Reexamining the Neural Network Involved in Perception of Facial Expression: A Meta-analysis

Abstract

Perception of facial expression is essential for social interactions. There have been numerous attempts to map brain regions to facial expression processing. Although a few competing models have enjoyed some success, they are also facing difficult challenges. A main locus of the disagreement among them has been the role of the fusiform face area (FFA) and superior temporal sulcus (STS). In a broader context, this has also been a question of how other brain regions in the associated ventral and dorsal streams participate in a distributed neural network for facial expression processing. To appraise these competing models and to overcome a number of limitations suffered by the past meta-analyses, the current study used an updated activation likelihood estimation (ALE) method of meta-analysis to explore the involvement of brain regions in facial expression processing. The sample contained 96 functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies of healthy adults with the results of whole-brain analyses. The key findings revealed that the ventral pathway, especially the left FFA region, was more responsive to facial expression. In particular, the left posterior FFA showed strong involvement when participants passively viewing emotional faces without being asked to judge the type of expression or other attributes of the stimuli. Through meta-analytic connectivity modeling (MACM) of the main brain regions in the ventral pathway, we constructed a co-activating neural network as a revised model of facial expression processing that assigns prominent roles to the amygdala, FFA, the occipital gyrus, and the inferior frontal gyrus.

Introduction

Facial expressions convey emotional signals through certain configuration of facial muscle contractions (Darwin, 1872; Ekman et al., 1972; Izard, 1997). Research has revealed that perceiving facial expressions engages a distributed neural network, including fusiform face area (FFA), occipital face area (OFA), superior temporal sulcus (STS), amygdala, and insula (Adolphs and Spezio, 2006; Haxby et al., 2002). However, there is at present no consensus on relative role of these areas for facial expression processing.

In the model of face perception developed by Haxby et al. (2000), the FFA in the ventral stream plays a key role in processing the invariant aspects of the face, such as identity or gender, whereas the STS in the dorsal stream processes changeable aspects of the face including facial expression (Haxby et al., 2000; Hoffman and Haxby, 2000). There is some evidence for the role of the dorsal pathway in expression processing (Adolphs, 2002; Calder and Young, 2005; Haxby et al., 2000; Ishai, 2008; Pessoa and Padmala, 2006). For example, STS neurons show preferential responses to different facial expressions in both macaques and humans (Hasselmo et al., 1989; Ojemann et al., 1992). STS also responds more strongly to emotional faces than to neutral faces (Engell and Haxby, 2007). Furthermore, multi-voxel pattern analysis (MVPA) of activities in anterior and posterior parts of STS can successfully predict which facial expression a participant has seen (Said et al., 2010).

However, the division of labor between the ventral and the dorsal streams for face processing has turned out to be far less clear-cut than being suggested by Haxby et al. (2000). There is substantial evidence that facial expression is not only processed by the dorsal pathway, including middle temporal (MT) visual area and STS, but also by the ventral pathway, including FFA and OFA. For example, several studies reported greater FFA activation to emotional faces relative to neutral faces in numerous fMRI studies (Morris, 1998; Breiter et al., 1996; Kesler/West et al., 2001; Vuilleumier et al., 2001; Derntl et al., 2012). The FFA shows higher activation when different facial expressions are presented from one trial to another compared to when the same expression is unchanged (Ganel et al., 2005). Higher FFA activations could be observed even without being accompanied by an activation in a dorsal area like STS during an exposure to emotional facial expression (Rauch et al., 2007; Williams et al., 2006). Furthermore, a perceived facial expression can be accurately predicted from the pattern of FFA activation using the MVPA method (Harry et al., 2013). Remarkably, patterns of the FFA produce the highest accuracy among seven brain regions for discriminating facial expressions (Wegrzyn et al., 2015). Based on evidence like this, Bernstein and Yovel (2015) revised the model of Haxby et al. (2000) by proposing that the ventral stream handles information of form (such as facial identities and facial expressions) whereas the dorsal stream processes the information of motion. However, there is no consensus whether perception of facial expression is exclusively a ventral function.

Given these rather conflicting accounts of face perception, a thorough synthesis of the existing data throws some light on the roles of the dorsal and ventral streams in perceiving facial expressions. Indeed, a number of meta-analyses have provided some clues in this direction. Using activation likelihood estimation (ALE) method work, Fusar-Poli et al. (2009) identified stronger left FFA activation to disgusted or happy faces relative to neutral faces, as well as stronger bilateral FFA activation to fearful faces relative to neutral faces. Subsequently, Sabatinelli and colleagues (2011) found similar responses to emotional faces in numerous areas, including the bilateral and post FFA, inferior frontal gyrus (IFG), middle frontal gyrus (MFG), amygdala, parahippocampal gyrus, left superior frontal gyrus and right middle temporal gyrus. A more recent study by Schirmer (2018) has also identified higher activation in bilateral amygdala, middle occipital gyrus (MOG), right FFA, left IFG and inferior occipital gyrus (IOG) when comparing emotional faces with neutral faces. These meta-analyses seem to suggest that the ventral stream rather than the dorsal stream plays an imperative role in emotional expression perception. They pose a serious challenge to the influential model by Haxby et al. (2000). The competing model proposed by Bernstein and Yovel (2015) has also met challenges. After evaluating neural responses to dynamic and static faces through a meta-analysis, both Arsalidou et al. (2011) and Zinchenko et al. (2018) found increased activation in FFA, STS, amygdala, and IFG to these stimuli. Their results suggested an involvement of both ventral and dorsal pathways in processing facial motion. Hence the suggested functional division in Bernstein and Yovel’s model is also not supported.

However, the past meta-analyses suffer from some limitations. An important limitation is that they all depended on the false discovery rate (FDR) correction. The method is no longer recommended for ALE meta-analyses because it is highly susceptible to false positive results thus is inadequate for analyzing the continuous and spatially smoothened neuroimaging data (Chumbley and Friston, 2009; Eickhoff et al., 2016). Recommended by Eickhoff et al. (2016), the cluster-level family wise error (FWE) thresholding strikes a balance between specificity and sensitivity as required by ALE meta-analyses (Eickhoff et al., 2012). Furthermore, due to the technical limitation of the time, the coordinates from region-of-interest (ROI) analyses were included in Fusar-Poli et al.’s (2009) meta-analysis. This method is no longer recommended because of its prior assumption of interested regions (Müller et al., 2018). ALE meta-analyses test convergence of brain activations across studies against the null hypothesis that all voxels in the whole brain have the same possibility of being activated. However, ROI studies do not concern voxels outside their regions of interest, which could result in exaggerated significant activations for these regions. Furthermore, the updated GingerALE software fixed its documented implementation errors for FDR multiple-comparison correction in version 2.3.3 in 2015 and the errors for FWE correction in version 2.3.6 in 2016 (Eickhoff et al., 2017). The developers recommend that past results of meta-analyses conducted through the old software be re-analyzed.

A meta-analysis of the N170 component in event-related potentials (ERPs) research has also provided evidence that, areas involved in face processing, such as the STS or the FFA, are sensitive to facial expressions (Hinojosaa, Mercadoc, and Carretié, 2015). However, due to the low spatial resolution of ERPs, it is unclear whether the dorsal or ventral pathway is more important. Given this and other technical limitations of the past meta-analyses, a re-analysis of the literature is necessary to obtain a more precise picture of the extent to which the ventral stream and the rest of the brain are involved in processing facial expressions. This was the first goal of this study.

Another related objective of this study was to perform meta-analytic connectivity modeling (MACM) to investigate the connectivity network for the brain areas responsible for emotion processing from faces. The MACM technique detects the brain regions that co-activate above chance, using the brain volume of interest as the seed region (Robinson et al., 2010). To our knowledge, prior meta-analyses did not use this method on the topic. By applying it in this study, we aimed to identify the connectivity between the core regions for perception of facial expression.

The third goal of this study was to examine the roles of dorsal and ventral streams in processing dynamic facial expressions. Unlike the existing meta-analyses that often included studies of other kinds of facial motion, such as comparing neural responses to rotating versus stationary heads (Lee et al., 2010), we have limited our interest solely to the effect of dynamic facial expression. Hence studies using rigid head motion or nonrigid motion other than facial expression such as talking, sneezing, or yawning were excluded from our meta-analysis.

The final goal of this study was to investigate the neural networks involved in top-down (task driven) and bottom-up (stimulus driven) processing of facial expression. Prior research by Fusar-Poli et al. (2009) and Müller et al. (2018) has evaluated this by comparing neural responses to facial expression in tasks with different attentional demands, where participants either identified facial expressions (explicit task) or attributes other than facial expressions (implicit task). It was found that explicit tasks were associated with greater activation of the FFA, amygdala, IFG, IOG and MFG, whereas the implicit tasks were associated with greater activation of the posterior FFA and insula (Fusar-Poli et al., 2009). Conjunction analyses of explicit and implicit tasks (gender evaluation only) revealed significant convergence in the bilateral amygdala, IFG, right mid FFA and right IOG (Müller et al. 2018).

These studies attempted to delineate the top-down route for facial expression processing by comparing activations of the brain areas for different types of tasks. The identified route seems to overlap with both the ventral and dorsal streams. Unlike the top-down route, the bottom-up route for facial expression processing needed to be studied by comparing neural activities under passive viewing with other tasks. However, this has seldom been studied except that by Dricu and Frühholz (2016), who examined the contrast of passive viewing versus explicit tasks but found no significant results. No studies have yet investigated the contrast of passive viewing versus implicit tasks, which could provide useful information about the brain regions sensitive to attention elicited by facial expressions. We therefore decided to provide a further meta-analytic comparison of them in this study.

To sum up, two competing models of face perception have attempted to formulate functional divisions between ventral and dorsal streams for facial expression processing. While Haxby et al. (2000) assign the role to the STS in the dorsal stream, Bernstein and Yovel (2015) treat it as a FFA function of the ventral stream. Although both models have gathered supporting evidence, they have also been challenged. Past meta-analyses have provided valuable insights for ways to resolve debate about the neurofunctional network underlying facial expression perception. However, the evidence they provide is often no longer adequate due to the limitation in methodology. To capitalize on the improved assumption of the current meta-analyses technique, the present study aims to: (i) determine the role of dorsal and ventral stream in perception of facial expression via an up-to-date ALE algorithm and statistical method; (ii) investigate the co-activation patterns of the brain regions responsible for facial expression perception utilizing MACM; (iii) investigate the role of dorsal and ventral streams in processing dynamic facial expressions; (iv) examine the role of ventral and dorsal streams in top-down and bottom-up processing of facial expression.

Method

Search strategies

Following the guidance of Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA; Liberati et al., 2009), we selected multiple online citation indexing services, including Web of Science, PubMed and Google Scholar. Two of the authors (LMT and ZS) conducted the search separately. One used combinations of terms containing fMRI, PET, emotional (or neutral) facial expression (or faces) and perception in Web of Science, PubMed and Google Scholar. The other searched the PubMed with the terms including facial expression, emotion, explicit processing or implicit processing, neuroimaging, or fMRI. A combination of terms (e.g., fMRI/PET and neutral faces/happy faces/sad faces/angry faces/fearful faces/disgusted faces/surprised faces) was also used for search in the PubMed. The search included articles published between January 1995 and November 2019. In addition, we checked relevant articles from previous meta-analyses and references of crucial studies. All the obtained articles were included in the initial pool.

The articles in the initial pool were further evaluated against the following inclusion and exclusion criteria to create a final pool of articles for this meta-analysis:

Inclusion Criteria

1) Original articles based on empirical research, published in English in a peer-reviewed journal with full-text available; 2) employing healthy adult participants with an average or median age between 18 and 60 years old who were not under the influence of medicine, alcohol or medical intervention; 3) using functional magnetic resonance imaging (fMRI) or positron

emission tomography (PET); 4) containing whole-brain analyses; 5) using photographs or movies of human faces as stimuli and investigating facial expression perception; 6) reporting data in standard stereotactic coordinates, either Talairach or Montreal Neurological Institute (MNI) space.

Exclusion Criteria

1) The study was excluded if it was not a primary empirical study available in English in a peer-reviewed journal. 2) Participants with an average or median age greater than 60 years old, or younger than 18 years old were excluded, because these age groups are known to have different brain activation compared to the rest of population when processing facial expressions (Deeley et al., 2008; Iidaka et al., 2002; Taylor et al., 2004). Studies containing interventions such as medication and alcohol intake were excluded to avoid their influence on face processing. 3) Other types of neuroimaging studies than fMRI or PET did not have enough spatial resolution. 4) Studies only performing ROI analyses were excluded because the method breaks the assumption of ALE’s null-hypothesis that voxels have the same possibility to be activated (Eickhoff et al., 2012). 5) Studies that did not report data in standard stereotactic coordinates. 6) Studies mainly focusing on other psychological processes such as attention, memory were not considered due to the scope of our focus. 7) Studies using schematic faces, robotic faces, or emoji as stimuli (Fusar-Poli et al., 2009). 8) Studies that did not report data in standard stereotactic coordinates.

Selection and data extraction

The selection process and data extraction were conducted in accordance with the PRISMA guideline. One of the authors selected the articles based on the inclusion and exclusion criteria and performed the data extraction. Another author double-checked the selection and the extracted data. Discrepancies were discussed until a consensus was reached. Activation foci and relevant information were extracted from the selected articles, including the publication year, sample size, mean age and gender of participants, types of face paradigm, types of comparison and formats of standard stereotactic coordinates.

ALE meta-analysis

A series of ALE meta-analyses were carried out in the standard space of MNI using the BrainMap GingerALE software (version 3.0.2). Coordinates reported in the format of Talairach were transformed into the MNI space using the tool provided by GingerALE, which employed the method of tal2icbm_spm transmission (Lancaster et al., 2007). We also considered the differences in the coordinate normalization performed by the original studies using different software such as SPM (Ashburner, 2012), FSL (Jenkinson et al., 2012), or other and transformed these data separately into the MNI, SPM format. Then, the coordinates were accumulated into text files for different contrasts with the proper format required by GingerALE for the subsequent coordinate-based meta-analyses. ALE estimates the significantly activated brain foci in independent studies with similar topics by computing the probability of at least one activated focus that is located in a voxel and determines ALE values. The calculated ALE values were compared with values in a null distribution in order to obtain a 3D p value image. Subsequently, a cluster-level FWE correction was applied to the p value image with the cluster level FWE threshold set to 0.05, threshold permutations set to 1000 and cluster-forming threshold of $p < 0.001$.

For each ALE meta-analysis calculated in GingerALE, a minimum of 17 experiments were needed to be surpassed or achieved by the volume of a data set. A quantity less than that would fail to promise a stable performance of ALE algorism or a reliable result (Eickhoff et al., 2016). Additionally, when encountering any studies with multiple contrasts or sub-contrasts over the same group of participants, the most representative one was selected for each of our interested contrasts, to avoid the negative impact of sample overlap, which, also denoted as the within-group effect, stems from the finding that participant groups involved in multiple experiments would create a stronger impact on ALE results than groups involved in a single experiment (Turkeltaub et al., 2012). The method we chose was one of the recommended approaches to compensate for the sample overlapping issue (Müller et al., 2018).

Contrast and conjunction analyses in GingerALE were used to assess the influence of task form. ALE maps were constructed separately for tasks that were either explicit (i.e., participants were asked to judge facial expressions), implicit (i.e., participants were asked to judge attributes such as gender, age, identity, color of the face, or the orientation of arrowheads that were presented simultaneously with the face stimuli), or passive viewing (participants only had to look at the face stimuli without performing any specific task). We only included the contrasts between emotional faces and neutral faces under the three kinds of tasks, in order to explore the roles of the dorsal and ventral pathways in top-down and bottom-up processing of information in emotional facial expressions. The three ALE maps were also pooled for every two of the three tasks. Subtraction analyses of both directions of contrasts and conjunction analyses were conducted for the every two of the tasks. The threshold of the results of our subtraction analyses was set to $p < 0.01$, with p value permutations set to 10000, and the min volume of clusters set to 100 mm^3.

Meta-analytic Connectivity Modeling

In order to investigate the neural co-activations, we also employed a methodology called meta-analytic connectivity modeling, which combines the functions of Sleuth and GingerALE, both developed by BrainMap. We extracted 4 volumes of interest (VOIs) from the significant cluster-level results of the emotional faces versus neutral faces comparisons, which included the bilateral amygdala (cluster 1, 2), bilateral occipital gyrus (cluster 3, 4), left FFA (cluster 5), and right IFG (cluster 6). Neuroimaging studies that reported activations and located these seed regions were collected from BrainMap database, with their activated coordinates downloaded in MNI format as well. The other criteria set to limit the included studies were “Activation Only”, “Normal Mapping” for the experimental context. The activated coordinates were then sent to meta-analyses using GingerALE, with the parameters set to cluster level FWE < 0.05, threshold permutations = 1000 and cluster-forming threshold of $p < 0.001$. Table 1 shows the VOIs that passed the criteria, along with their associated numbers of experiments, participants, and foci.

Table 1

Summary of the location-based search in the BrainMap database of the 4 VOIs for MACM analyses.

Volumes of Interest	Number of Experiments	Number of Participants	Number of Foci
Bilateral amygdala	658	10273	8259
Bilateral occipital gyrus	543	8090	8705
Left FFA	146	2254	2486

Right IFG	129	2399	2083

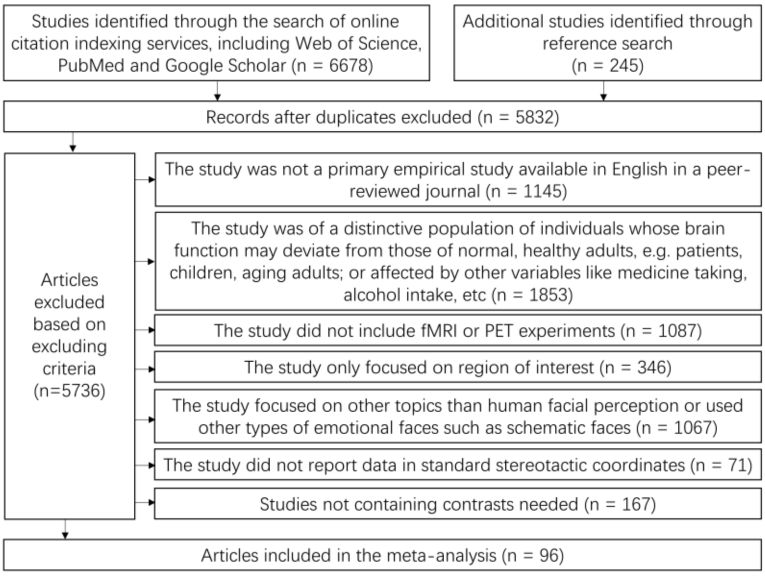

Fig. 1. Procedure of the study selection.

Results

Outcomes of searching

A total number of 96 studies were included in our meta-analyses after selection and extraction (see details in Fig. 1, Supplementary Table 1). Of these, 94 were based on fMRI, and 2 on PET; 45 used MNI as normalized coordinates, and 51 reported results in Talairach space. A total of 1794 participants (861 female) were included. The mean age was 28.4 years.

Effects of facial expressions

Primarily, we examined the contrasts of perceiving emotional versus neutral faces in 69 experiments from 67 studies, among which two studies included two groups of participants in two experiments separately, with a total number of 1256 participants, and 643 foci. The six basic types of facial expressions were happiness, sadness, fear, disgust, anger, and surprise. We detected greater activations for emotional face stimuli in the bilateral amygdala, bilateral parahippocampal gyrus (BA34), right uncus (BA28), right IOG (BA18, 19), right declive, left MOG (BA37, 19), left FFA (BA19, 37, 36), left sub-lobar thalamus (ventral lateral nucleus), and right IFG (BA9; Fig. 2, Supplementary Table 2).

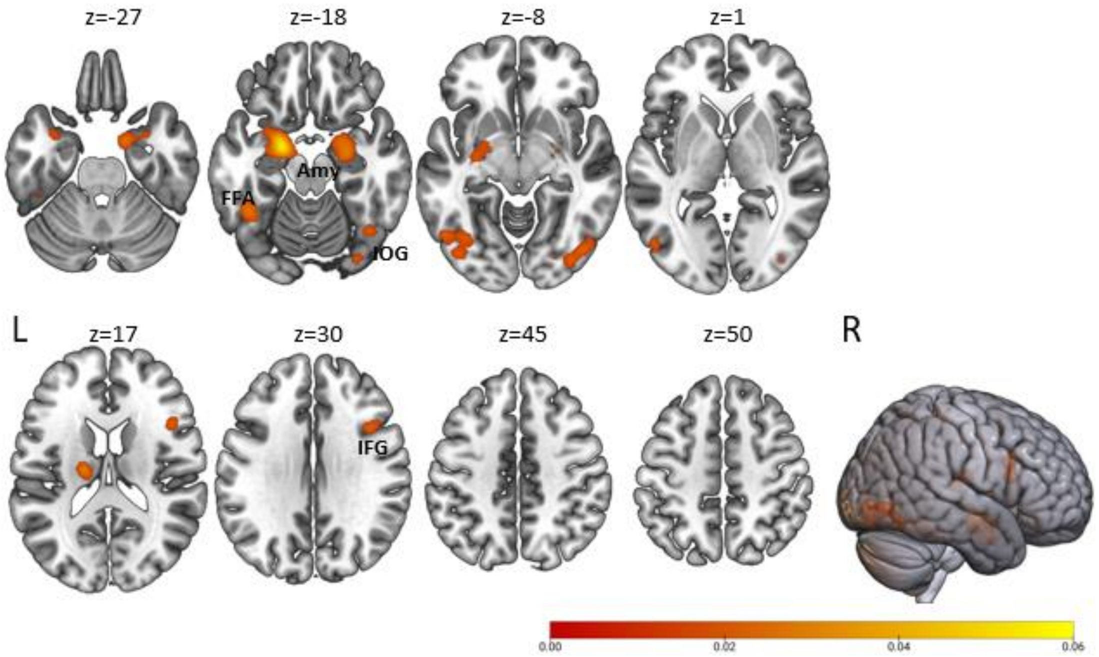

Fig. 2. Regions showing higher activations to emotional faces as compared neutral faces. Clusters threshold: $p < 0.05$ (cluster-level FWE correction). Coordinates are MNI152 standard stereotaxic spaces. Figure was created using Mango (http://ric.uthscsa.edu/mango). Abbreviations: Amy, amygdala; FFA, fusiform face area; IFG, inferior frontal gyrus; IOG, inferior occipital gyrus; L, left; R, right.

Effects of facial perception tasks

The meta-analyses for explicit, implicit tasks and passive viewing designs included 21, 33, and 17 experiments separately, each with 517, 486, and 240 participants, 201, 269, and 179 foci. The differences and similarities of the brain activities related to emotional face perception through the three kinds of tasks (i.e., explicit task, implicit task, and passive viewing) were shown in Supplementary Table 3. Relative to explicit tasks, passive viewing leads to greater activation in the left fusiform gyrus (BA19), the posterior part of the fusiform gyrus and containing the posterior FFA (Weiner and Grill-Spector, 2012). Relative to the implicit tasks, passive viewing results in greater activation in the left fusiform and lingual gyrus (BA19). Compared with explicit tasks, implicit tasks elicit more activation in the bilateral parahippocampal gyrus (BA35, 28), right lateral globus pallidus, and left amygdala. Conjunction analyses revealed activations of the left parahippocampal gyrus and subcallosal gyrus (BA34) in both explicit tasks and implicit tasks. The conjunction of significant activation was found in the left parahippocampal gyrus (BA34) for explicit tasks and passive viewing tasks; and in the left amygdala for implicit tasks and passive viewing tasks (Fig. 3; Supplementary Fig. S1).

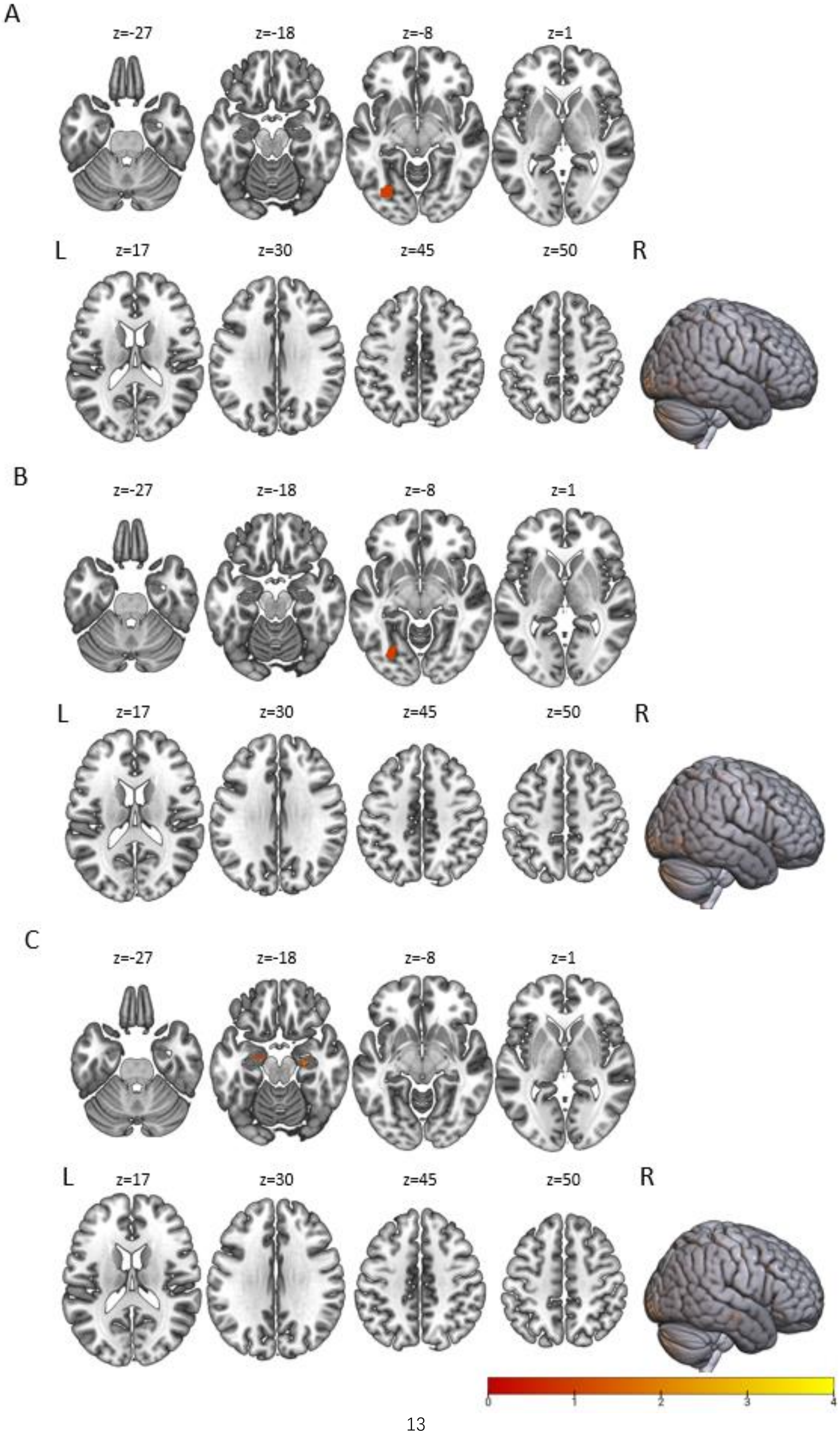
A
z=-27
z=-18
z=-8
z=1
L
z=17
z=30
z=45
z=50
R
B
z=-27
z=-18
z=-8
z=1
L
z=17
z=30
z=45
z=50
R
C
z=-27
z=-18
z=-8
z=1
L
z=17
z=30
z=45
z=50
R
0
1
2
3
4

Fig. 3. Results of the contrast analyses. A. Passive viewing versus explicit tasks. B. Passive viewing versus implicit tasks. C. Implicit versus explicit tasks. Clusters threshold: $p < 0.01$ with 10000 permutations. Coordinates are MNI152 standard stereotaxic spaces. Figure was created using Mango (http://ric.uthscsa.edu/mango). Abbreviations: L, left; R, right.

Effects of dynamic facial expressions

The meta-analyses of dynamic versus static or neutral facial expressions involved 17 experiments from 16 studies, among which a study used two groups of participants in two experiments separately, with 188 foci and 287 participants. The results showed that the dynamic facial expression elicit more activation in the bilateral fusiform gyrus (BA37, 19, including the FFA), bilateral MT (BA21, 22, 37), left amygdala/parahippocampal gyrus, left MOG (BA19), and right STS (BA22) than static and neutral facial expressions (Fig. 4, Supplementary Table 4).

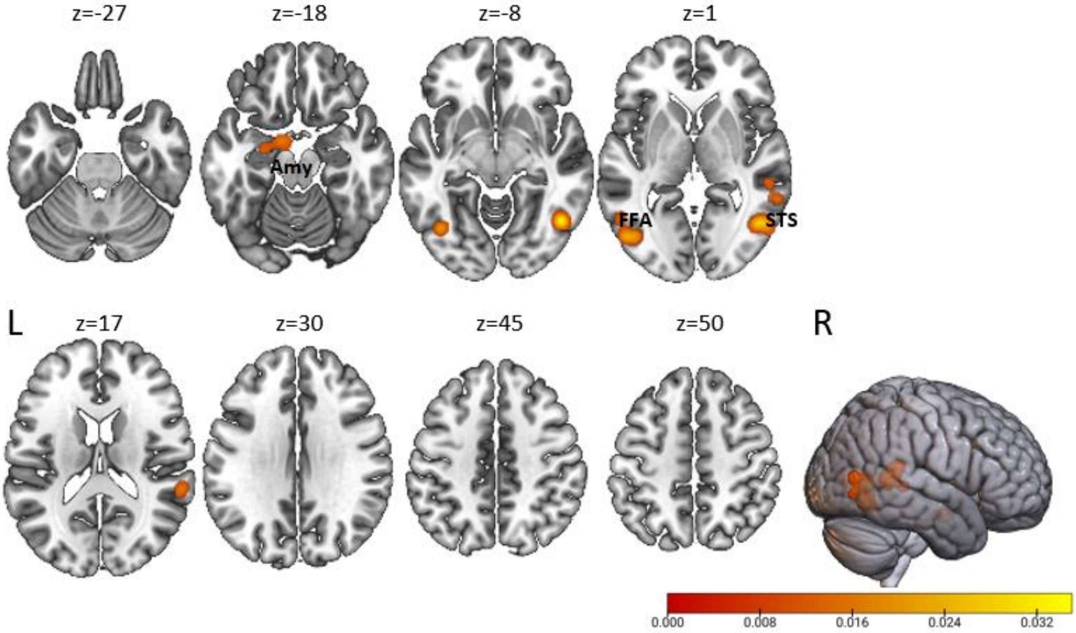

Fig. 4. Regions showing higher activations for dynamic facial expressions. Clusters threshold: $p < 0.05$ (cluster-level FWE correction). Coordinates are MNI152 standard stereotaxic spaces. Figure was created using Mango (http://ric.uthscsa.edu/mango). Abbreviations: Amy, amygdala; FFA, fusiform face area; L, left; R, right; STS, superior temporal sulcus.

Effect of emotional faces

To separate neural responses to emotional faces from non-face factors, we used the baseline conditions consisted of fixation, scrambled faces, scrambled pictures, mosaic, shapes or other non-facial stimuli. The meta-analyses of emotional faces versus baseline involved 19 experiments from 19 studies, with 294 foci and 343 participants. The results showed that emotional faces elicited stronger activations in the right IFG (BA9), right MFG (BA6), bilateral amygdala/parahippocampal gyrus, right declive, right fusiform gyrus (BA19), right superior frontal gyrus (BA6), right STS (BA41), and bilateral culmen/fusiform gyrus (BA37) relative to baseline (Fig. 5, Supplementary Table 5).

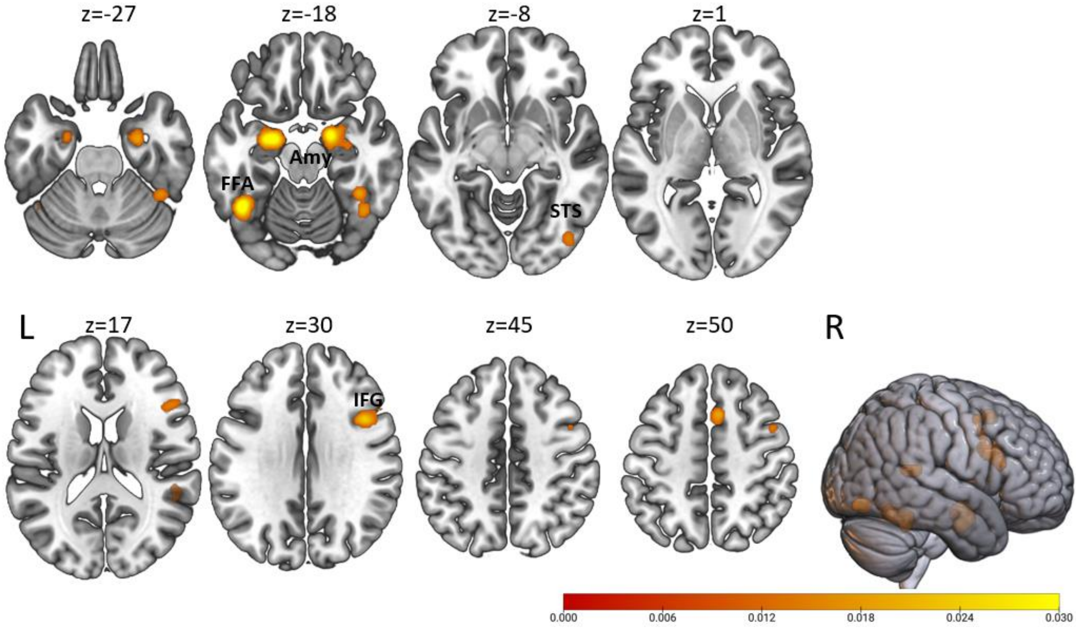

Fig. 5. Regions showing higher activations when processing emotional faces as compared to baseline. Clusters threshold: $p < 0.05$ (cluster-level FWE correction). Coordinates are MNI152 standard stereotaxic spaces. Figure was created using Mango (http://ric.uthscsa.edu/mango). Abbreviations: Amy, amygdala; FFA, fusiform face area; IFG, inferior frontal gyrus; STS, superior temporal sulcus; L, left; R, right.

MACM results

Our analyses of co-activation patterns for the left FFA (BA19, 36, 37) showed significant co-activations with the bilateral IFG, left MFG, left medial frontal gyrus, left MT, bilateral superior parietal lobule, left inferior parietal lobule, right IOG, and MOG (Supplementary Table 6). For the right IFG (BA9), the co-activation patterns were observed in the bilateral MFG, bilateral cingulate gyrus, left MT, left inferior parietal lobule, right superior parietal lobule, bilateral fusiform gyrus, and right thalamus (Supplementary Table 7). For the bilateral amygdala, the co-activation patterns were found in the bilateral FFA, bilateral IFG, left MFG, right IOG, bilateral insula, bilateral candidate, bilateral thalamus, right hypothalamus, bilateral MT, right STS, left superior frontal gyrus, and left superior cingulate (Supplementary Table 8). Furthermore, the bilateral occipital gyrus (BA18, 19, 37) co-activated with the bilateral FFA, bilateral IFG, left amygdala/parahippocampal gyrus, bilateral thalamus, and bilateral MFG (Supplementary Table 9, Fig. 6).

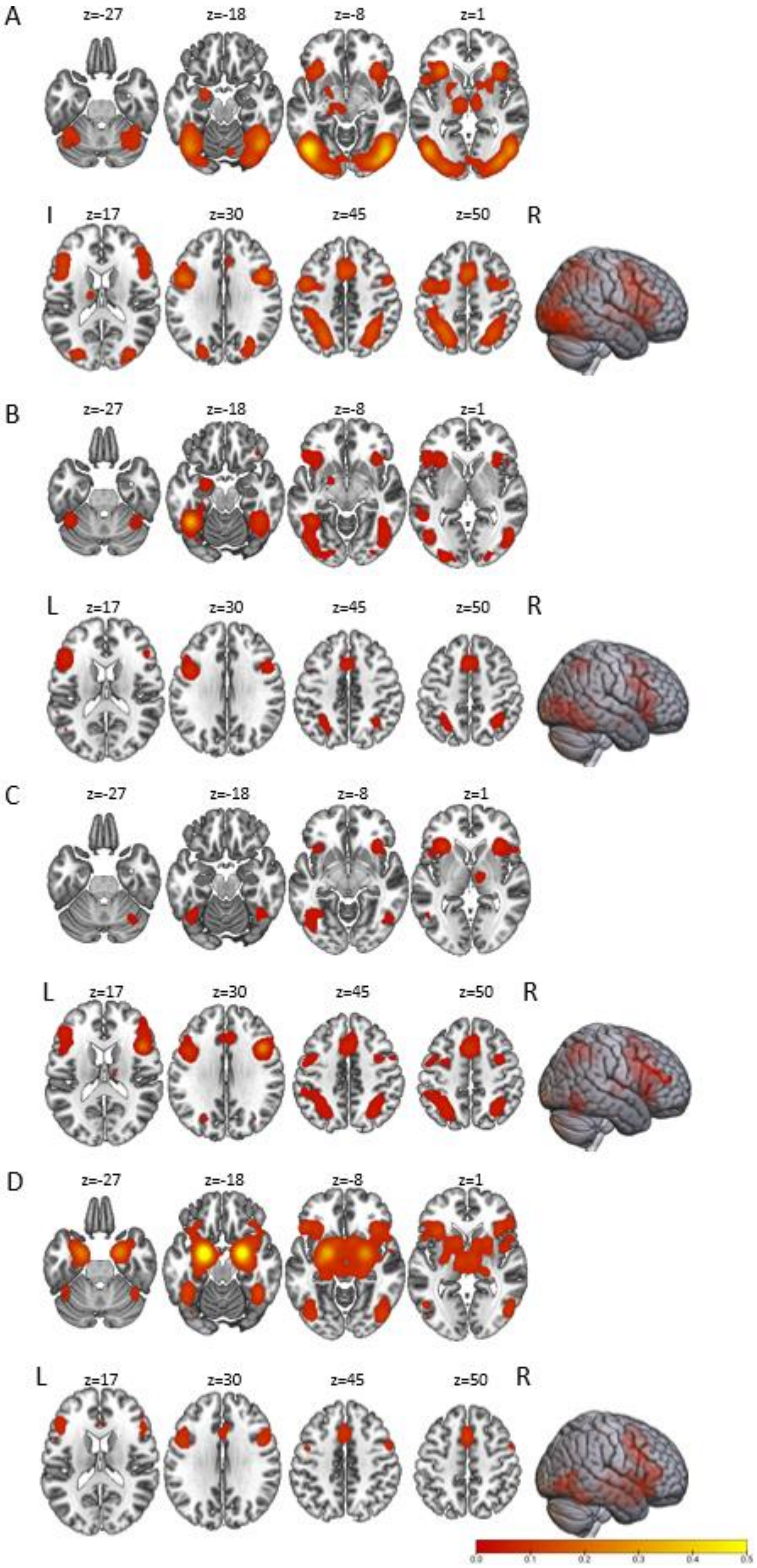
A
z=-27
z=-18
z=-8
z=1
I
z=17
z=30
z=45
z=50
R
B
z=-27
z=-18
z=-8
z=1
L
z=17
z=30
z=45
z=50
R
C
z=-27
z=-18
z=-8
z=1
L
z=17
z=30
z=45
z=50
R
D
z=-27
z=-18
z=-8
z=1
L
z=17
z=30
z=45
z=50
R
0.0
0.1
0.2
0.3
0.4
0.5

Fig. 6. Connectivity maps of the MACM analyses. Co-activation patterns for bilateral occipital gyrus (A), left FFA (B), right IFG (C), and bilateral amygdala (D). Clusters threshold: $p < 0.05$ (cluster-level FWE correction). Coordinates are MNI152 standard stereotaxic spaces. Figure was created using Mango (http://ric.uthscsa.edu/mango). Abbreviations: L, left; R, right.

Discussion

The aim of this meta-analysis was to elucidate the roles of the dorsal and ventral pathways in perception of facial expressions. Utilizing the latest GingerALE to overcome limitations in the past meta-analyses, we re-analyzed the brain areas that have stronger responses to emotional faces than to neutral faces or non-facial stimuli. Furthermore, we examined the effects of tasks and dynamic facial expressions, and applied MACM to explore the co-activation networks for perception of facial expressions using the 4 clusters elicited by emotional faces than neutral faces as VOIs. In what follows, we discuss the implications of the key findings for the roles of ventral and dorsal pathways, effects of task demands on these pathways and their relationship to bottom-up and top-down face processing, brain regions for dynamic facial expression, and results of MACM analysis. We then present a revised model for perception of facial expression, followed by acknowledgements of certain limitations in our meta-analysis.

4.1 The roles of the ventral and dorsal pathways

The results of our meta-analysis suggested that the ventral stream is more involved in the facial expression processing than the dorsal stream. Greater responses to emotional faces relative to neutral faces were found engaging a distributed neural network. These include the right IOG (containing the right OFA), left MOG, left FFA, and right IFG. Apart from these regions that are associated with the ventral stream, the responsive areas also included bilateral amygdala, bilateral parahippocampal gyrus, right uncus, and right declive, that are part of the emotion processing network. In contrast, the STS did not produce the same effect.

The finding of the left FFA activation from our meta-analysis is consistent with several neuroimaging studies (Derntl et al., 2012; Duan et al., 2010; Kesler/West et al., 2001). For example, research has shown that FFA is sensitive to facial expression changes after adaptation

(Xu and Biederman, 2010), and the type of emotional expression can be reliably predicted from the pattern of FFA activities (Harry et al., 2013). Further support for the role of the ventral stream comes from our findings of the greater responses of this region to facial expressions, including the right IOG (BA18, BA19) and left MOG (BA37, BA19). The OFA in the IOG has been included in most face perception models (Bernstein and Yovel, 2015; Haxby et al., 2000; O'Toole et al., 2002), with the function of processing facial expressions and form information (Deeley et al., 2008; Holtmann et al., 2013; N'Diaye et al., 2009). Classified as a part of the ventral pathway in Bernstein and Yovel's (2015) model, the OFA, having high connectivity with FFA but not with STS, is thought to be involved in processing information about form but not motion. In the results of our meta-analysis, the stronger responses in the right IOG to facial expressions confirmed its role in relaying information of facial expressions to the FFA.

The hyperactive response of right IFG and right declive to emotional faces are not included in the prior models of face processing (Bernstein and Yovel, 2015; Haxby et al., 2000; O'Toole et al., 2002). The significantly active cluster containing the IFG when processing emotional faces than neutral faces is the sixth largest cluster with the extreme value of 0.23, while the one containing IFG and MFG for perceiving emotional faces than baseline (non-face stimuli) is the largest cluster with the extrema value of 0.26. These results suggest a higher level of involvement of the IFG and MFG in processing emotional than neutral faces, which can be further interpreted as both the facial expression and face perception contributing to the activations of the IFG and MFG. Therefore, it is possible that the top-down effect in the IFG and MFG is more apparent for emotional than neutral faces. There has also been evidence for the roles of the IFG and right declive in facial emotion processing (Amting et al., 2010; Dal Monte et al., 2013; Lee et al., 2008; Uono et al., 2016). Other studies found that right IFG is active when processing social interaction information (Liu et al., 2015, 2016). It might be suggested this region was responsible for maintaining attention to the social information in the perception of facial expression. Taking this evidence into account, we also included the IFG and the MFG in the top-down stream of facial expression perception in our revised model (see the section 4.5).

4.2 Effects of task demands on the ventral and dorsal pathways

The finding from our meta-analysis suggests that the left FFA plays a critical role in processing facial expressions through the comparison from the three types of facial expression tasks. During passive viewing, the activation in the left FFA (BA 19) is greater relative to that in the explicit or implicit tasks. However, no cluster was found when subtracting passive viewing from explicit tasks , or passive viewing from implicit tasks. This may be due to passive viewing allows for more attentional resources on the face stimuli and thus elicits the left FFA, whereas explicit and implicit tasks divert these resources to the task itself. Similar FFA activation has also been reported elsewhere. The face-selective N170 component, measured at the occipito-temporal cortex containing the FFA and modulated by emotionality of facial expressions, has been more frequently observed in passive viewing than other tasks (Schindler and Bublatzky, 2020). Moreover, attention enhances the stimulus-driven gamma oscillations, which occur when participants experience a coherent visual perception in the fusiform gyrus (Tallon-Baudry et al., 2005).

Conjunction analyses demonstrate significant activations in the parahippocampal gyrus and subcallosal gyrus (BA34) for explicit and implicit tasks; parahippocampal gyrus (BA34) for explicit and passive viewing tasks; and amygdala for implicit and passive viewing tasks. These results demonstrated that the limbic system is consistently activated by facial expressions regardless of tasks.

4.3 The roles of the ventral and dorsal pathways in perceiving dynamic facial expressions

Our results also confirmed the role of FFA for both dynamic and static facial expressions. Dynamic facial expressions, relative to static and neutral facial expressions trigger greater activation in the bilateral fusiform gyrus (containing the bilateral FFA), middle temporal gyrus (containing bilateral MT), left amygdala, left MOG, and right STS. It is well known that the dorsal pathway of the face processing network preferentially responds to dynamic faces and socially meaningful facial motions (Campbell et al., 2001). However, research on whether the FFA in the ventral pathway also responds this way has resulted in mixed conclusions. Echoed with a number of authors have reported stronger FFA responses to dynamic facial expressions relative to static images (Arsalidou et al., 2011; LaBar, 2003; Sato et al., 2004; Schultz and Pilz, 2009; Trautmann et al., 2009), we found equal FFA activations for both dynamic and static facial expressions, which is in line with Furl et al., (2013, 2015). Consistent with Bernstein and Yovel (2015) and O’Toole et al. (2002), the results of our meta-analysis for the STS support its role in facial motion processing. STS showed no significantly higher responses to emotional faces than neutral ones, whilst the STS has stronger responses to dynamic facial expressions relative to static or neutral faces. It is reasonable to speculate that the FFA is more responsible for the form of facial expressions while STS is more involved in the extraction of dynamic information. This is also inconsistent with the Haxby et al.'s (2000) proposal that the STS is responsible for processing facial expression.

4.4 The co-activation network of emotion processing from faces

When neural responses to emotional faces are contrasted with neutral faces, our MACM analysis revealed co-activation patterns of four VOIs, which include the bilateral amygdala (cluster 1, 2), bilateral occipital gyrus (cluster 3, 4), left FFA (cluster 5), and right IFG (cluster 6). The patterns describe the connectivity of these regions and the co-activated brain areas in MACM results which used them as seed regions. The results of our MACM meta-analysis (Fig. 7) show that these interested brain regions have similar co-activation patterns, because each VOI shared co-activation with several other regions. This suggests a high level of interactions among these components within the system for facial expression processing. The details of each component are as follows.

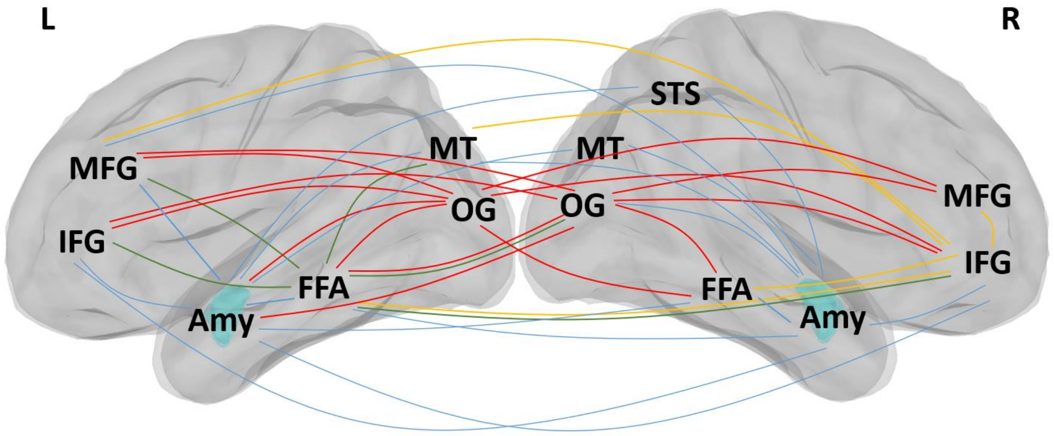

Fig. 7. Co-activation patterns derived from the MACM results. Abbreviations: Amy, amygdala; FFA, fusiform face area; IFG, inferior frontal gyrus; MFG, middle frontal gyrus; MT, middle temporal visual area; OG, occipital gyrus; STS, superior temporal sulcus.

The Left FFA. This VOI showed a co-activation pattern with bilateral IFG, left MFG, left MT, bilateral superior parietal lobule, left inferior parietal lobule, right IOG and MOG. Its connectivity with the IFG, right IOG and MOG is in line with Dima et al.’s (2011) finding that the VPFC (containing the IFG) receives information of facial affect directly from the FFA. Furthermore, the MACM results add support for the connectivity between FFA and MT as observed within visual association network (including the FFA) and dorsal attention network (including the MT) reported in Popal et al. (2020).

The Right IFG. This VOI showed significant co-activation with bilateral MFG, bilateral cingulate gyrus, left MT, left inferior parietal lobule, right superior parietal lobule, bilateral FFA, and right thalamus. There is already evidence that the IFG is responsible for recognition of facial expressions (Kret and De Gelder, 2012; Ruigrok et al., 2014; Sabatinelli et al., 2011; Schirmer, 2018). Like Sato et al. (2012), we also found enhanced connectivity between the MT and IFG during processing dynamic emotional faces relative to static ones. We further observed connectivity between the IFG and MFG, which might be due to their direct anatomical connection (Vogt and Pandya, 1987). This is in line with Ćurčić-Blake et al. (2012) who showed a similar connectivity during emotional learning. Our MACM results also indicate a co-activation of the FFA with the IFG when the IFG serves as a seed region, providing novel evidence for the connectivity between the IFG and FFA.

The OG. The seeds of the occipital gyrus that contain the right IOG and the left MOG have consistently displayed stronger responses to emotional faces than to neutral faces. The occipital gyrus was co-active with bilateral IFG, MFG, FFA, thalamus, and left amygdala. The connectivity between the OG and FFA is supported by the co-activation of the FFA with OG in the MACM analysis. The co-active pattern for the amygdala and OG, accompanied by their connectivity with FFA, is congruent with the results reported by Fairhall and Ishai (2007). OG has no direct anatomical connection with IFG and MFG. Its connectivity with the IFG is supported by the evidence that facial expressions modulate the coupling from the IOG to the VPFC, which contains the IFG (Dima et al., 2011). The connectivity between the OG and MFG is also in line with the finding by Foley et al., (2012), who found effective connectivity between the MFG and IOG during the period of processing dynamic facial expressions, while using the voxel in the IOG as a seed.

The Amygdala. This VOI was co-active with the bilateral FFA, IFG, insula, candidate, thalamus, MT, right hypothalamus, right STS, right IOG, left superior frontal gyrus, left MFG, and left superior cingulate. There is already evidence for the connectivity between the amygdala, IFG (Ćurčić-Blake et al., 2012), FFA (Fairhall and Ishai, 2007), and OG (Fairhall and Ishai, 2007). Corroborating the finding by Foley and colleagues (2012), who used the voxel in the amygdala as a seed in processing of dynamic angry facial expressions, our MACM analysis also suggests that the amygdala has effective connectivity with MFG and MT. In addition, our finding of the connectivity between the amygdala and right STS echoes the results from the study by Davies-Thompson and Andrews (2012).

It is worth noting that all the four seed regions co-activate with the MFG, suggesting that the MFG plays a key role in this network. Previously this brain region has been found to couple with amygdala and modulate its response to emotional stimuli (Sebastian et al., 2017). In addition, there is evidence that the MFG processes facial expression (Kale et al., 2019; Seitz et al., 2008). In our result it was also more activated for faces than for non-face stimuli, which may suggest that it also processes other properties related to faces apart from facial expression.

The connectivity of these four seed regions shown in Fig. 7 reveals a neural network for processing of emotional facial expressions. The amygdala is functionally connected with all face-sensitive regions including the FFA, STS, OG, IFG, and MFG. Similar brain regions were identified in the four-area model of facial affect processing by Dima et al. (2011), who suggested that the VPFC (containing the IFG) receives information of facial affect directly from the IOG, FFA, and amygdala. Compatible with their findings, we found a co-active pattern for these four areas when the amygdala serves as a seed region. The FFA, which plays an important role in processing facial expressions, is connected with the OG, amygdala, IFG, and MFG, suggesting the existence of a stream for facial expression processing originating from the OG and recruiting the FFA to extract form information from facial expressions and delivering the information to the amygdala, IFG, and MFG. No matter whether IFG or FFA was used as the seed region, these two regions always co-activated in our analysis. Based on the finding that the IFG is involved in processing of facial expressions (Uono et al., 2016) and that both the FFA and IFG but not STS have greater responses to emotional faces than to neutral faces, we could infer that the IFG receives information of facial expressions extracted by the FFA but not the STS.

The IOG, containing the OFA, is in charge of facial processing at an early stage (Pitcher et al., 2007); while the MOG is a region sensitive to faces (Puce et al., 1995) and to emotion intensity (N'Diaye et al., 2009). The connectivity of the OG with the IFG, MFG, FFA, and amygdala suggests that the involvement of the OG in delivering early-processed facial information to those regions. Notably, the results of our MACM meta-analysis show that the STS does not have co-activation with the OG, thus supporting Bernstein and Yovel's (2015) notion that the OFA has high connectivity with the FFA rather than the STS, and is involved in form information processing in the ventral stream. These results pose a challenge to the functional route in Haxby et al.'s (2000) model, where the OFA delivers facial information to the STS for extracting information of facial expressions.

4.5 A revised model for facial expression processing based on results of meta-analysis including MACM

Based on the results of this meta-analysis, we propose a revised model for facial expression processing. As illustrated in Fig. 8, a key feature of this model is that the OG and FFA in the ventral stream plays a more prominent role for processing facial expression. This differs from the models of Haxby et al. (2000) and O'Toole et al. (2002), which assign the function to the STS in the dorsal stream. Our model also differs from Bernstein and Yovel (2015) because unlike the connection between the FFA and the STS in their model, the FFA in our model is only connected to the IFG/MFG within the ventral system. The connectivity between the brain areas involved in facial expression processing is defined by the results of our MACM analysis. In Bernstein and Yovel's model, the IFG, like the STS, responds more strongly to dynamic faces. However, the results of our meta-analysis showed no significant IFG/MFG responses to dynamic facial expressions. Moreover, the MT and STS did not respond more to emotional faces than neutral faces, although they were activated by dynamic facial expressions. Both the results suggest that the MT and STS are likely to be involved in processing face motion as proposed by Bernstein and Yovel, but not facial expression. Finally, our model classifies the brain regions responsible for processing facial expression into the bottom-up and top-down types, with the former containing the OG and FFA, and the latter containing the IFG and MFG. Being sensitive to emotional stimuli but not face-specific, the amygdala and limbic system are outside the ventral and dorsal pathways.

As suggested by Haxby et al. (2000), these regions receive input from the dorsal pathway. The engagement of the bilateral amygdala, parahippocampal gyrus, right uncus, and left thalamus found in the results of our meta-analysis supports the role of the limbic system in processing facial expressions. However, these results also suggest these areas may also receive information about facial expression from the OFA and FFA in the ventral stream.

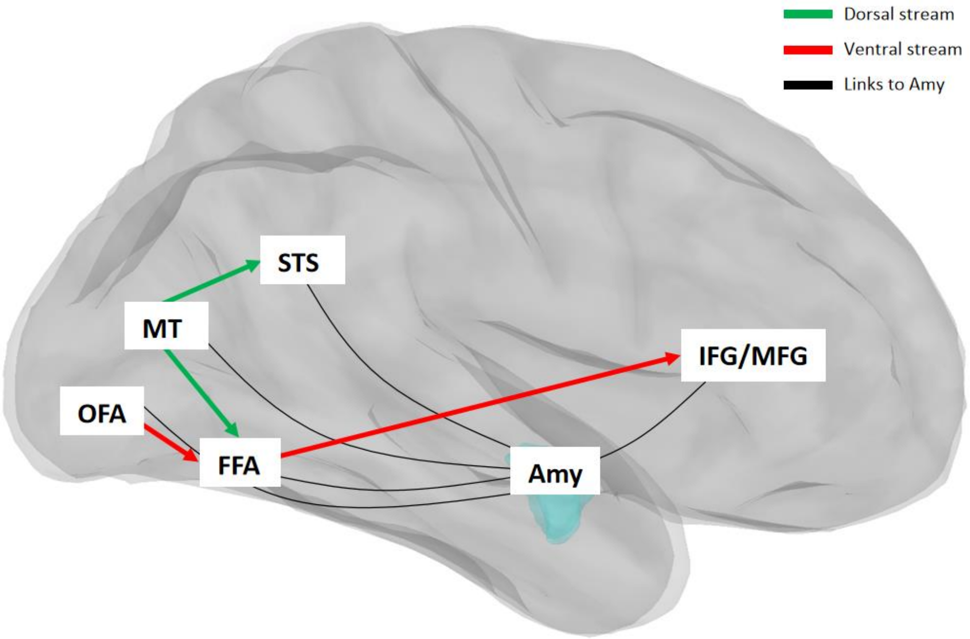

Fig. 8. A revised neural network for processing facial expressions. The ventral stream, including OFA, FFA, IFG/MFG is involved in facial expression processing, whereas, the dorsal stream, including MT, STS, is involved in motion processing. The arrows indicate the bottom-up processing flow. Abbreviations: FFA, fusiform face area; IFG, inferior frontal gyrus; MFG, middle frontal gyrus; MT, middle temporal visual area; OFA, occipital face area; STS, superior temporal sulcus; Amy, Amygdala.

4.6 Limitations

This meta-analysis has several limitations. First, because most studies included in this analysis only used static face stimuli, the neural representation of emotional facial expressions may not extend to dynamic materials. This limitation restricts us from investigating the involvement of the ventral and dorsal streams in processing facial expressions. Second, factors such as age, gender, culture, and task difficulty could also bias the results of our meta-analysis. There has been evidence for the effects of age and gender on emotional face perception (Fusar-Poli et al., 2009; Stevens and Hamann, 2012). Effects of other covariates like culture and task difficulty on facial expression perception awaits future meta-analyses. Moreover, because of limited numbers of studies (less than 17), we were unable to conduct separate contrasts for different facial expressions, especially for the expressions of surprise, sadness and disgust. Most existing neuroimaging studies only used happy, fearful, and angry faces as stimuli. The results regarding the roles of the ventral and dorsal streams in processing facial expressions are therefore confined to these well-studied facial expressions. This could lead to limited generalization of facial expressions in our meta-analysis. Further studies should contrast the perception of surprised, sad or disgusted facial expressions with the perception of neutral faces to overcome the bias in our analysis.

4.7 Conclusions

Our meta-analysis provides comprehensive evidence for the role of the ventral stream in the perception of facial expression. This conclusion is drawn from three key findings. The first is the higher activation for emotional faces in the ventral stream including the left FFA, right IOG, left MOG, and right IFG. The second is the involvement of the left FFA in bottom-up processing of facial expression. The third is the involvement of FFA in processing dynamic facial expression. Dynamic facial expression is often seen as a function of the STS, but the results of our meta-analysis have shown clear involvement of multiple regions including bilateral FFA, MT, left amygdala/parahippocampal gyrus, left MOG in addition to the right STS. Apart from these key findings, the results also show the role of amygdala/parahippocampal gyrus in facial expression perception, which is consistently involved in processing facial expressions, regardless of the kind of task used in the studies.

References

Adolphs, R., 2002. Recognizing emotion from facial expressions: psychological and neurological mechanisms. Behavioral and Cognitive Neuroscience Reviews 1, 21–62. https://doi.org/10.1177/1534582302001001003

Adolphs, R., Spezio, M., 2006. Role of the amygdala in processing visual social stimuli, in: Progress in Brain Research. Elsevier, pp. 363–378. https://doi.org/10.1016/S0079-6123(06)56020-0

Amting, J.M., Greening, S.G., Mitchell, D.G.V., 2010. Multiple Mechanisms of Consciousness: The Neural Correlates of Emotional Awareness. Journal of Neuroscience 30, 10039–10047. https://doi.org/10.1523/JNEUROSCI.6434-09.2010

Arsalidou, M., Morris, D., Taylor, M.J., 2011. Converging evidence for the advantage of dynamic facial expressions. Brain Topogr 24, 149–163. https://doi.org/10.1007/s10548-011-0171-4

Ashburner, J., 2012. SPM: A history. NeuroImage 62, 791–800. https://doi.org/10.1016/j.neuroimage.2011.10.025

Benuzzi, F., Meletti, S., Zamboni, G., Calandra-Buonaura, G., Serafini, M., Lui, F., Baraldi, P., Rubboli, G., Tassinari, C.A., Nichelli, P., 2004. Impaired fear processing in right mesial temporal sclerosis: a fMRI study. Brain Research Bulletin 63, 269–281. https://doi.org/10.1016/j.brainresbull.2004.03.005

Bernstein, M., Yovel, G., 2015. Two neural pathways of face processing: a critical evaluation of current models. Neuroscience & Biobehavioral Reviews 55, 536–546. https://doi.org/10.1016/j.neubiorev.2015.06.010

Breiter, H.C., Etcoff, N.L., Whalen, P.J., Kennedy, W.A., Rauch, S.L., Buckner, R.L., Strauss, M.M., Hyman, S.E., Rosen, B.R., 1996. Response and habituation of the human amygdala during visual processing of facial expression. Neuron 17, 875–887. https://doi.org/10.1016/S0896-6273(00)80219-6

Calder, A.J., Young, A.W., 2005. Understanding the recognition of facial identity and facial expression. Nature Reviews Neuroscience 6, 641–651. https://doi.org/10.1038/nrn1724

Campbell, R., MacSweeney, M., Surguladze, S., Calvert, G., McGuire, P., Suckling, J., Brammer, M.J., David, A.S., 2001. Cortical substrates for the perception of face actions: an fMRI study of the specificity of activation for seen speech and for meaningless lower-face acts (gurning). Cognitive Brain Research 12, 233–243. https://doi.org/10.1016/S0926-6410(01)00054-4

Chumbley, J., Friston, K., 2009. False discovery rate revisited: FDR and topological inference using Gaussian random fields. NeuroImage 44, 62–70.

https://doi.org/10.1016/j.neuroimage.2008.05.021

Ćurčić-Blake, B., Swart, M., Aleman, A., 2012. Bidirectional information flow in frontoamygdalar circuits in humans: a dynamic causal modeling study of emotional associative learning. Cerebral Cortex 22, 436–445. https://doi.org/10.1093/cercor/bhr124

Dal Monte, O., Krueger, F., Solomon, J.M., Schintu, S., Knutson, K.M., Strenziok, M., Pardini, M., Leopold, A., Raymont, V., Grafman, J., 2013. A voxel-based lesion study on facial emotion recognition after penetrating brain injury. Social Cognitive and Affective Neuroscience 8, 632–639. https://doi.org/10.1093/scan/nss041

Darwin, C., 1872. The expression of the emotions in man and animals. John Murray, London. https://doi.org/10.1037/10001-000

Davies-Thompson, J., Andrews, T. J., 2012. Intra- and interhemispheric connectivity between face-selective regions in the human brain. Journal of Neurophysiology, 108, 3087–3095. https://doi:10.1152/jn.01171.2011

Deeley, Q., Daly, E.M., Azuma, R., Surguladze, S., Giampietro, V., Brammer, M.J., Hallahan, B., Dunbar, R.I.M., Phillips, M.L., Murphy, D.G.M., 2008. Changes in male brain responses to emotional faces from adolescence to middle age. NeuroImage 40, 389–397. https://doi.org/10.1016/j.neuroimage.2007.11.023

Derntl, B., Habel, U., Robinson, S., Windischberger, C., Kryspin-Exner, I., Gur, R.C., Moser, E., 2012. Culture but not gender modulates amygdala activation during explicit emotion recognition. BMC Neuroscience 13, 54. https://doi.org/10.1186/1471-2202-13-54

Dima, D., Stephan, K.E., Roiser, J.P., Friston, K.J., Frangou, S., 2011. Effective connectivity during processing of facial affect: evidence for multiple parallel pathways. Journal of Neuroscience 31, 14378–14385. https://doi.org/10.1523/JNEUROSCI.2400-11.2011

Dricu, M., Frühholz, S., 2016. Perceiving emotional expressions in others: activation likelihood estimation meta-analyses of explicit evaluation, passive perception and incidental perception of emotions. Neuroscience & Biobehavioral Reviews 71, 810–828. https://doi.org/10.1016/j.neubiorev.2016.10.020

Duan, X., Dai, Q., Gong, Q., Chen, H., 2010. Neural mechanism of unconscious perception of surprised facial expression. NeuroImage 52, 401–407. https://doi.org/10.1016/j.neuroimage.2010.04.021

Eickhoff, S.B., Bzdok, D., Laird, A.R., Kurth, F., Fox, P.T., 2012. Activation likelihood estimation meta-analysis revisited. NeuroImage 59, 2349–2361. https://doi.org/10.1016/j.neuroimage.2011.09.017

Eickhoff, S.B., Laird, A.R., Fox, P.M., Lancaster, J.L., Fox, P.T., 2017. Implementation errors in the GingerALE software: description and recommendations. Human Brain Mapping 38, 7–11. https://doi.org/10.1002/hbm.23342

Eickhoff, S.B., Nichols, T.E., Laird, A.R., Hoffstaedter, F., Amunts, K., Fox, P.T., Bzdok, D., Eickhoff, C.R., 2016. Behavior, sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. NeuroImage 137, 70–85. https://doi.org/10.1016/j.neuroimage.2016.04.072

Ekman, P.M., Friesen, W., Ellsworth, P., 1972. Emotion in the human face: guidelines for research and an integration of findings. https://doi.org/10.1016/S0005-7967(73)80022-1

Engell, A. D., Haxby, J. V., 2007. Facial expression and gaze-direction in human superior temporal sulcus. Neuropsychologia, 45, 3234–3241. https://doi.org/10.1016/j.neuropsychologia.2007.06.022

Fairhall, S.L., Ishai, A., 2007. Effective connectivity within the distributed cortical network for face perception. Cerebral Cortex 17, 2400–2406. https://doi.org/10.1093/cercor/bhl148

Foley, E., Rippon, G., Thai, N.J., Longe, O., Senior, C., 2012. Dynamic facial expressions evoke distinct activation in the face perception network: a connectivity analysis study. Journal of Cognitive Neuroscience 24, 507–520. https://doi.org/10.1162/jocn_a_00120

Furl, N., Henson, R.N., Friston, K.J., Calder, A.J., 2015. Network interactions explain sensitivity to dynamic faces in the superior temporal sulcus. Cerebral Cortex 25, 2876–2882. https://doi.org/10.1093/cercor/bhu083

Furl, N., Henson, R.N., Friston, K.J., Calder, A.J., 2013. Top-down control of visual responses to fear by the amygdala. Journal of Neuroscience 33, 17435–17443. https://doi.org/10.1523/JNEUROSCI.2992-13.2013

Fusar-Poli, P., Placentino, A., Carletti, F., Landi, P., Allen, P., Surguladze, S., Benedetti, F., Abbamonte, M., Gasparotti, R., Barale, F., Perez, J., McGuire, P., Politi, P., 2009. Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. Journal of Psychiatry & Neuroscience: 34, 418–432. https://doi.org/10.1111/j.1365-2850.2009.01434.x

Ganel, T., Valyear, K.F., Goshen-Gottstein, Y., Goodale, M.A., 2005. The involvement of the “fusiform face area” in processing facial expression. Neuropsychologia 43, 1645–1654. https://doi.org/10.1016/j.neuropsychologia.2005.01.012

Harry, B., Williams, M.A., Davis, C., Kim, J., 2013. Emotional expressions evoke a differential response in the fusiform face area. Frontiers in Human Neuroscience 7. https://doi.org/10.3389/fnhum.2013.00692

Hasselmo, M.E., Rolls, E.T., Baylis, G.C., 1989. The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. Behavioural Brain Research 32, 203–218. https://doi.org/10.1016/S0166-4328(89)80054-3

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2002. Human neural systems for face recognition and social communication. Biological Psychiatry, Social Anxiety: From Laboratory Studies to Clinical Practice 51, 59–67. https://doi.org/10.1016/S0006-3223(01)01330-0

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends in Cognitive Sciences 4, 223–233. https://doi.org/10.1016/S1364-6613(00)01482-0

Hinojosa, J.A., Mercado, F., Carretié, L., 2015. N170 sensitivity to facial expression: a meta-analysis. Neuroscience & Biobehavioral Reviews 55, 498–509. https://doi.org/10.1016/j.neubiorev.2015.06.002

Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nature Neuroscience 3, 80–84. https://doi.org/10.1038/71152

Holtmann, J., Herbort, M.C., Wüstenberg, T., Soch, J., Richter, S., Walter, H., Roepke, S., Schott, B.H., 2013. Trait anxiety modulates fronto-limbic processing of emotional interference in borderline personality disorder. Frontiers in Human Neuroscience 7. https://doi.org/10.3389/fnhum.2013.00054

Iidaka, T., Okada, T., Murata, T., Omori, M., Kosaka, H., Sadato, N., Yonekura, Y., 2002. Age-related differences in the medial temporal lobe responses to emotional faces as revealed by fMRI. Hippocampus 12, 352–362. https://doi.org/10.1002/hipo.1113

Itier, R.J., 2004. N170 or N1? Spatiotemporal differences between object and face processing using ERPs. Cerebral Cortex 14, 132–142. https://doi.org/10.1093/cercor/bhg111

Ishai, A., 2008. Let's face it: it's a cortical network. NeuroImage 40, 415–419. https://doi.org/10.1016/j.neuroimage.2007.10.040

Izard, C.E., 1997. Emotions and facial expressions: a perspective from differential emotions theory, in: Russell, J.A., Fernández-Dols, J.M. (Eds.), The Psychology of Facial Expression. Cambridge University Press, pp. 57–77. https://doi.org/10.1017/CBO9780511659911.005

Jenkinson, M., Beckmann, C.F., Behrens, T.E.J., Woolrich, M.W., Smith, S.M., 2012. FSL. NeuroImage 62, 782–790. https://doi.org/10.1016/j.neuroimage.2011.09.015

Kale, E.H., Üstün, S., Çiçek, M., 2019. Amygdala–prefrontal cortex connectivity increased during face discrimination but not time perception. European Journal of Neuroscience 50, 3873–3888. https://doi.org/10.1111/ejn.14537

Kesler/West, M.L., Andersen, A.H., Smith, C.D., Avison, M.J., Davis, C.E., Kryscio, R.J., Blonder, L.X., 2001. Neural substrates of facial emotion processing using fMRI. Cognitive Brain Research 11, 213–226. https://doi.org/10.1016/S0926-6410(00)00073-2

Kret, M.E., De Gelder, B., 2012. A review on sex differences in processing emotional signals. Neuropsychologia 50, 1211–1221. https://doi.org/10.1016/j.neuropsychologia.2011.12.022

LaBar, K.S., 2003. Dynamic perception of facial affect and identity in the human brain. Cerebral Cortex 13, 1023–1033. https://doi.org/10.1093/cercor/13.10.1023

Lancaster, J.L., Tordesillas-Gutiérrez, D., Martinez, M., Salinas, F., Evans, A., Zilles, K., Mazziotta, J.C., Fox, P.T., 2007. Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. Human Brain Mapping 28, 1194–1205. https://doi.org/10.1002/hbm.20345

Lee, L.C., Andrews, T.J., Johnson, S.J., Woods, W., Gouws, A., Green, G.G.R., Young, A.W., 2010. Neural responses to rigidly moving faces displaying shifts in social attention investigated with fMRI and MEG. Neuropsychologia 48, 477–490. https://doi.org/10.1016/j.neuropsychologia.2009.10.005

Lee, K.-U., Khang, H.S., Kim, K.-T., Kim, Y.-J., Kweon, Y.-S., Shin, Y.-W., Kwon, J.S., Ho, S.-H., Garfinkel, S.N., Chae, J.-H., Liberzon, I., 2008. Distinct processing of facial emotion of own-race versus other-race: NeuroReport 19, 1021–1025. https://doi.org/10.1097/WNR.0b013e3283052df2

Liberati, A., Altman, D.G., Tetzlaff, J., Mulrow, C., Gøtzsche, P.C., Ioannidis, J.P.A., Clarke, M., Devereaux, P.J., Kleijnen, J., Moher, D., 2009. The PRISMA Statement for reporting systematic reviews and meta-analyses of studies that evaluate health care interventions: explanation and elaboration. PLoS Medicine 6, e1000100. https://doi.org/10.1371/journal.pmed.1000100

Lieberman, M.D., Eisenberger, N.I., Crockett, M.J., Tom, S.M., Pfeifer, J.H., Way, B.M., 2007. Putting feelings into words. Psychological Science 18, 421–428. https://doi.org/10.1111/j.1467-9280.2007.01916.x

Liu, T., Saito, H., Oi, M., 2015. Role of the right inferior frontal gyrus in turn-based cooperation and competition: a near-infrared spectroscopy study. Brain and Cognition 99, 17–23. https://doi.org/10.1016/j.bandc.2015.07.001

Liu, T., Saito, H., Oi, M., 2016. Obstruction increases activation in the right inferior frontal gyrus. Social Neuroscience 11, 344–352. https://doi.org/10.1080/17470919.2015.1088469

Molenberghs, P., Johnson, H., Henry, J.D., Mattingley, J.B., 2016. Understanding the minds of others: a neuroimaging meta-analysis. Neuroscience & Biobehavioral Reviews 65, 276–291. https://doi.org/10.1016/j.neubiorev.2016.03.020

Morris, J., 1998. A neuromodulatory role for the human amygdala in processing emotional facial expressions. Brain 121, 47–57. https://doi.org/10.1093/brain/121.1.47

Müller, V.I., Cieslik, E.C., Laird, A.R., Fox, P.T., Radua, J., Mataix-Cols, D., Tench, C.R., Yarkoni, T., Nichols, T.E., Turkeltaub, P.E., Wager, T.D., Eickhoff, S.B., 2018. Ten simple rules for neuroimaging meta-analysis. Neuroscience & Biobehavioral Reviews 84, 151–161. https://doi.org/10.1016/j.neubiorev.2017.11.012

N’Diaye, K., Sander, D., Vuilleumier, P., 2009. Self-relevance processing in the human amygdala: gaze direction, facial expression, and emotion intensity. Emotion 9, 798–806. https://doi.org/10.1037/a0017845

Ojemann, J.G., Ojemann, G.A., Lettich, E., 1992. Neuronal activity related to faces and matching in human right nondominant temporal cortex. Brain 115, 1–13. https://doi.org/10.1093/brain/115.1.1

O’Toole, A.J., Roark, D.A., Abdi, H., 2002. Recognizing moving faces: a psychological and neural synthesis. Trends in Cognitive Sciences 6, 261–266. https://doi.org/10.1016/S1364-6613(02)01908-3

Pessoa, L., Padmala, S., 2006. Decoding near-threshold perception of fear from distributed single-trial brain activation. Cerebral Cortex 17, 691–701. https://doi.org/10.1093/cercor/bhk020

Pitcher, D., Walsh, V., Yovel, G., Duchaine, B., 2007. TMS evidence for the involvement of the right occipital face area in early face processing. Current Biology 17, 1568–1573. https://doi.org/10.1016/j.cub.2007.07.063

Popal, H., Quimby, M., Hochberg, D., Dickerson, B.C., Collins, J.A., 2020. Altered functional connectivity of cortical networks in semantic variant Primary Progressive Aphasia. NeuroImage: Clinical 28, 102494. https://doi.org/10.1016/j.nicl.2020.102494

Puce, A., Allison, T., Gore, J.C., McCarthy, G., 1995. Face-sensitive regions in human extrastriate cortex studied by functional MRI. Journal of Neurophysiology 74, 1192–1199. https://doi.org/10.1152/jn.1995.74.3.1192

Rauch, A.V., Ohrmann, P., Bauer, J., Kugel, H., Engelien, A., Arolt, V., Heindel, W., Suslow, T., 2007. Cognitive coping style modulates neural responses to emotional faces in healthy humans: a 3-T fMRI study. Cerebral Cortex 17, 2526–2535. https://doi.org/10.1093/cercor/bhl158

Robinson, J.L., Laird, A.R., Glahn, D.C., Lovallo, W.R., Fox, P.T., 2010. Metaanalytic connectivity modeling: delineating the functional connectivity of the human amygdala. Human Brain Mapping 31, 173–184. https://doi.org/10.1002/hbm.20854

Rotshtein, P., Vuilleumier, P., Winston, J., Driver, J., Dolan, R., 2007. Distinct and convergent visual processing of high and low spatial frequency information in faces. Cerebral Cortex 17, 2713–2724. https://doi.org/10.1093/cercor/bhl180

Ruigrok, A.N.V., Salimi-Khorshidi, G., Lai, M.-C., Baron-Cohen, S., Lombardo, M.V., Tait, R.J., Suckling, J., 2014. A meta-analysis of sex differences in human brain structure. Neuroscience & Biobehavioral Reviews 39, 34–50. https://doi.org/10.1016/j.neubiorev.2013.12.004

Sabatinelli, D., Fortune, E.E., Li, Q., Siddiqui, A., Krafft, C., Oliver, W.T., Beck, S., Jeffries, J.,

2011. Emotional perception: meta-analyses of face and natural scene processing. NeuroImage 54, 2524–2533. https://doi.org/10.1016/j.neuroimage.2010.10.011

Sadeh, B., Podlipsky, I., Zhdanov, A., Yovel, G., 2010. Event-related potential and functional MRI measures of face-selectivity are highly correlated: a simultaneous ERP-fMRI investigation. Human Brain Mapping 31, 1490–1501. https://doi.org/10.1002/hbm.20952

Said, C.P., Moore, C.D., Engell, A.D., Todorov, A., Haxby, J.V., 2010. Distributed representations of dynamic facial expressions in the superior temporal sulcus. Journal of Vision 10, 11–11. https://doi.org/10.1167/10.5.11

Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., Matsumura, M., 2004. Enhanced neural activity in response to dynamic facial expressions of emotion: an fMRI study. Cognitive Brain Research 20, 81–91. https://doi.org/10.1016/j.cogbrainres.2004.01.008

Sato, W., Toichi, M., Uono, S., Kochiyama, T., 2012. Impaired social brain network for processing dynamic facial expressions in autism spectrum disorders. BMC Neuroscience 13, 99. https://doi.org/10.1186/1471-2202-13-99

Schindler, S., Bublatzky, F., 2020. Attention and emotion: an integrative review of emotional face processing as a function of attention. Cortex 130, 362–386. https://doi.org/10.1016/j.cortex.2020.06.010

Schirmer, A., 2018. Is the voice an auditory face? An ALE meta-analysis comparing vocal and facial emotion processing. Social Cognitive and Affective Neuroscience 13, 1–13. https://doi.org/10.1093/scan/nsx142

Schultz, J., Pilz, K.S., 2009. Natural facial motion enhances cortical responses to faces. Experimental Brain Research 194, 465–475. https://doi.org/10.1007/s00221-009-1721-9

Sebastian, C.L., McCrory, E.J., De Brito, S.A., Viding, E., 2017. Modulation of amygdala response to task-irrelevant emotion. Social Cognitive and Affective Neuroscience 12, 643–650. https://doi.org/10.1093/scan/nsw174

Seitz, R.J., Schäfer, R., Scherfeld, D., Friederichs, S., Popp, K., Wittsack, H.-J., Azari, N.P., Franz, M., 2008. Valuating other people’s emotional face expression: a combined functional magnetic resonance imaging and electroencephalography study. Neuroscience 152, 713–722. https://doi.org/10.1016/j.neuroscience.2007.10.066

Stevens, J.S., Hamann, S., 2012. Sex differences in brain activation to emotional stimuli: a meta-analysis of neuroimaging studies. Neuropsychologia 50, 1578–1593. https://doi.org/10.1016/j.neuropsychologia.2012.03.011

Tallon-Baudry, C., Bertrand, O., Hénaff, M.-A., Isnard, J., Fischer, C., 2005. Attention modulates gamma-band oscillations differently in the human lateral occipital cortex and fusiform gyrus. Cerebral Cortex 15, 654–662. https://doi.org/10.1093/cercor/bhh167

Taylor, M.J., Batty, M., Itier, R.J., 2004. The faces of development: a review of early face processing over childhood. Journal of Cognitive Neuroscience 16, 1426–1442. https://doi.org/10.1162/0898929042304732

Trautmann, S.A., Fehr, T., Herrmann, M., 2009. Emotions in motion: dynamic compared to static facial expressions of disgust and happiness reveal more widespread emotion-specific activations. Brain Research 1284, 100–115. https://doi.org/10.1016/j.brainres.2009.05.075

Turkeltaub, P.E., Eickhoff, S.B., Laird, A.R., Fox, M., Wiener, M., Fox, P., 2012. Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. Human Brain Mapping 33, 1–13. https://doi.org/10.1002/hbm.21186

Uono, S., Sato, W., Kochiyama, T., Sawada, R., Kubota, Y., Yoshimura, S., Toichi, M., 2016. Neural substrates of the ability to recognize facial expressions: a voxel-based morphometry study. Social Cognitive and Affective Neuroscience nsw142. https://doi.org/10.1093/scan/nsw142

Vogt, B.A., Pandya, D.N., 1987. Cingulate cortex of the rhesus monkey: II. Cortical afferents. Journal of Comparative Neurology 262, 271–289. https://doi.org/10.1002/cne.902620208

Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an event-related fMRI Study. Neuron 30, 829–841. https://doi.org/10.1016/S0896-6273(01)00328-2

Weiner, K.S., Grill-Spector, K., 2012. The improbable simplicity of the fusiform face area. Trends in Cognitive Sciences 16, 251–254. https://doi.org/10.1016/j.tics.2012.03.003

Williams, L.M., Liddell, B.J., Kemp, A.H., Bryant, R.A., Meares, R.A., Peduto, A.S., Gordon, E., 2006. Amygdala–prefrontal dissociation of subliminal and supraliminal fear. Human Brain Mapping 27, 652–661. https://doi.org/10.1002/hbm.20208

Xu, X., Biederman, I., 2010. Loci of the release from fMRI adaptation for changes in facial expression, identity, and viewpoint. Journal of Vision 10, 36–36.

https://doi.org/10.1167/10.14.36

Zinchenko, O., Yaple, Z.A., Arsalidou, M., 2018. Brain responses to dynamic facial expressions: a normative meta-analysis. Frontiers in Human Neuroscience 12, 227. https://doi.org/10.3389/fnhum.2018.00227