, 2012; Lindquist et al., 2012). While the way that emotions are represented in the brain has long been debated (Hamann, 2012), the neuropsychological mechanisms of facial expression recognition are also complicated. It has been proposed that two psychological processes might be involved, including perception of geometric configuration of facial features and recognition of emotions expressed (Fusar-Poli et al., 2009b). Given face processing is evolutionarily special (Johnson, 2005; Vuilleumier et al., 2003), whether the neuroimaging evidence for facial expression recognition supports current models of emotion processing in the brain remains unclear.

Here, we explore neurocognitive mechanisms of facial expression recognition on the basis of brain activation and connectivity in recognition of facial emotions. We first review classical models of emotion recognition and hypotheses of the emotional brain, as well as their relationships with facial expression recognition. Next, we conduct a set of meta-analyses to examine brain organizations in recognition of facial expressions. Specifically, we 1) identify brain activity and connectivity profiles in discrete and dimensional emotions; 2) compare common and distinctive patterns of brain maps across discrete and dimensional emotions; 3) decode functional characterizations of the identified brain networks; 4) explore asymmetry of the brain for facial expressions recognition. We then generate characteristics of brain organizations in facial expression recognition, in support of the theoretical models. Finally, we discuss limitations of the current meta-analyses and make suggestions for future studies.

1.1. Emotion recognition and facial expression recognition

The brain system for recognizing emotions varies with stimuli types, sensory modalities, and facial characteristics (Calder and Young, 2005). While emotion recognition from scenes is especially associated with the lateral occipital cortex (LOC) and thalamus, emotion recognition from faces uniquely engages the fusiform face area (FFA) and middle temporal gyrus (MT), both of which share a set of brain areas including the amygdala, medial prefrontal cortex (mPFC), orbitofrontal cortex (OFC), inferior temporal cortex (IT), and extrastriate occipital cortex (see Sabatinelli et al., 2011 for a meta-analysis). Voice-specific and face-specific neural representations have also been consistently shown in the superior temporal cortex (ST) and MT, respectively (Schirmer, 2018). Based on the classical dual neural pathway model of face processing (Haxby JV et al., 2000), a recent model has been proposed that static and dynamic facial expressions are processed by the ventral and dorsal face neural pathway, respectively (Bernstein and Yovel, 2015). However, common and distinct neural representations of specific facial expressions remain unclear. There is a lack of persuasive evidence and direct comparison among different categories of facial expressions in support of current models of emotion processing.

1.2. Psychological models of emotion processing

There are two classical psychological models of emotion processing: the basic emotion model and the dimensional emotion model. These two models center around whether the basic constituent units of emotions are discrete or dimensional (Hamann, 2012). The basic emotion model, proposed by Ekman and Friesen (1971), assumes that there are essentially six basic emotion categories - happiness, anger, sadness, fear, disgust, and surprise - that are inherently discrete and psychophysiologically distinct. These six basic emotions can interact with each other and combine to form other “complex emotions” such as jealousy, love etc. (Darwin and Prodger, 1998; Ortigue and Bianchi-Demicheli, 2011). The dimensional model, by contrast, argues that emotions consist of fundamental dimensions, such as arousal (Osgood et al., 1957; Russell, 1979), valence (positive and negative emotions) and motivation (approach and withdrawal) (Barrett and Wager, 2006; Davidson et al., 1990a). This model holds that all emotions are a combination of these independent continuous dimensions that are not specific to any single emotion category. Taking anger as an example, it can be viewed as a combination of high arousal, negative valence and a motivational tendency to approach the trigging situation. Although there have been findings showing discrete neural underpinnings of basic emotions (for a meta-analysis, see Vytal and Hamann, 2010), a mounting body of evidence supports the dimensional model (Barrett and Wager, 2006; Wager et al., 2015). Focusing on the valence of the dimensional model, there are different neural accounts proposing that positive and negative emotions are underpinned by i) a common but bipolar brain system, ii) independent brain systems, or iii) flexible valence-general brain systems (Lindquist et al., 2016). Therefore, neuroimaging studies provide important evidence for brain mechanisms underlying emotion processing in support of these potential hypotheses.

1.3. Neuroimaging hypotheses of the emotional brain

Neuroimaging findings of emotion processing converge on two main hypotheses based on models of emotion. The locationist hypothesis assumes that each category of discrete emotion is localized in a specific brain area or network, whereas the psychological constructionist hypothesis proposes that emotions are constructed from combinations of basic psychological operations and neural elements of the brain network that are domain-general, rather than specific to emotion (Lindquist et al., 2012). Each specific emotion is underpinned by the network comprising brain regions more or less specialized in that emotion and brain regions involved in other functions. For example, the amygdala, which has extensive connections with both the cortical and subcortical regions, is broadly involved in attention, perception, decision-making and emotion (Pessoa, 2010). Although there has been a number of meta-analyses of neuroimaging studies conducted to examine these hypotheses in general emotion processing (Dricu and Fruhholz, 2016; Fusar-Poli et al., 2009b; Lindquist et al., 2012; Murphy et al., 2003; Vytal and Hamann, 2010; Wager et al., 2003) or to compare the processing of faces to that of other stimuli (Dricu and Fruhholz, 2016; Sabatinelli et al., 2011), the brain organization specific to facial expression recognition remains unclear. Despite that a previous meta-analytic study has shown neuroimaging evidence for discrete brain activations of basic emotions in recognition of facial expressions (Fusar-Poli et al., 2009b), brain responses to perception of facial geometric configuration might be involved given that emotional faces were compared with non-facial stimuli in their analyses. Additionally, the inclusion of ROI-based studies in that meta-analytic study could also have led to potential biases to predefined ROIs.

In addition to brain activation patterns of facial expression recognition, recent studies have shown that dissociated neural pathways are engaged, depending on facial expressions (Meaux and Vuilleumier, 2016). For instance, interactions between the anterior cingulate cortex (ACC) and superior frontal gyrus (SFG), and interactions between the superior temporal sulcus (STS) and inferior frontal gyrus (IFG), are engaged distinctively in processing of dynamic facial expressions, while the neural pathway from the STS to amygdala is selectively involved in the integration of distinct processes of dynamic facial expression (Skiba and Vuilleumier, 2020). Although connectivity patterns of the amygdala have been shown to characterize dynamic signatures of prototypical basic emotions (Diano et al., 2017; Ziaei et al., 2017), Jamieson et al. (2021) has shown that connectivity from the amygdala and dorsal lateral prefrontal cortex (dlPFC) responds to dimensional characteristics that are different between sad and fearful facial expressions. However, it is difficult to obtain a complete picture of emotional face processing circuitry in the human brain based on these heterogeneous findings from various tasks and analyses.

Methodologically, the recently proposed meta-analytic connectivity modelling (MACM) approach has been widely used to delineate the functional connectivity of specific brain regions (Robinson et al., 2010). Making use of many task-based fMRI studies included in the BrainMap database, it identifies brain regions that coactivate with pre-defined regions of interest (ROIs) and rebuilds indirect connections within a network. Previous studies have also shown that networks identified by the task-based MACM method are highly consistent with those built from seed-based resting-state functional connectivity (Gu et al., 2019; Hartwigsen et al., 2019). Therefore, the MACM approach would be advantageous for the identification of brain networks involved in recognition of discrete and dimensional facial expressions.

1.4. Asymmetry of the emotional brain

The classical overall right-hemisphere dominance hypothesis of emotion processing has been proposed for a long time (Schwartz et al., 1975), however, it is unsupported by a couple of meta-analyses (Fusar-Poli et al., 2009a; Wager et al., 2003). Instead, the valence-specific lateralization of emotion has recently been shown in the amygdala and PFC (Fusar-Poli et al., 2009a; Wager et al., 2003). The frontal asymmetry of emotion has also been proposed for the positive-negative dimensional model, with the left PFC responding to positive emotions and the right PFC responding to negative emotions (van

Honk and Schutter, 2006). These lateralization patterns have also been shown in the approach-withdrawal motivational-direction model (Harmon-Jones, 2004; Murphy et al., 2003). It has also been proposed that the asymmetrical emotion organization is underpinned by the lateralized homeostatic afferent activation of the anterior insula (AI) (Craig, 2005). Therefore, a systematic meta-analytic summary of these fragmentary findings is necessary to elaborate the (a)symmetry of the brain for recognizing facial expression.

1.5. Meta-analysis of neuroimaging studies on facial expression recognition

In the current meta-analysis, we examined brain organizations in recognition of discrete/dimensional facial expressions based on previous neuroimaging studies. Given that six basic emotion categories of the basic emotion model, including anger, sadness, fear, disgust, happiness and surprise, are universal across cultures and races (Ekman and Friesen, 1971) and are most reliably recognized from facial expressions (Adolphs, 2002b), we included this widely accepted six basic emotion model in the present meta-analysis, though other emotions such as pride and shame have also been proposed to be basic emotions (Tracy and Matsumoto, 2008). For the dimensional emotion models, we focused on positive and negative emotions for affective-valence model, and approach and withdrawal for the motivational-direction model, in line with Murphy et al. (2003) and

Wager et al. (2003). In support of the locationist hypothesis for facial expression recognition, the activation or co-activation (connectivity) patterns of specific brain regions would show consistently for a given category of discrete/dimensional emotion. In contrast, common category- or dimension-general brain activation/ connectivity patterns would support the psychological constructionist hypothesis for recognizing facial expressions.

2. Methods

2.1. Study identification

A step-wise procedure was used to identify functional imaging studies of facial expression recognition (**Fig. 1**). First, candidate studies (published up to the 14th of June, 2018) were selected through search on PubMed. Search terms included combination of the following three categories: (i) emotion types: "emotion" OR "affect" OR "happy" OR "angry" OR "fear" OR "sad" OR "disgust" OR "surprise" OR "valence" OR "pleasant" OR "unpleasant"; (ii) emotional stimuli: "face" OR "facial" OR "expression"; (iii) research methods: "fMRI" OR "functional MRI" OR "functional magnetic resonance imaging" OR "PET" OR "positron emission tomography" OR "neuroimaging". To maximize the probability that all potential studies were included, we also included studies from previous emotion-related meta-analyses (Garcia-Garcia et al., 2016; Kober et al., 2008; Murphy et al., 2003; Phan et al., 2002; Satpute et al., 2015; Sergerie et al., 2008; Stevens and Hamann, 2012) and/or those cited by previous review articles. These emotion-related meta-analytic studies and reviews were also obtained from the above literature search. All candidate articles were assessed using the following inclusion criteria: 1) making use of fMRI or PET; 2) including healthy participants; 3) including adult participants (age ≥ 18); 4) including emotional facial stimuli; 5) reporting whole-brain-wise imaging results; 6) using a neutral face as the control condition; 7) using facial stimuli that can be categorized into a single subtype of discrete or dimensional emotions.

2.2. Contrast definition and data extraction

In the current meta-analysis, we focused on brain activation of the contrast between emotional and neutral faces. To examine our hypotheses, we conducted separate meta-analyses for each category of discrete and dimensional emotions. It should be noted that a happy face is the only category of positive facial expression based on the basic emotion model in the present study. For the meta-analysis of faces in approach motivation, we included both happy and angry faces, according to previous studies (van Honk and Schutter, 2006; Wilkowski and Meier, 2010). We also classified the “surprise” emotion (4 studies in total) into the approach dimension based on its definition that ensures interruption of ongoing processes and diverts cognitive resources (e.g., attention) to "approach" unexpectedness (Horstmann, 2015; Meyer et al., 1997) . If there were more than two experiments conducted in the same sample for a specific contrast, we combined the coordinates of these experiments together (Turkeltaub et al., 2012). For each study, we extracted the following data: 1) study ID (first author and publication year); 2) sample size; 3) contrast; 4) normalization space (MNI or Talairach); 5) smoothing kernel; 6) brain region location information (x/y/z coordinates of the peak coordinates; 7) categories of emotions.

2.3. Activation likelihood estimation (ALE) analysis

The activation likelihood estimation (ALE) meta-analyses were performed using GingerALE 2.3.6 (http://www.brainmap.org/ale/; see Eickhoff et al., 2009, 2012). Coordinates reported in Talairach space were transformed into MNI space using the automated transformation tool implemented in GingerALE. The clustering maps between experiments were calculated by modelling each focus of the study as the center of a three-dimensional Gaussian distribution with the full width half-maximum (FWHM) weighted by sample size and probabilities of activation in each voxel. The cluster determining threshold (CDT) was set at a cluster-wise $p < 0.05$ and a cluster-forming $p < 0.001$ with 1,000 permutations to correct for multiple comparisons.

2.4. Conjunction and contrast analyses

To assess common brain activation across emotion categories, conjunction analyses were conducted by identifying the intersection among corrected ALE maps of each emotion category. To examine the distinct or unique brain areas for each discrete emotion category, we conducted separate contrast analyses between each category and the others. Specifically, we conducted ALE analyses for each basic emotion and the other four basic emotions combined by pooling coordinates of these four basic emotions together. Then we computed voxel-wise differences between these two ensuing ALE maps. All experiments contributing to either ALE map were then randomly divided into two groups, with the same sample sizes as those in the original ones to correct for study sizes (Eickhoff et al., 2011). We then conducted ALE analyses on these two randomly assembled groups and computed the corresponding voxel-wise differences. The real difference of the ALE values against the voxel-wise null-distribution of label-exchangeability was examined by conducting a permutation test with 5,000 repetitions corrected for multiple comparisons using a whole-brain-wise false-discovery rate (FDR) of 0.05.

2.5. Meta-analytic connectivity modelling (MACM) analyses

To identify connectivity/co-activation patterns of brain areas that respond to each discrete emotion, we conducted MACM analyses based on the BrainMap database (http://www.brainmap.org; Laird et al., 2009) by adding together all activated clusters of each emotion category to generate a category-specific combined seed (Darby et al., 2019). MACM delineates patterns of co-activation across studies from neuroimaging database and produces data-driven functional connectivity maps of predefined ROIs (Langner et al., 2014). Only neuroimaging studies reporting whole-brain-wise activation in standard stereotaxic space from healthy participants were included. Whole-brain peak coordinates of all those studies from BrainMap were extracted using the Sleuth toolbox (www.brainmap.org/sleuth) if the study reported at least one focus of activation within any cluster of each category of emotion. Next, coordinates were analyzed using the ALE algorithm to detect convergent areas that coactivated with each combined seed. Finally, the ALE maps were thresholded at the level of a cluster-wise $p < 0.05$ with a cluster-forming $p < 0.001$ with 1000 permutations to correct for multiple comparisons.

2.6. Functional decoding

A functional decoding analysis was performed via Neurosynth Image Decoder (https://neurosynth.org/decode/) to characterize the psychological function of the meta-analytic results of each emotion category. Specifically, we selected the meta-analytic map of 217 terms that bear clear biological significance in the Neurosynth database according to Cheng et al. (2017). We then calculated the voxel-wise spatial Pearson's correlation between the unthresholded ALE/MACM map of each emotion category and the meta-analytic map of each term (from the 217 terms). The word clouds were created by extracting ten terms with the highest correlation coefficients. From the 217 terms, we selected five basic emotional terms and extracted their correlation coefficients with each discrete/dimensional emotion category in order to find out whether these terms specifically decode each discrete and dimensional emotion category.

2.7. Laterality analysis

To examine the consistency of hemispheric lateralization in facial expression recognition across neuroimaging studies, laterality index (LI) was calculated using equation (1) under both discrete and dimensional emotions.

$$LI = \frac{R-L}{R+L} \quad (1)$$

, where R and L represent average ALE values from right and left ROIs. Given the distinguished roles of the unilateral amygdala, anterior insula cortex (AI), and ventral medial prefrontal cortex (vmPFC) in emotion processing (for a review, see Gainotti, 2019), these three ROIs were selected and defined from the automated anatomical labelling (AAL) template (Tzourio-Mazoyer et al., 2002).

3. Results

Of the 3331 publications initially found by systematic search in the available databases, 141 studies with 3138 participants in 145 subject groups were included in this meta-analysis (See **Fig. 1** for details of the inclusion procedure and **Tables 1, 2 and 3** for characteristics of the included studies and the demographic details of the participants).

3.1. Brain activity and connectivity of discrete emotions

The meta-analyses for each category of emotion showed that 1) the left amygdala consistently responded to happy faces; 2) the left pallidum, bilateral amygdala and right fusiform face area (FFA) were commonly activated when processing angry faces; 3) a set of brain regions, including the left ventral lateral PFC (vlPFC), bilateral pallidum, amygdala, FFA and occipital face area (OFA), were consistently activated when recognizing fearful faces; 4) the left amygdala also responded to sad faces; 5) bilateral OFA were activated for recognizing disgusted faces (**Fig. 2A**). Given that Eickhoff et al. (2016) has shown that at least 20 experiments should be included in an ALE meta-analysis to obtain sufficient power for moderate effects, we didn’t conduct ALE meta-analysis on surprise of the discrete emotion model due to the very small number of studies (n = 4).

The MACM analyses of the combined seeds showed that 1) brain regions consistently activated in recognition of happy faces were connected to the left caudate, left OFA, bilateral putamen, amygdala and FFA, which are important for emotion processing; 2) brain areas responding to angry faces were connected to the anterior PFC, left AI, bilateral vlPFC, ventral striatum (VS), amygdala and OFA; 3) brain regions responding to fearful faces were connected to the bilateral dorsal lateral PFC (dlPFC), vlPFC, AI, VS, amygdala, OFA; 4) brain regions responding to sad faces were connected to the left AI, bilateral VS and amygdala; 5) brain regions responding to disgusted faces were connected to the right dlPFC, AI, bilateral striatum and OFA (**Fig. 2B**).

3.2. Common and distinct patterns of brain activation and connectivity in discrete emotions

Conjunction analyses of brain activations among discrete emotions revealed that the left amygdala consistently responded to all the happy, angry, fearful and sad faces, but not the disgusted faces, whereas the right amygdala responded to both angry and fearful faces (**Fig. 3A**). Conjunction analyses of brain connectivity showed common connections of the combined seeds to the vlPFC, VS, left FFA across the five discrete emotions, and to the frontoparietal control network across fear, anger and disgust (**Fig. 3B**). Contrast analyses revealed unique weaker responses of the IT to angry faces, stronger responses of the right OFA to disgusted faces, stronger responses of the right dlPFC to fearful faces, weaker responses of the left amygdala to happy faces, compared with other categories of facial expression (**Fig. 3C**). There were no significant clusters found for sad faces.

3.3. Brain activation and connectivity profiles for dimensional emotions

Meta-analyses of the motivation-direction dimension showed that the bilateral amygdala, middle occipital gyrus, right FFA and middle temporal gyrus consistently responded to faces in the approach direction, whereas bilateral vlPFC, amygdala, OFA, middle and superior temporal gyri were commonly activated for recognizing facial expressions in the withdrawal direction (**Fig. 4A**). To recognize faces in the negative dimension, consistent activation was observed in bilateral vlPFC extending to the insula, amygdala, FFA, middle/superior temporal and occipital gyri, while consistent responses of the left amygdala to positive (happy) faces were found (**Fig. 4A**).

The MACM analyses showed that the combined seeds of the approach dimension were connected to bilateral amygdala, anterior insula, ventral striatum, dorsal anterior cingulate cortex, vmPFC and FFA in emotion processing; the same connectivity patterns were also found in the withdraw and negative dimensions (**Fig. 4B**).

3.4. Common and distinct brain activation and connectivity in dimensional emotions

Conjunction analyses of brain activations in dimensional emotions showed common activation of bilateral amygdala between approach and withdraw, and common activation of the left amygdala between positive and negative emotion (**Fig. 5A**). Conjunction analyses of connectivity revealed common connectivity of the combined seed with the FFA, bilateral amygdala, VS, vlPFC and frontoparietal network in the motivational dimension, with bilateral amygdala and VS, left FFA and vlPFC in the valence dimension (**Fig. 5B**). Contrast analyses revealed higher activation in the left vlPFC, amygdala and right middle occipital gyrus (MOG) for recognizing negative than positive faces (**Fig. 5C**). There were no significant clusters found between withdrawal and approach.

3.5. Functional characterization of identified patterns of activation

Functional decoding results showed that the meta-analytic activation and coactivation-based connectivity map in both discrete and dimensional emotions were all characterized by emotion- and face-related processes (**Fig S1-S4**). The decoding patterns were highly consistent across the five basic emotional terms in both discrete and dimensional emotions (**Fig. 6**).

3.6. Asymmetry in the amygdala, AI and vmPFC

Both the amygdala and AI showed left hemispheric lateralization in processing both discrete and dimensional emotions, while the vmPFC showed left hemispheric dominance for processing sad faces but right hemispheric lateralization in response to happy faces (**Fig. 7, Table S1**).

4. Discussion

The universality of basic emotions has been the dominant view since Ekman's pioneering studies (Ekman and Friesen, 1971; Ekman et al., 1983), though it has been challenged by some recent findings (Crivelli et al., 2016; Jack et al., 2012). Numerous studies have been devoted to brain organizations of these emotions. Previous meta-analytic studies compared the locationist hypothesis with the psychological constructionist hypothesis in general emotion processing, indiscriminating stages of emotional recognition and experience processes (Lindquist et al., 2012). However, brain activation patterns have been shown to be distinctive between emotion recognition and experience processes

(Garcia-Garcia et al., 2016; Sabatinelli et al., 2011). There are also other perspectives that processes of emotional recognition could involve emotional experience (see Phillips et al., 2003 for a review), e.g., observation of other people's emotional faces could also trigger activation of brain areas responsible for one's own experience of the same emotion (Wicker et al., 2003). By using the recently proposed meta-analytic connectivity modelling (MACM) approach (Robinson et al., 2010), we examined brain network organizations of facial expression recognition by conducting a set of meta-analyses based on different hypotheses. Our results provide the first network-based meta-analytical evidence for the psychological constructionist hypothesis in recognizing facial emotions.

Although the debate over the nature of emotion between discrete and dimensional models has lasted for a long time, this is the first examination of the neurocognitive mechanisms of facial expression recognition by conducting meta-analytic connectivity modelling analyses on neuroimaging studies. Despite that discrete activation patterns of basic emotions have been shown in the current meta-analysis, the common or indiscriminate brain regions activated across different categories of emotions go against specificity of the basic emotion model. For instance, the left amygdala responded to happy, angry, fearful and sad faces, supporting the idea of common brain activation distributions composing a 'core' affect system (Lindquist et al., 2012; Russell and Barrett, 1999; Wager et al., 2015). Consistent with previous findings in general emotion processing (Barrett and Wager, 2006), these results, at least partly, suggest that it is currently difficult to characterize discrete emotions by specific biological features (Barrett, 2006). While the dissimilarity between brain responses to positive/approach but similarity of those in negative/withdrawal dimensions goes against the polarity hypothesis which assumes common neural underpinnings responding monotonically across valences, shared amygdala activation and common connectivity patterns in both directions contradict the bivalent hypothesis that supposes distinct neural systems underlying positive and negative valences. Consistent with the ideas proposed for emotional processing (Lindquist et al., 2016), these results suggest a flexible valence-general brain system underpins the dimensional model of facial expression recognition.

4.1. Locationist vs. psychological constructionist hypotheses

Inconsistent with the hypothesis of emotion-brain-location correspondence (Ekman and Cordaro, 2011), the common activation of the amygdala and connectivity patterns across different categories of discrete/dimensional emotional models goes against the assumption that each category of discrete/dimensional emotion associates with unique/discriminable brain areas. Brain responses to discrete/dimensional emotions commonly connected to the amygdala suggests that the amygdala is the hub of the distributed network for representing the core affect, preferentially to exteroceptive sensations (Lindquist et al., 2012). The functional decoding results showed that neural mechanisms of different emotion categories converged to facial and emotional functions, further validating our meta-analytic findings in support of the psychological constructionist hypothesis.

The current meta-analyses showed the left amygdala responds to all discrete emotions but disgust. Three in 24 studies included in the meta-analysis showed activation of the amygdala in response to disgust (Anderson et al., 2007; Phillips et al., 1998; Wicker et al., 2003). A large meta-analysis showed higher proportions of studies on emotion experience than emotion perception that found involvement of the amygdala in disgust (Lindquist et al., 2012), indicating potentially various degrees of activation in the amygdala between emotion experience and emotion perception. Given that the present meta-analysis was only focused on facial expression recognition, the distinctive and common neural underpinnings between recognition and experience of disgust could be examined in future studies.

The psychological constructionist hypothesis assumes that emotion consists of the combination of the core affect with categorization for the emotional meaning of the core affect (Lindquist and Barrett, 2012; Lindquist et al., 2012). The facial recognition related OFA (Bernstein and Yovel, 2015) and FFA (Kanwisher et al., 1997), executive attention related vlPFC (Corbetta et al., 2008), as well as the goal-directed control related dlPFC

(Corbetta and Shulman, 2002), may jointly constitute the recognition of the core affect of facial expressions. The AI may play pivotal network-based roles in both representing the core affect of interoceptive sensations (Craig, 2003, 2005, 2009) and creating affective feeling (Lindquist and Barrett, 2012). It has been shown that the AI is widely associated with a broad range of basic and social emotions (Lamm and Singer, 2010). The AI has also been shown to be responsible for processing disgusted facial expressions (Phillips et al., 1998; Phillips et al., 1997; Sprengelmeyer et al., 1998). Although activation of bilateral middle occipital gyrus rather than the AI was consistently observed in response to disgusted facial expressions in the current meta-analysis, we found strongly consistent connectivity to the AI in recognition of disgusted faces. Abundant empirical and meta-analytic neuroimaging evidence for facial emotion recognition has shown that disgust is the most difficult one of the five basic emotions to recognize (Gur et al., 2002; Kohler et al., 2004; Ruffman et al., 2008; Widen and Russell, 2013). Therefore, one explanation might be that the augmented activation in visual areas is necessary in response to the difficulty of recognizing disgusted faces. Consequently, connectivity from visual areas to the AI is speculated to be engaged for processing the disgusted emotion.

Together, these results showed a set of common/shared brain areas across discrete/dimensional emotions, though there were also distinct activations in some brain regions, such as the left amygdala, the IT, right OFA, dlPFC and MOG. Although these areas showed increased or decreased degrees of responses to some discrete/dimensional emotions than the others, they were not specific for any discrete/dimensional emotion. Consistent with a previous meta-analysis (Lindquist et al., 2012), these results also support the psychological constructionist model. Importantly, our meta-analytic connectivity modeling analyses showed that the common brain areas of core affect are connected to distributed networks, which are widely involved in cognitive control and conceptualization (Kober et al., 2008; Lindquist et al., 2012; Wager et al., 2015). These findings provide converged neuroimaging evidence for the psychological constructionist account.

4.2. The asymmetrical brain in facial expression recognition

Consistent with previous findings on asymmetry of the emotional brain (Duerden et al., 2013; Gainotti, 2019), our results suggest that there are laterality effects on facial expression recognition, with different asymmetrical brain patterns for different categories of emotions. In the current meta-analysis, there were no consistent results to support the overall right-hemisphere dominant hypothesis. Instead, there was consistent and common left amygdala activation across all discrete emotion categories, except for disgust, suggesting the dominant role of the left amygdala in facial emotion recognition. Consistently, asymmetric analysis with the amygdala as the ROI showed higher activation in the left than in the right amygdala across emotion categories. This is consistent with results of a previous meta-analytic study that showed stronger activation in the left amygdala than in the right across different types of emotion (Baas et al., 2004). The majority of neuroimaging studies included in the present meta-analysis are related to conscious emotion processing, supporting the asymmetric model proposed by Morris et al. (1998), which proposes that the left amygdala mainly responds to conscious emotion processing, whereas processing emotions below conscious awareness preferentially activates the right amygdala.

The results of ROI-based asymmetric analysis of the AI showed increased activation in the left rather than the right AI, regardless of emotion category. These results are consistent with previous meta-analytic findings (Duerden et al., 2013) but inconsistent with the hypothesis proposed by Craig (2005), which posits that positive affect is associated with the left AI, while negative affect is associated with the right AI. However, it may support the idea that lateralized homeostatic sensory activity is selectively activated in response to different facial expressions (Craig, 2005). One explanation for such a discrepancy is that the facial emotion processing in our meta-analysis is mainly about emotion recognition, while Craig’s model is based on the experience of emotion. Future studies are necessary to distinguish the neural processes between emotion recognition and emotion experience. The right lateralized activation in the vmPFC for recognizing all facial expressions except “anger” and “sadness” is inconsistent with the affective-valence hypothesis on frontal asymmetry that proposed the left PFC responds to approach/ positive affect while the right PFC responds to withdrawal/negative affect (Davidson et al., 1990b; Schwartz et al., 1975). In contrast, consistent with previous findings on the engagement of the left PFC in anger (van Honk and Schutter, 2006) and the roles of the right PFC in fear and disgust (Harmon-Jones, 2004), the current meta-analytic findings suggest a more flexible frontal asymmetry system. Taken together, while the results showed limited evidence for frontal asymmetry and valence-selective lateralization, these findings converge to a more complex asymmetrical representations of emotions than a straightforward overall right-hemisphere dominance hypothesis and classical affective-valence/motivational-direction model.

It should be noted that we also included studies with tasks on implicit processing of facial expressions in the current meta-analyses. There are three types of paradigms widely used to induce facial emotion recognition, including incidental processing (e.g., subjects are instructed to judge the gender of faces), passive perception, and explicit evaluation of emotional expressions (Garcia-Garcia et al., 2016). Numerous studies have shown that facial emotion recognition is an automatic process (Stenberg et al., 1998; Tracy and Robins, 2008), which suggests that it happens even if the subjects are not explicitly instructed to recognize facial emotion. Studies have shown that recognition happens when facial emotion stimuli are presented subliminally (Whalen et al., 1998; Winkielman et al., 2005). Facial expression recognition has been proposed as a continuous spectrum that ranges from subliminal/unconscious perception, incidentally task-irrelevant processing, and passive perception, to the explicit identification of facial expressions (Dricu and Fruhholz, 2016). Future studies are necessary to examine the common and distinctive brain organizations between explicit and implicit processing of facial expression recognition.

5. Limitations

Some limitations of the current meta-analysis should be noted. As with previous meta-analyses of emotion processing, we could not conduct meta-analyses to assess the valence-arousal model and the surprise emotion, given there are few neuroimaging studies measuring arousal independently (Barrett and Wager, 2006; Wager et al., 2003). Future studies that separately measure the brain underpinnings of arousal and valence are needed. Studies on brain responses to surprise are also necessary. Another limitation of the current meta-analyses is that we only focused on contrasts between activation of emotional and neutral faces, rather than monotonically changed brain activation in the valence dimension of the bipolarity hypothesis (Wundt, 1897). However, our results revealed that brain activation patterns were distinct between positive and negative but common between approach and withdrawal directions, which goes against the view of a shared brain system for the two poles of the valence dimension. The current meta-analysis only focused on emotion processing under the visual model of facial expressions, which is one of the most important and common mediums of emotion expression. Neural mechanisms underlying recognition of emotion categories under other classes (e.g., natural scenes) and modalities (e.g., audio) are yet to be tested. Emotional processes can also be generally classified as emotion recognition and emotion experience, which process others' and one's own emotions, respectively (Hamann, 2012). In this study, we only focused on facial expression recognition rather than emotion experience, the differences between and similarities of which are still unclear. Given the low time resolution of the fMRI technique, dissociation of these two processes also needs to be examined in future studies.

6. Conclusions

In summary, the current meta-analytic findings show relatively consistent engagement of the amygdala and its connectivity with distributed networks across discrete and dimensional emotions. In support of the psychological constructionist hypothesis, these networks are widely involved in the processing of attention, motivation, memory, language, and cognitive control. The left-hemisphere dominance of the amygdala and AI across emotions, but category-specific lateralization of the vmPFC, suggest a more complex asymmetrical representations of emotions than the straightforward overall right-hemisphere dominance hypothesis and the classical affective-valence/motivational-direction model. This work provides the first network-based meta-analytic evidence and theoretical insight for understanding the functional brain architecture of facial expression recognition.

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Figure Captions

Figure 1. Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) flow diagram for the procedure of study identification.

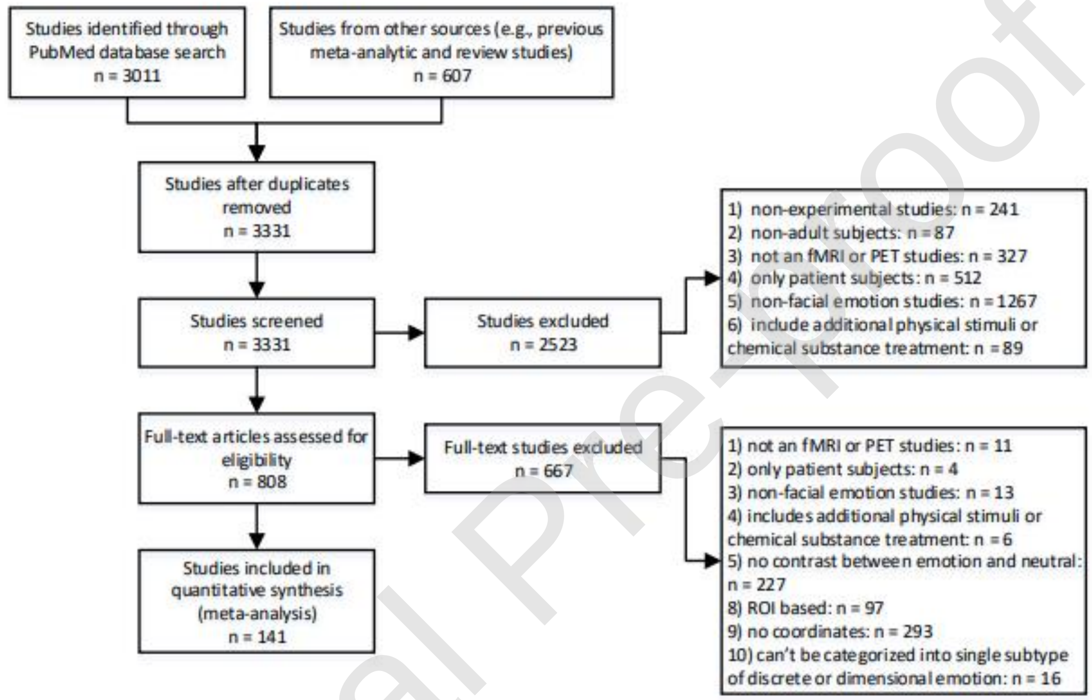


Figure 2. Brain regions significantly activated in the A) activation likelihood estimation (ALE) meta-analyses and B) meta-analytic connectivity modeling (MACM) analyses of discrete emotions (happiness, anger, disgust, sadness, fear). Activation maps were thresholded at a voxel-wise uncorrected $p < 0.001$, with cluster-wise FWE-corrected $p < 0.05$, with 1,000 permutations to correct for multiple comparisons. AMG, amygdala; FG, fusiform gyrus; MTG, medial temporal gyrus; MOG, middle occipital gyrus; PFG, posterior fusiform gyrus; MFG, middle frontal gyrus; IFG, inferior frontal gyrus.

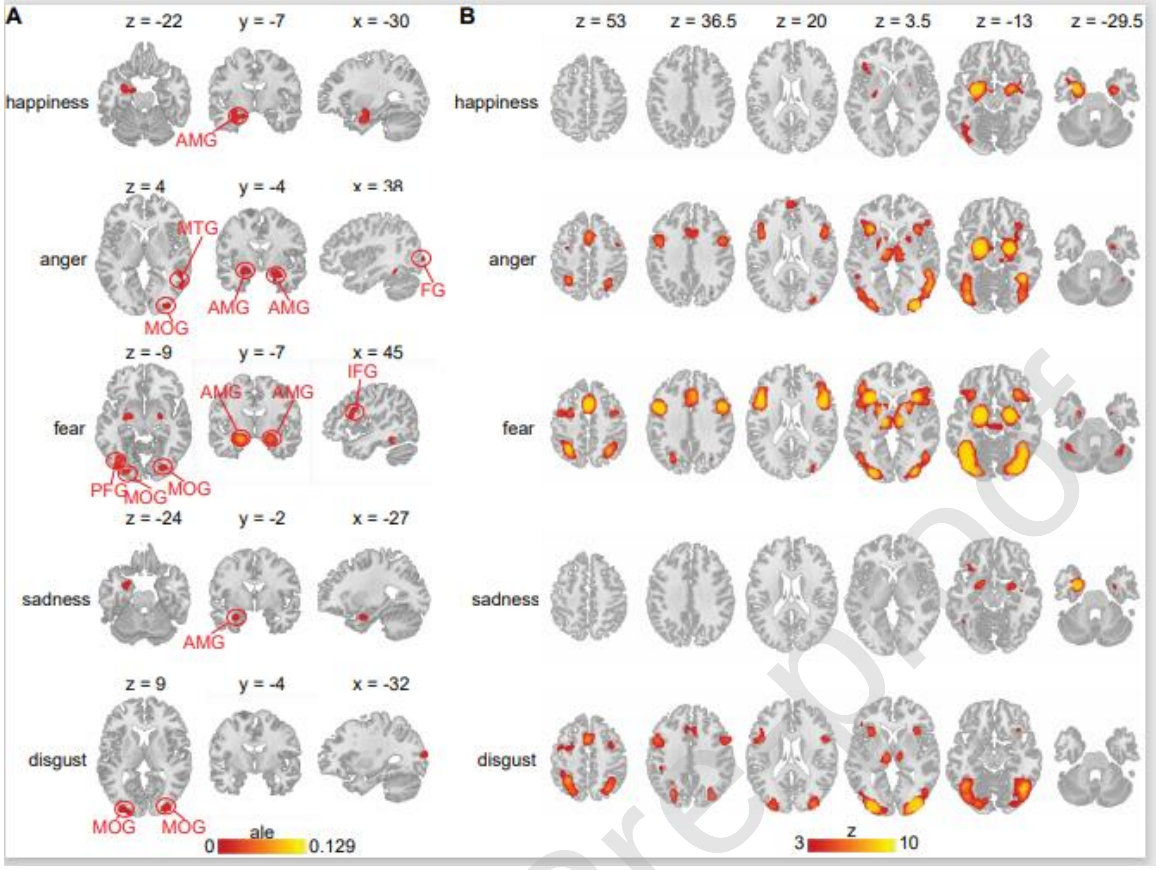
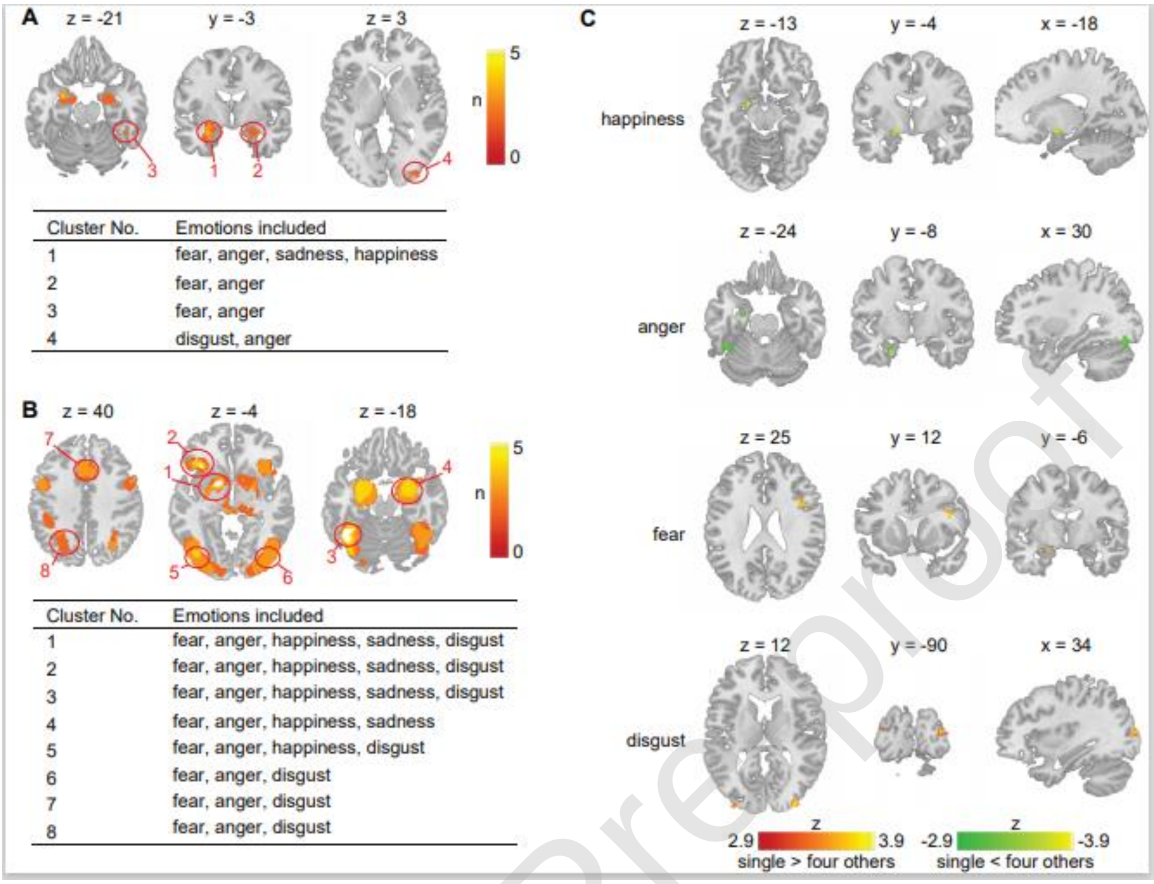


Figure 3. Common and distinct brain activation and connectivity of discrete emotions. (A) Conjunction of brain activation across discrete emotions. Yellow indicates a higher number of basic emotions with overlapped brain activation. The table shows the type of emotions that overlapped in each numbered cluster. (B) Conjunction of the meta-analytic connectivity modeling (MACM) based brain networks of discrete emotions. (C) Distinct brain activation between each single basic emotion and the combination of the other four emotions. Red (yellow) indicates higher (lower) activation of the single emotion when compared with the other four emotions.



Cluster No.	Emotions included
1	fear, anger, sadness, happiness
2	fear, anger
3	fear, anger
4	disgust, anger

Cluster No.	Emotions included
1	fear, anger, happiness, sadness, disgust
2	fear, anger, happiness, sadness, disgust
3	fear, anger, happiness, sadness, disgust
4	fear, anger, happiness, sadness
5	fear, anger, happiness, disgust
6	fear, anger, disgust
7	fear, anger, disgust
8	fear, anger, disgust

Figure 4. Brain regions consistently activated in the A) activation likelihood estimation (ALE) meta-analyses and B) meta-analytic connectivity modeling (MACM) analyses of dimensional emotions (approach, withdraw; positive, negative). Activation maps were thresholded at a voxel-wise uncorrected $p < 0.001$, with cluster-wise FWE-corrected $p < 0.05$ with 1,000 permutations to correct for multiple comparisons. AMG, amygdala; FG, fusiform gyrus; MTG, medial temporal gyrus; MOG, middle occipital gyrus; STG, superior temporal gyrus; ITG, inferior temporal gyrus; IOG, inferior occipital gyrus; MFG, middle frontal gyrus; IFG, inferior frontal gyrus.

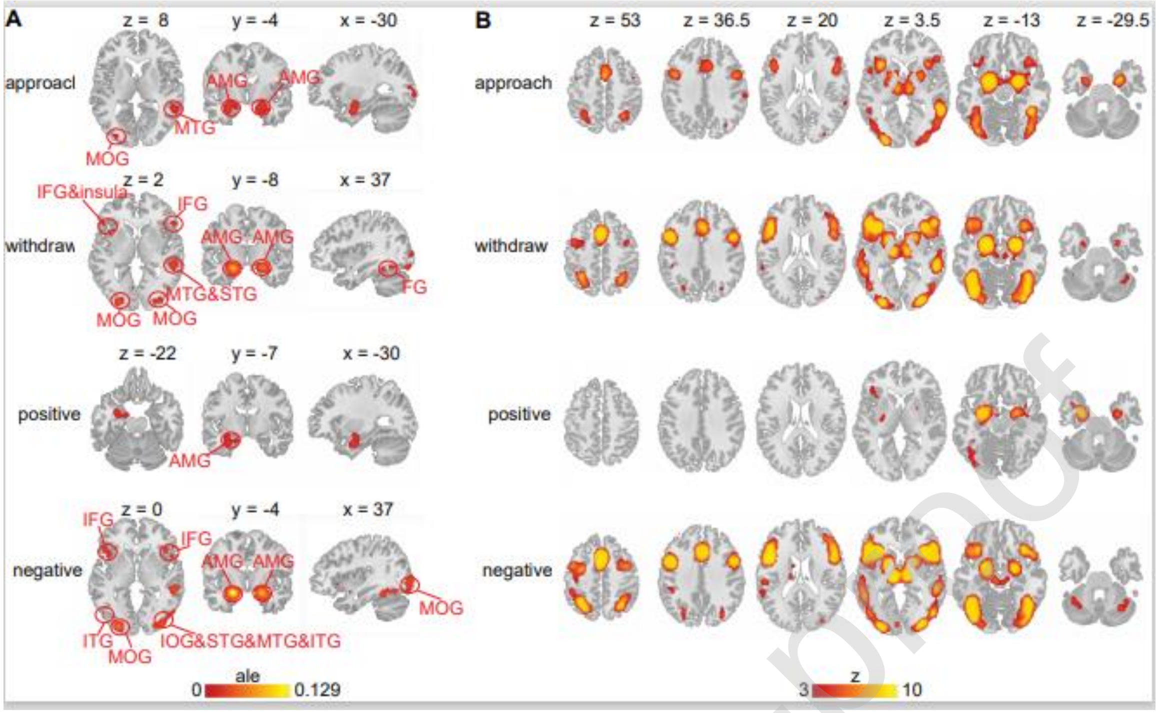


Figure 5. Common and distinct brain activation and connectivity of dimensional emotions. (A) Conjunction of brain activation across dimensional emotions. The overlapped brain regions between the two dimensions are highlighted in red. (B) Conjunction of the meta-analytic connectivity modeling (MACM) based brain networks of dimensional emotions. The overlapped connectivity between the two dimensions is highlighted in red. (C) Distinct brain activation between negative and positive emotion. Red indicates higher activation of the negative emotion in comparison with positive emotion.

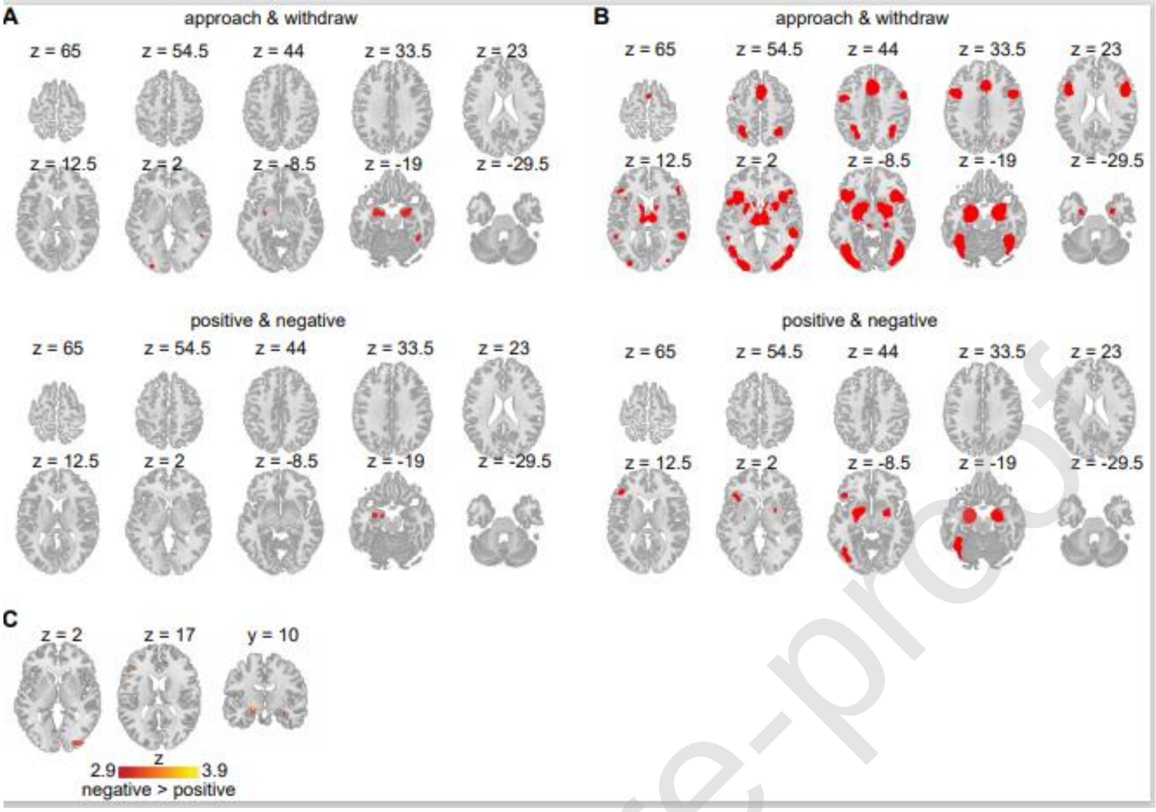


Figure 6. Functional fingerprint based on brain activation and connectivity of discrete and dimensional emotions. A) Associations between brain activation of discrete emotions in the present meta-analyses and those of five basic emotional terms in the Neurosynth database; B) Associations between the meta-analytic connectivity modeling (MACM) based brain networks of discrete emotions and the meta-analytic results of five basic emotions extracted from the Neurosynth database; C) Associations between brain activation of dimensional emotions in the present meta-analyses and those of five basic emotional terms in the Neurosynth database; D) Associations between the meta-analytic connectivity modeling (MACM) based brain networks of dimensional emotions and the meta-analytic results of five basic emotions extracted from the Neurosynth database.

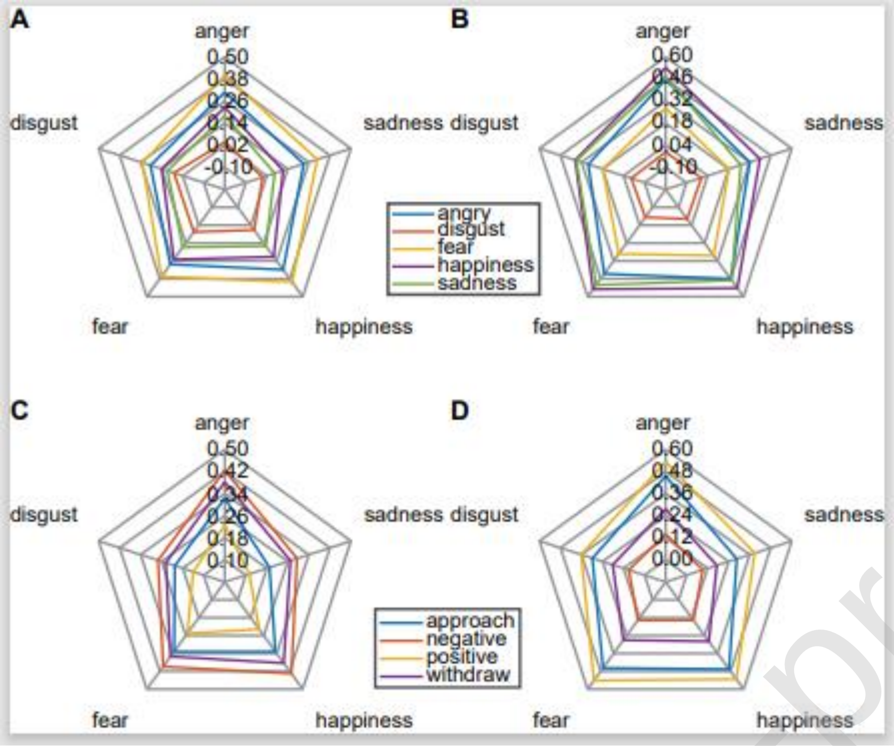
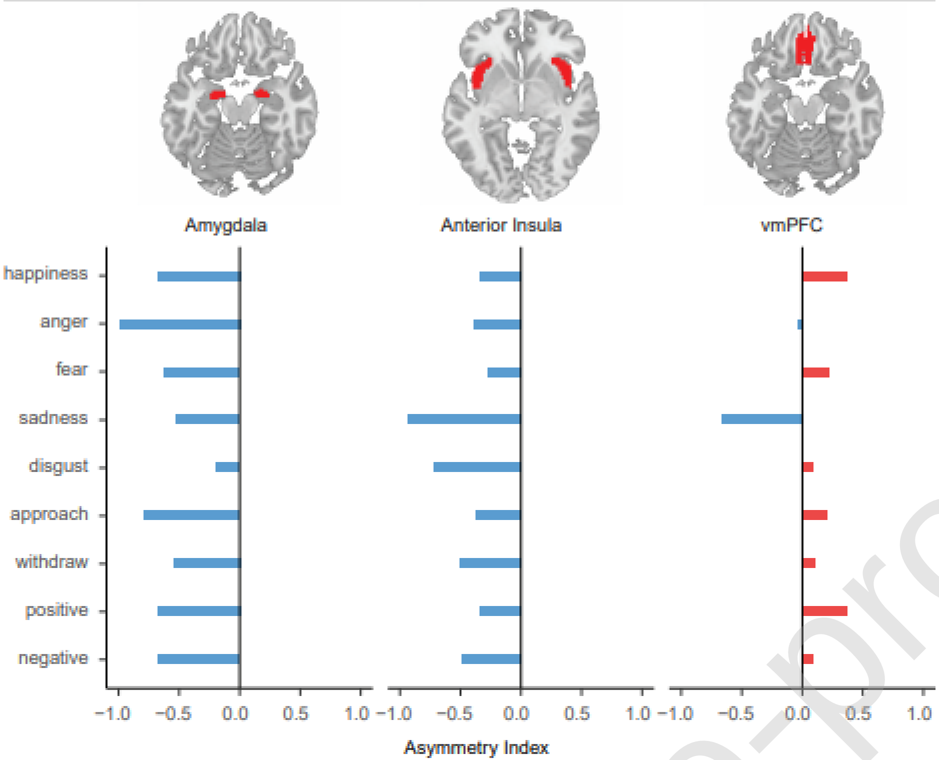


Figure 7. Laterality indices for the amygdala, anterior insula, vmPFC in both discrete and dimensional emotions. Positive values (red) indicate rightward asymmetry, while negative values (blue) indicate left asymmetry. vmPFC, ventral medial prefrontal cortex.


Amygdala
Anterior Insula
vmPFC
happiness
anger
fear
sadness
disgust
approach
withdraw
positive
negative
−1.0
−0.5
0.0
0.5
1.0
Asymmetry Index

Tables

Table 1. Demographic characteristics of studies included in meta-analysis.

Study	Emotions	Task	N (male)	Age (SD)	FWHM*
(Abel et al., 2003)	fear	gender decision	8(8)	23-42	11
(Amir et al., 2005)	disgust	valence decision	11(3)	24.1(5.2)	7.5
(Amting et al., 2010)	negative	valence decision	16(6)	24.88(2.71)	4
(Anderson et al., 2007)	disgust, fear	gender decision	12(12)	24.7(5.8)	10
(Andersson et al., 2008)	fear	object categorization	16(7)	15.03(5.51)	8
(Ashwin et al., 2007)	fear	stimulus detection	13(13)	25.6(5.1)	6
(Baeken et al., 2009)	happiness, negative	passive viewing	40(0)	23.8(3.9)	8
(Baeken et al., 2010)	happiness, negative	passive viewing	20(0)	26.6(6.9)	8
(Basile et al., 2011)	negative	identify self-emotion	22(9)	26.8(3)	8
(Batut et al., 2006)	fear, happiness, sadness	gender decision	15(6)	22-45	8
(Benuzzi et al., 2004)	fear	gender decision	14(7)	21-27	8
(R. J. Blair et al., 1999)	anger	gender decision	13(13)	25.25	12
(K. Blair et al., 2008)	negative	gender decision	17(9)	31.2(9.1)	6
(Botvinick et al., 2005)	pain	passive viewing	12(0)	20-30	12
(Britton et al., 2006)	anger, fear, happiness, sadness	mixed	12(6)	21.4(2.2)	6
(Budell et al., 2010)	pain	intensity decision and movement discrimination	18(9)	18-25	8
(Canli et al., 2002)	fear	not mentioned	15(4)	-	8
(Chakrabarti et al., 2006)	anger, disgust, happiness, sadness	stimulus detection	26(13)	23.4(4.23)	7

(Chan et al., 2016)	anger	gender decision	54(21)	23(2.4)	8
(Ciumas et al., 2017)	fear, happiness	valence decision	11(8)	9.2(2.3)	8
(Cremers et al., 2010)	anger, fear, sadness	gender decision	60(23)	21-56	8
(Dannlowski et al., 2007)	negative	implicit valence intensity rating	23(12)	38.7(12.6)	6
(De Winter et al., 2016)	fear	oddball task	20(11)	66.6(6.1)	8
(Deeley et al., 2007)	disgust, fear, happiness	gender decision	9(9)	27(5)	7.2
(Deeley et al., 2008)	disgust, fear	gender decision	40(40)	24(9.6)	-
(Deeley et al., 2006)	fear, happiness	gender decision	15(15)	-	-
(Del-Ben et al., 2005)	aversive	gender decision	12(12)	24.7(5.8)	10
(Dima et al., 2011)	negative	valence decision	40(20)	31.5(10.4)	8
(Dolan et al., 1996)	happiness	passive viewing	8(8)	20-27	-
(Domes et al., 2010)	fear	intensity rating	16(0)	24.2(2.5)	12
(Duan et al., 2010)	happiness, surprise	face recognition	18(5)	23.6(1.3)	8
(El Khoury-Malhame et al., 2011)	negative	dot detection	17(9)	31.7(6.7)	6
(Engell et al., 2007)	anger, disgust, fear, surprise	face recognition	13	22-33	6
(Etkin et al., 2004)	fear	color decision	17(9)	20-33	8
(Faivre et al., 2012)	happiness	valence decision	18(6)	18-35	8
(Fan et al., 2011)	fear	valence decision	25(12)	21-58	8
(Fenker et al., 2005)	fear	learning word	20(6)	19-27	8
(Fernandez-Egea et al., 2009)	pain	valence decision	10(10)	23-31	5
(Fischer et al., 2005)	anger	passive viewing	46	-	-
(Gilman et al., 2012)	fear	passive viewing	14(14)	25(5.16)	6
(Gowin et al., 2016)	fear	passive viewing	32(27)	-	6
(Grant et al., 2011)	happiness, sadness	gender decision	16(6)	31.1(9.2)	8
(Haas et al., 2009)	fear, happiness, sadness	gender decision	29(15)	22.4(2.8)	8
(Hennenlotter et al., 2005)	happiness	passive viewing	12(6)	24.5	8

(Hennenlotter et al., 2004)	disgust	gender decision	9(5)	37.4(5.4)	10
(Holtmann et al., 2013)	fear	Eriksen Flanker task	24(23)	26.83(5.35)	8
(Hooker et al., 2008)	fear, happiness	passive viewing	12(5)	21	8
(Hornboll et al., 2013)	anger, fear	gender decision	23(14)	31.8(6.5)	8
(Hortensius et al., 2016)	fear	oddball task	12	-	-
(Hurlemann et al., 2008)	anger, happiness	gender decision	14(7)	25.4(2.4)	8
(Ihme et al., 2014b)	anger, fear, happiness	valence decision	48(25)	24(3)	6
(Ihme et al., 2014a)	anger, happiness	valence decision	50(24)	18-29	6
(Iidaka et al., 2001)	negative	gender decision	12(6)	25.1(5)	8
(Jackson et al., 2008)	anger	face recognition	35(20)	29	8
(Jehna et al., 2011a)	anger, disgust	valence recognition	15(10)	30.27(10.61)	5
(Jehna et al., 2011b)	anger, disgust	valence decision	30(9)	36.3(14.3)	5
(Ji et al., 2015)	anger	valence decision	37(20)	20-42	10
(Jogia et al., 2008)	sadness	valence decision	8	-	8
(Kempton et al., 2009)	fear	valence decision	74(40)	18-65	8
(Kesler-West et al., 2001)	anger, fear, happiness, sadness	passive viewing	21(11)	18-45	-
(Kilts et al., 2003)	anger, happiness	intensity rating	13(9)	22-26	9
(M. J. Kim et al., 2008)	fear	object matching	12(7)	29(6.2)	8
(H. Kim et al., 2003)	fear, surprise	passive viewing	16(8)	22.3(1.84)	6
(LaBar et al., 2003)	negative	object judgement	10(5)	21-30	8
(Lange et al., 2003)	fear	intensity rating	9(9)	21-42	11
(K. U. Lee et al., 2008)	happiness, sadness	gender decision	13(13)	24.8(3.6)	-
(T. W. Lee et al., 2006)	anger, happiness, sadness	passive viewing	18(9)	26	8
(Lennox et al., 2004)	happiness, sadness	intensity rating	12(6)	32.6(10.7)	12
(Lenzi et al., 2009)	happiness	imitate and observe	16(0)	23-42	8

(Lichev et al., 2015)	happiness	word evaluation	46(23)	23.5(2.7)	6
(Liddell et al., 2005)	fear	passive viewing	22(11)	32(13)	8
(Luo et al., 2014)	fear	face recognition	25(25)	23.14(1.83)	8
(Madsen et al., 2016)	aversive	gender decision	76(67)	25.63(5.23)	8
(McCloskey et al., 2016)	fear	valence decision	20(12)	32.8	8
(McLellan et al., 2012)	happiness, sadness	valence decision	7(0)	26.86(4.67)	8
(Michalopoulou et al., 2008)	fear	gender decision	9(5)	32(6)	-
(Miskowiak et al., 2007)	fear	gender decision	24(16)	-	5
(Mitchell et al., 2007)	fear	gender decision	15(6)	26.1(4.32)	6
(Morawetz et al., 2016)	anger	passive viewing	60(30)	30.48(11.1)	8
(Moriguchi et al., 2005)	fear	passive viewing	32(12)	20-60	8
(Morris et al., 1998)	fear, happiness	gender decision	5(4)	42.8	12
(Morris et al., 1999)	anger	Conditioned Stimulus	10(10)	32.7	12
(Mothersill et al., 2014)	anger	passive viewing	81(43)	-	10
(Mourao-Miranda et al., 2012)	happiness	valence decision	18(2)	30(9)	6
(Muller et al., 2011)	happiness	passive viewing	35(15)	-	8
(Noesselt et al., 2005)	fear	oddball task	12(7)	22.6	8
(Nomura et al., 2004)	anger	valence decision	12	-	8
(Palm et al., 2011)	anger, fear, happiness	valence recognition	16(0)	34(13)	10
(Paradiso et al., 2003)	sadness	passive viewing	17(9)	65(7.3)	6.5
(Park et al., 2016)	negative	emotional one-back task	19(12)	25.9(2.7)	8
(Passamonti et al., 2012)	anger, sadness	gender decision	30(13)	25.1(3.2)	8
(Phillips et al., 1999)	anger, disgust, fear	gender decision	5	22-43	11
(Phillips et al., 1997)	anger, fear	gender decision	7(2)	27	11
(Phillips et al., 2004)	disgust, fear	passive viewing	10(8)	25-36	11
(Phillips et al., 1998a)	happiness	valence decision	8(7)	26-39	11
(Phillips et al., 1998b)	disgust, fear	gender decision	6(6)	25-43	11

(Rauch et al., 2007)	anger, fear, happiness	passive viewing	20(10)	-	6
(Reeck et al., 2012)	fear	stimulus detection	25(12)	19-34	9
(Reinders et al., 2005)	fear	stimulus detection	15(7)	18-36	11
(Reker et al., 2010)	happiness, sadness	valence decision	33(0)	24.8(3.4)	6
(Robins et al., 2009)	anger, fear	passive viewing	10(3)	18-33	7
(Sagaspe et al., 2011)	fear	gender decision	14	18-25	8
(Sambataro et al., 2006)	disgust	gender decision	24(11)	26.8(5.6)	10
(Sato et al., 2004)	anger	gender decision	10(5)	24.4(7.8)	6
(Schroeder et al., 2004)	disgust, surprise	gender decision	20(10)	32.5(8.3)	8
(Schulz et al., 2009)	happiness, sadness	valence decision	24(16)	18-35	8
(Schwabe et al., 2013)	fear	intensity rating	80(40)	23.53(0.34)	8
(Sebastian et al., 2017)	anger	gender decision	20(20)	30.25(4.31)	8
(Seubert et al., 2010)	disgust, happiness	valence decision	44(21)	-	8
(Spilka et al., 2015)	anger, fear, happiness	passive viewing	27(13)	40.7(11.1)	7
(Sprengelmeyer et al., 1998)	anger, disgust, fear	gender decision	6(2)	23.5(1.3)	9
(Straube et al., 2004)	anger	valence decision	10(4)	23.2(3.9)	8
(Surguladze et al., 2003)	disgust, fear, happiness, sadness	gender decision	9(5)	23-63	-
(Surguladze et al., 2010)	disgust, fear	gender decision	9(5)	39.7(14.6)	7.2
(Suslow et al., 2009)	happiness, sadness	valence decision	51(28)	28.5(7.9)	6
(Suslow et al., 2010)	happiness, sadness	valence decision	30(0)	23.9(1.84)	6
(Thielscher et al., 2007)	disgust, fear	valence decision	25(10)	23(3)	8
(Trautmann et al., 2009)	disgust, happiness	passive viewing	16(0)	21.6(2.3)	8
(Tsukiura et al., 2003)	happiness	intensity rating	11	21.7(2.26)	8
(Villalta-Gil et al., 2013)	fear	valence matching	31(15)	25.57(4.8)	8
(von dem Hagen et al., 2009)	disgust	intensity rating	27(13)	27(8)	10
(Vuilleumier et al., 2004)	fear	passive viewing	13(7)	35.9(8.6)	8

(Vuilleumier et al., 2003)	fear	passive viewing	13(6)	18-37	8
(Vuilleumier et al., 2001)	fear	object matching	12(6)	23-35	8
(Wabnegger et al., 2015)	anger, disgust, fear, sadness	intensity rating	22(11)	51.8(9.8)	8
(Wang et al., 2005)	sadness	circle detection	12(5)	25.9(4.4)	8
(Weisenbach et al., 2014)	anger, fear, happiness, sadness	valence decision	138(63)	18-65	5
(Wicker et al., 2003)	disgust, happiness	passive viewing	14(14)	20-27	6
(Leanne M. Williams et al., 2006)	fear	mixed	15(7)	35.8(9.06)	8
(Williams et al., 2001)	fear	gender decision	11(11)	30	-
(Williams et al., 2005)	anger, disgust, fear	gender decision	13(5)	24(8)	-
(Williams et al., 2004b)	fear	gender decision	22(14)	-	-
(L. M. Williams et al., 2006a)	fear	passive viewing	15(7)	35.8(9.04)	8
(Williams et al., 2004a)	fear	gender decision	22(15)	27.5(8.2)	-
(L. M. Williams et al., 2006b)	fear	passive viewing	13(7)	34.8(8.5)	8
(Winston et al., 2003)	fear	gender decision	13(6)	22-44	8
(Wright et al., 2003)	fear	passive viewing	20(8)	20-54	5
(Wright et al., 2006)	fear	passive viewing	36(12)	21-81	7
(Yang et al., 2012)	fear	stimulus orientation detection	27(14)	22.45(1.78)	3
(Zeki et al., 2008)	anger	press key when stimulus disappear	17(10)	34.8	9
(Zsoldos et al., 2016)	fear	valence decision	34	-	-

Note: * FWHM = full width half-maximum.

Table 2. Summary of included studies of both discrete and dimensional emotions

	Emotions	Experiments[*]	Subjects	Foci
Discrete Emotions				
Happiness	Happiness	44	1018	362
Anger	Anger	39	1042	224
Sadness	Sadness	23	603	179
Disgust	Disgust	24	415	202
Fear	Fear	78	1595	620
Dimensional Emotions				
Positive	Happiness	44	1018	362
Negative	Sadness, Anger, Fear, Disgust, Pain, Aversive	136	2966	1455
Approach	Happiness, Surprise, Anger	72	1693	615
Withdraw	Sadness, Fear, Disgust, Pain	107	2230	1100

Note: [*] There might be more than one experiment in one study.

Table 3. Summary of retrieved studies from Sleuth for MACM analysis

	Emotions	**Experiments**[*]	**Subjects**	**Foci**
Discrete Emotions				
Happiness	Happiness	158	2552	2427
Anger	Anger	411	6377	6843
Sadness	Sadness	68	1055	988
Disgust	Disgust	168	2480	3417
Fear	Fear	921	14217	15480
Dimensional Emotions				
Positive	Happiness	158	2552	2427
Negative	Sadness, Anger, Fear, Disgust, Pain, Aversive	1472	21970	23519
Approach	Happiness, Surprise, Anger	519	7899	8922
Withdraw	Sadness, Fear, Disgust, Pain	1116	16682	18084

Note: [*] There might be more than one experiment in one study.