
The Preponderant Role of Fusiform Face Area for the Facial Expression Confusion Effect: A MEG Study

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Abstract

Although the recognition of facial expressions seems automatic and effortless, discrimination of expressions can still be error prone. Common errors are often due to visual similarities between some expressions, e.g., fear and surprise are easily confused with each other. Little is known of what neural mechanisms are involved in such confusion effect. To address this question, we recorded the magnetoencephalography (MEG) while subjects judged facial expressions that were either easily confused with or easily distinguish from other expressions. Results showed that it was the fusiform face area (FFA) rather than the posterior superior temporal sulcus (pSTS) played a preponderant role in discriminating confusable facial expressions. No difference between high confusion and low confusion conditions was observed on the M170 component in either the FFA or the pSTS, whilst a difference between two conditions started to emerge in the late positive potential (LPP), with the low confusion condition eliciting a larger LPP amplitude in the FFA. In addition, the power of delta was also stronger in the time window of LPP component. This confusion effect was reflected in the FFA which might be associated with the perceptual-to-conceptual shift.

Key words: facial expression, confusion, FFA, LPP, delta rhythm

Introduction

Facial expression provides a wealth of information for social communication. The ability to process such information may be part of our biological heritage (Darwin &

Disease, 1978). Cross-cultural studies have identified six basic emotional facial expressions, including anger, fear, surprise, sadness, happiness and disgust (Ekman & Friesen, 1971; Elfenbein, Mandal, Ambady, Harizuka, & Kumar, 2002; Matsumoto, 1992). Although these emotional expressions appear to be universally recognized (Ekman & Friesen, 1971), the recognition rates vary across these emotions (Beaudry, Roy-Charland, Perron, Cormier, & Tapp, 2014; Tracy & Robins, 2008). Happiness is typically identified most accurately, followed by anger and surprise, while disgust, fear and sadness have been found more difficult to recognize (Ekman & Friesen, 1971; Ekman, Friesen, & Emotion, 1986; Izard, 1994; Tracy & Robins, 2008; Vassallo, Cooper, & Douglas, 2009). Recognition accuracy often depends on how easily an expression is confused with other expressions. Studies have shown that both children and adults tended to confuse surprise with fear but not easily confuse it with anger, sadness, or disgust (Gagnon, Gosselin, Hudon-ven der Buhs, Larocque, & Milliard, 2010; Gosselin & Simard, 1999; Jack, Blais, Scheepers, Schyns, & Caldara, 2009; Matsumoto & Hwang, 2011; Russell & Bullock, 1986). Fear and surprise look very similar because both of them involve wide eyes and open mouths (Schroeder et al., 2004; Duan et al., 2010). Recent evidence suggests that pairing a facial expression with another visually similar expression can make them more difficult to distinguish (Said et al., 2010; Brooks et al., 2019; Sormaz et al., 2016). Pairs such as surprise-happiness, sadness-surprise and happiness-disgust are less similar than fear-anger and surprise-fear (Brooks et al., 2019). However, where and when such confusion occurs in the brain remains largely unknown. According to the current

knowledge, a number of interconnected and distributed brain regions are involved in recognition of facial expression or other information such as face identity (Bruce & Young, 2011; Haxby, Hoffman, & Gobbini, 2000; Hoffman & Haxby, 2000; Young, Newcombe, de Haan, Small, & Hay, 1993). Haxby et al (2000) proposed a widely-accepted theory that face processing depends on the division of labor between the FFA and the pSTS regions. According to this model, the FFA in the ventral pathway is involved in the representation of invariant aspects of the face, such as face identity, while the pSTS in the dorsal pathway, is known to activate in response to facial expressions (Allison, Puce, & McCarthy, 2000). Although some empirical studies document the role of pSTS in emotion recognition (Allison, Puce, & McCarthy, 2000; Fox, Hanif, Iaria, Duchaine, & Barton, 2011; David, 2014), recent studies have convinced that the FFA is also involved in the processing of facial expression. For example, neuroimaging studies on healthy subjects (Dolan et al., 1996; Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005; Luiz, Shruti, David, & Ungerleider, 2006; Nicholas, Henson, Friston, & Calder, 2013; Pessoa, Mckenna, Gutierrez, & Ungerleider, 2002; Pujol et al., 2009; Surguladze et al., 2003; Vuilleumier, Armony, Driver, & Dolan, 2001; Winston, O'Doherty, & Dolan, 2003) and electrocorticography recordings in patients (Hiroto et al., 2012; Kawasaki et al., 2012) found significantly greater responses in the FFA to emotional faces compared to neutral faces. And strong responses can be found in the FFA than the pSTS while subjects viewed static as well as dynamic facial expressions by recording intracranial responses (Kawasaki et al., 2012).

If both of the FFA and the pSTS are involved in the processing of facial expression, which one is more responsible for processing perceptual similarities of facial expressions? Using multi-voxel pattern analysis (MVPA) of functional magnetic resonance imaging (fMRI) data, Said, Moore, Engell, Alexander, & Haxby (2010) found that the patterns of activation corresponding to individual facial expressions can be decoded in the pSTS. Furthermore, the structure that represents similarity in the pSTS correlated significantly with the structure of perceived similarity of the expressions. A subsequent study has also shown that different categories of emotional expression elicited distinct patterns of neural activation in the pSTS region (Said, Moore, Norman, Haxby, & Todorov, 2010). Sormaz et al (2016) further found that the perceptual similarity of expressions could be predicted from the patterns of neural response in the pSTS, but not in the FFA. However, there has been contradictory evidence showing that perception of different facial expressions can be predicted by the pattern of neural activation in the right FFA rather than pSTS (Brooks et al., 2019; Harry, Williams, Davis, & Kim, 2013). Recently, Brooks et al (2019) found that the conceptual structure of emotion categories (i.e. emotion-concept knowledge) could shape the perceptual structure of those categories' multi-voxel representations in the FFA. With classification analysis, Harry et al (2013) demonstrated that most emotional expressions that participants perceived could be reliably predicted from the neural pattern of activity in the FFA, suggesting the role of FFA in the perception of emotional expressions.

Accompanying the inconsistent result reviewed above is a variety of experimental tasks used in these studies. Some used memory tasks that required responding to repeated presentation of the same facial expression (Harry et al, 2013) or judging whether the probe expression appeared in the previous set (Said, Moore, Engell, Alexander, & Haxby, 2010). Some required passively viewing different facial expressions without responding (Brooks et al., 2019; Sormaz et al., 2016). Some also required viewing computer generated videos of emotional expressions and indicating whether the expression was closer to fear or anger (Said, Moore, Norman, Haxby, & Todorov, 2010). All these tasks were unable to reveal a clear relationship between facial expression and the neural responses in two face-selective brain regions, pSTS and FFA. In this study, we specifically concerned about it is the pSTS or the FFA that in charge of confusion effect among facial expressions.

Researchers in the literature of emotion recognition often employ a six-alternative forced choice (6AFC) task, in which subjects are asked to match a face image with one of the six basic expression labels (Kessels, Montagne, Hendriks, Perrett, & de Haan, 2014; Zhao, Yan, Chen, Zuo, & Fu, 2013). This allows for an evaluation of recognition accuracy for each facial expression relative to others, but does not provide a straightforward explanation as to why certain expressions are not recognized as accurately as the others from the results. To illustrate this question, Zhao, Zhao, Zhang, Cui, & Fu (2017) measured the effect of confusability by employing a two-alternative forced choice (2AFC) task, in which subjects had to choose between a pair of emotion labels that described the expression of a face image.

This method can be more advantageous than the 6AFC method because when a pair of alternative expressions such as surprise-fear produces poorer discrimination than another pair such as surprise-disgust, the question of which pair is more confusable or similar is self-evident, thus no extra step of analysis is necessary. A 2AFC task is also easier because of reduced alternatives, to investigate the neural mechanisms of this confusion effect, we measured neural activities with MEG while subjects performed the two-alternative forced facial expression recognition task. We chose MEG because it combines direct and noninvasive access to the electrophysiological activity of the brain with sub-millisecond temporal resolution, and because its advantage of locating neural activities in cerebral regions with minimum spatial bias (Baillet, 2017).

This study consisted of two parts. The first part required rating visual similarity across pairs of facial expressions. Based on the similarity rating scores, the second part tested how high-confusion (HC) and low-confusion (LC) pairs affected expression recognition performance. A MEG scan was recorded while subjects performed the task in the second part.

Method

Subjects

Two separate groups of subjects were recruited for the two tasks in this study. Thirty subjects (14 males) aged 21.5 ± 2.58 years performed the similarity rating task, and 17 subjects (8 males) aged 20.5 ± 1.24 years performed the 2AFC task with MEG recording. All were right-handed, free of neurological or psychiatric diseases, and had

normal or corrected-to-normal vision. They were paid 30 and 150 RMB for their participation in similarity rating and MEG task, respectively. The experiment was approved by the Institutional Review Board of the Institute of Psychology, Chinese Academy of Sciences.

Materials

The face stimuli consisted of images of five basic facial expressions (anger, fear, surprise, sadness, and disgust) posed by 10 models (5 males, 5 females) from the Ekman database (Ekman & Friesen, 1976). We excluded the happy expression because of its low confusability with other emotions. Fifty gray-scaled images were trimmed to 192×220 pixels, which measured 5.0×7.5 degrees of visual angle.

Based on the principle of combination, we created 10 pairs of face stimuli from the five expression types for each face model. In the similarity rating task, the face images within each emotion pair came from the same model to control the influence of identity. In the expression recognition task, 10 emotion pairs were presented in blocks with random presentation of 10 models within each block.

Based on the results of the similarity rating task, the pairs of face in the expression recognition task were classified into HC and LC conditions. The HC condition comprised of disgust-anger, fear-surprise, sadness-disgust, anger-sadness, and anger-fear, whereas the LC condition consisted of sadness-fear, fear-disgust, surprise-anger, surprise-sadness, and surprise-disgust. In addition to these face stimuli,

we also used five text labels (“anger”, “disgust”, “fear”, “sadness”, “surprise”) for the response screen in the expression recognition task.

Procedure

Similarity rating task. Pairs of face images were presented on the screen side by side simultaneously. Subjects were asked to judge the similarity degree of each pair and rate on a scale which ranged from 0 to 100 (from extremely different to extremely similar). The 100 pairs of face stimuli were shown randomly in a total of 100 trials (10 models \times 10 pairs), and each pair of images came from the same identity.

Facial expression recognition task with MEG recording. This part of the experiment followed the same study protocol described in Zhao, Zhao, Zhang, Cui, and Fu (2017), which was a modified version of Brief Affect Recognition Test (Ekman & Friesen, 1974). As Figure 1 illustrates, each trial began with a black central fixation cross presented against a neutral gray background for 200 ms. A blank screen was then presented from 300 to 500 ms. It is followed by a probe face for 100 ms. In order to accurately characterize the processing of the confusion effect, we set a 900 ms blank interval after the presentation of probe face. After the blank interval, a pair of text labels was shown on the screen, which exhibited the names of the two target expressions in that block. Subjects were instructed to perform a 2AFC task, in which they judged which facial expression label correctly described the emotion on the probe face. They were required to respond by pressing the key “1” for the first/left label or “2” for the second/right label. The response screen disappeared after the key

response. The correct answer for the left/right positions of the labels was counterbalanced. The inter-trial interval (ITI), lasting 1500-1800 ms, was inserted between two trials.

Each block tested a pair of facial expressions, and each trial only showed one emotional face. Figure 1 shows an example trial from the fear-surprise block, where a fearful face was presented. Half of the trials in this block presented fearful faces with this expression posed by the 10 models as the probe, and the remaining trials of the block presented faces with a surprised expression from the same models. The text labels were always “fear” and “surprise” in this block. The left-right position of the two labels was counterbalanced. The design amounted to 20 trials in each block, with 10 trials for each expression of a pair. This led to a total of 200 trials (10 blocks × 20 trials) in this task. The order of the 20 faces within each block was random. The order of 10 blocks for the 10 expression pairs was also randomized across subjects.

Data acquisition

MEG data were recorded with a 275-channel, axial-gradiometer SQUID-based sensory system (CTF MEG International Services LP, Coquitlam, British Columbia, Canada) at a sampling rate of 1200 Hz in a magnetically shielded and sound attenuated room in the Institute of Biophysics, Chinese Academy of Sciences. The head movement in relation to the MEG sensors was monitored continuously and

significant artefacts in a trial related to head motion were removed from subsequent analysis. After MEG recordings, each subject underwent anatomical MRI scans on a 3T GE scanner (Discovery MR750, GE Healthcare Systems, Milwaukee, WI) in the Institute of Psychology, Chinese Academy of Sciences to create individual head models. MEG data were co-registered with MRI structural images using the locations of the reference fiducial coil.

MEG pre-processing

MEG recordings were pre-processed using Brainstorm (Tadel et al., 2011), which is a collaborative tool developed with MATLAB and used for analyzing brain recordings. A co-registration of MRI data and MEG data was implemented with the digitization of head surface and reference points coils. Several trials containing additional bad segments like muscle noise and sensor artifacts were rejected by the function of detecting other artifacts in the Brainstorm software and visualizing all the trials before importing the epochs. At least 80 artifact-free epochs were averaged in each condition. Each epoch of the MEG recording was 3000 ms, with 1000 ms before the stimulus onset and 2000 ms after it. A delay of 32 ms was fixed in all the epochs.

MEG data evaluation

To compute the magnetic data and match it with the head shapes, we represented the subjects' folded cortical surfaces firstly by applying the overlapping sphere model (Huang, Mosher, & Leahy, 1999). We then estimated the distributed cortical

activations which determined the information collected by the sensors. The method of current density map and depth-weighted minimum norm imaging were used, which produced a linear L2- minimum norm estimate of current density, accompanying noise and source covariance matrices for compensation (Hämäläinen, Ilmoniemi, Engineering, & Computing, 1994).

For group analysis, sources of all the subjects were re-projected to the same source space using the Shepard's method. Continuous MEG data were band-passed at 0.5 to 40 Hz. Trials contaminated by eye blinks and movements were corrected using an independent component analysis (ICA) algorithm (Delorme & Makeig, 2004).

For each subject, epochs corresponding to either HC or LC condition were averaged, thus yielding two single-subject average waveforms (HC and LC), which were time-locked to the onset of each face image. Single-subject average waveforms were subsequently averaged to obtain group-level waveforms.

For each subject and each condition, we extracted the region of interest (ROI), according to the topographies (Figure 2) and the literature (Bernsterin & Yovel, 2015). These included FFA and pSTS in the right hemisphere. Each scout was set to 30-70 vertices, corresponding to 5-11 cm². The mean amplitude of the N170 (70 -140 ms) and LPP (200-1000 ms) were measured from the single-subject average waveforms (at pSTS and FFA regions), which were further compared between two experimental conditions (HC vs. LC) using a paired *t*-test.

To extract facial expression-elicited modulations of MEG oscillations on the time-frequency domain, the spectrograms were baseline-corrected (reference interval:

-300 to -200 ms relative to facial stimulus onset). The delta band rhythm (0.5-3 HZ) and theta band rhythm (4-8 HZ) were extracted for each subject from -1000 to 2000 ms. The spectrograms were then averaged based on the time and translated to a Z score based on a baseline (-300 to -200 ms). We then re-average the amplitudes of delta and theta band between two conditions, respectively. To maintain the same time window of M170 in the time domain analysis, we extracted the frequency values in the time window of 70 to 140 ms. Consistently with the component of LPP, we also extracted the frequency values in the time window of 200 to 1000 ms. For the delta and theta band rhythm, we conducted paired *t*-tests on two conditions separately.

Results

Results of the similarity rating task. Averaged rating score for each pair was shown in Table 1. The pairs were classified as HC and LC groups according to similarity scores. The degree of similarity in the HC condition ($M = 58.82$, $SE = 0.72$) was higher than for the LC condition ($M = 48.60$, $SE = 0.90$), $t(294) = 11.26$, $p < 0.001$.

Results of the expression recognition task. The indexes of sensitivity (d') were computed for each pair of facial expressions by subtracting the false alarm rate from the hit rate (Verde, Macmillan, & Rotello, 2006). Consistent with the similarity rating results, the discrimination index (d') was significantly lower for HC condition ($M = 3.91$, $SE = 0.32$) than for LC condition ($M = 5.94$, $SE = 0.38$), $t(14) = -5.58$, $p < 0.01$.

MEG results. Out of 17 subjects, 15 completed the study successfully. Two male subjects with head movements exceeding 0.5 cm in the MEG scan were excluded. For the components of M170 and LPP, we compared the mean amplitude between the two confusion conditions, respectively. For the M170 component in the FFA region, the grand averaged amplitudes were comparable between the HC ($M = -5.00$, $SE = 0.87$) and LC conditions ($M = -4.63$, $SE = 0.88$), $t = -2.00$, $p > 0.05$. The same was true for the M170 results in the pSTS region, where no difference was found between the HC ($M = -1.89$, $SE = 0.45$) and LC conditions ($M = -1.77$, $SE = 0.44$), $t = -0.89$, $p > 0.05$. These results suggest that the ventral and dorsal pathways are unable to discriminate the difference between the two conditions in the early processing stage. For the LPP component in the FFA region, the positive going amplitude was greater for LC ($M = -1.12$, $SE = 0.41$) than for HC condition ($M = -1.93$, $SE = 0.39$; $t = -5.00$, $p < 0.01$). The difference between the amplitudes of HC ($M = -0.48$, $SE = 0.24$) and LC ($M = -0.33$, $SE = 0.37$) in the pSTS region, however, did not reach the level of significance, $t = 0.88$, $p > 0.05$. These results suggest the ventral and dorsal pathways start to separate highly confusable expressions from more easily discriminable expressions at late processing stage.

The time-frequency results are shown in Figure 4. As for the delta rhythm in the time window of 70 to 140 ms, we found no difference between the amplitudes of HC ($M = 9.27$, $SE = 0.55$) and LC ($M = 9.56$, $SE = 0.59$) in the FFA region, $t = -1.42$, $p > 0.05$, neither a difference between the mean amplitudes of HC ($M = 10.77$, $SE = 0.21$) and LC ($M = 10.96$, $SE = 0.19$) in the pSTS region, $t = -0.93$, $p > 0.05$. As for the

theta rhythm, the mean amplitude from 70 to 140 ms in the FFA region showed no difference between HC ($M = 37.60$, $SE = 3.92$) and LC ($M = 37.23$, $SE = 3.92$), $t = 0.48$, $p > 0.05$. There was also no difference between the results of HC ($M = 36.44$, $SE = 2.07$) and LC ($M = 36.37$, $SE = 1.85$) in the pSTS region, $t = 0.05$, $p > 0.05$. Hence consistent with the time window of M170, the time frequency results on the delta rhythm also showed little processing of the visual information involved in confusable expressions in the ventral and dorsal pathways.

For the time window of LPP component, we also compared the grand averaged amplitude of delta and theta rhythm between two conditions. In the FFA region, the mean amplitude of delta rhythm from 200 to 1000 ms in the HC condition ($M = 5.14$, $SE = 2.08$) was lower than the LC condition ($M = 7.16$, $SE = 2.24$), $t = -2.15$, $p < 0.05$. However, in the pSTS region, no difference was found between the HC ($M = 10.26$, $SE = 1.54$) and LC ($M = 10.62$, $SE = 1.39$), $t = -0.46$, $p > 0.05$. For the theta rhythm in the FFA region, the mean amplitude of HC ($M = 4.63$, $SE = 1.43$) was comparable to LC ($M = 4.61$, $SE = 1.33$), $t = -0.46$, $p > 0.05$. Similar theta rhythm results were found in the pSTS region, where no difference was found between the HC ($M = 5.79$, $SE = 1.38$) and LC ($M = 7.55$, $SE = 2.90$) conditions, $t = -1.04$, $p > 0.05$.

To further examine whether the time domain results have a specific relationship with the delta rhythm rather than theta rhythm, we calculated the correlation efficient index in the time window of LPP at the FFA region. Results are plotted in Figure 5. The correlation between mean amplitudes of time domain and delta rhythm were 0.50, $p < 0.05$ for the HC condition, and 0.45, $p < 0.05$ for the LC condition. However, the

correlation between the mean amplitudes of time domain and theta rhythm was not significant for either for the HC or LC condition, all r 's < 0.30 , p 's > 0.05 .

Discussion

Our main interest in the present study was to uncover the neural mechanisms of the confusion effect in facial expression recognition. For both high confusion and low confusion conditions, M170 amplitude showed no difference in the FFA and the pSTS regions, while enhanced amplitude of LPP component was found in the FFA for low confusion condition rather than high confusion condition. Moreover, the delta rhythm (0.5-3Hz) was stronger in the FFA region for the low confusion condition than the high confusion condition, whilst no such difference was found in the pSTS region. Consistently, the grand averaged amplitude of LPP was positively correlated with the grand averaged amplitude of delta rhythm (0.5-3 Hz) in the FFA region.

M170/N170 is a negative occipito-temporal component maximally recorded in response to faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bentin & Deouell, 2000). It is regarded as the perceptual origin of the categorical perception effect of familiar facial identities (Campanella et al., 2000). Previous studies have found that the amplitude of M170/N170 could respond to perceptual characteristics including configured and integrated face processing (Jeffreys, 1996; Hinojosa, Mercado, Carretié, & Reviews, 2015; Itier, Latinus, & Taylor, 2006; Patrik Vuilleumier &

Pourtois, 2007). Our results demonstrated that the amplitude of M170 was the same between high and low confusion conditions at two brain regions of interest, which suggests that the M170 was not sensitive to the confusability dimension, and there was no difference in the processing of confusable facial expressions on the early perceptual encoding. In our study, we did not make a distinction among holistic processing, configured processing and featured processing (Beaudry et al., 2013; Bombari et al., 2013). Instead, the confusion effect of facial expression is what we are really interested in. Moreover, images used in each block coming from the same model control the influence of identity. Therefore, our results of M170 to some extent suggest that the confusability of different emotion categories occurs not in the early stage.

Another important component in processing emotional images, late positive potential, showed significant difference between high confusion and low confusion conditions. Larger amplitude of LPP was elicited in the LC condition than the HC condition in the FFA but not in the pSTS. It has been found that LPP might reflect an enhancement of top-down attention to the ongoing task (Margaret M. Bradley, 2009; M. M. Bradley & Lang, 2007; Carretié, Martín-Loeches, Hinojosa, & Mercado, 2001; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Schupp et al., 2000; Schupp et al., 2007). In the present study, the adoption of rapid facial expression recognition paradigm limited the time of viewing the images (100 ms), and it might be too hard to accomplish a complete processing, especially in a high confusion condition. Subjects needed to make a judgement of which emotion category the picture refers to, and

limited presentation time and confounding image in high confusion condition might drive them to jump into a decision, showing a lower level of LPP amplitude, leading to insufficient processing of facial expression.

Results of time frequency subsequently confirmed that the decreased LPP amplitude in high confusion condition could be attributed to the heavy cognitive load. The delta rhythm (0.5-3Hz) was stronger for the LC condition than the HC condition in the FFA region, whilst no difference was found in the pSTS region. It has been found that the activation level of the delta frequency is regulated by the cognitive load in several neurological disorders, such as schizophrenia (Bates, Kiehl, Laurens, & Liddle, 2009; Doege et al., 2010; Ergen, Marbach, Basar-Eroglu, & Demiralp, 2008; Ford, Roach, Hoffman, & Mathalon, 2008) and Alzheimer's disease (Güntekin, Saatçi, & Yener, 2008; Yener et al., 2012). Increased delta activity of Alzheimer's patients have been reported in the spontaneous EEG researches (Dierks et al., 1993; Huang et al., 2000; Jelic et al., 2000; Jeong, 2004; Babiloni et al., 2006, 2009). During cognitive tasks, delta response is also reduced in Alzheimer's disease (Yener et al., 2012; Güntekin et al., 2008; Caravaglios et al., 2008). Schmeichel et al (2014) proposed that cognitive load would distract attention away from the processing of emotional images and films in the presence versus absence of a concurrent cognitive task. In our study, more confusable emotion pairs (i.e. high confusion conditions) produce a larger cognitive load, leading to a reduction of delta rhythm. A strong correlation between the frequency domain and time domain results further confirmed these speculations. More confusable facial expression pairs lead to a heavier cognitive

load, accordingly demanding more decoding time and attentional resources involved. Due to the limited presentation time in each trial, high confusion pairs might not recruit enough attentional resources for complete processing in short time, leading to smaller LPP amplitude.

The differences of LPP component and delta rhythm between HC and LC were found only in the FFA region, but not in the pSTS region. These results were consistent with previous studies (Brooks et al., 2019; Harry, Williams, Davis, & Kim, 2013) which suggest the dominant role of FFA in the perception of emotional expressions. Because of excellent temporal and spatial resolution, MEG is particularly suited for investigating where and when the confusion effect occurs. Our clear-cut results confirmed that the dominant role of FFA in the processing facial similarity or confusability. Interestingly, we found that this discrepancy between high confusion and low confusion conditions occurs in the later stage but not in the early stage. As for the emotion recognition task itself, subjects were asked to perceive facial expressions and make judgments for each expression. This recognition process includes the stages of perception and concept extraction. The reduction of the LPP in the high confusion condition suggested that images presented in this condition may not have been encoded as well as images presented in the low confusion condition. This speculation echoed with some evidence in a recent study. Researchers used the representational similarity analysis to explore the relationship between the conceptual, perceptual, and neural computations of six facial expressions (Brooks, Chikazoe, Sadato, and Freeman, 2019). By a whole-brain searchlight and further region of

interest analyses, they found the representational dynamics in the right FFA region is corresponding to subject's prior conceptual knowledge about emotion. In other word, the FFA is involved in the processing of perceptual similarity, meanwhile, reflects the conceptual consistency. The LPP was also assumed to reflect a gateway to conscious recognition (Luck et al., 2000; Krancioch et al., 2003). Therefore, the results of our study to some extent reflected the idea that the shifting process from perceptual level to conceptual level locates in right FFA and this can be characterized by the LPP. What's more, our research revealed the neural responses of in the active processing of emotional contents on face, extending our understanding of brain activation in perceiving similarity facial expressions. Future researchers might determine whether the confusion effects were exactly engaged in the ventral rather the dorsal pathway. Further researchers should also enlarge the sample size to testify the gender difference underlie this effect.

Conclusion

The present study shows that: (1) the FFA area in the ventral road, rather than the pSTS in the dorsal pathway, plays an important role in characterizing the difference between confusable facial expressions; (2) the participation of the FFA in discriminating confusable facial expressions is in the late stage of facial expression

processing; (3) images of low confusion will induce a larger LPP amplitude and a stronger delta rhythm than that of high confusion, reflecting a higher efficiency in retrieving the concept of such facial expressions.

Figure Legends

Figure 1. An illustration of the facial expression recognition testing procedure.

Figure 2. Topographies of M170 and LPP for both of the LC and HC conditions. A shows the distributed topographies of M170 at 120 ms. B shows the distributed topographies of LPP at 300 ms. The blue circle highlight the regions of interest of FFA and pSTS.

Figure 3. Grand-averaged waveforms in both of the HC (blue line) and LC (red line) conditions. A and B demonstrate the waveforms for the FFA and pSTS regions, respectively.

Figure 4. The time frequency results in both of the HC (blue line) and LC (red line) conditions. A and B demonstrate the grand averaged waveforms for delta rhythm (0.5-3Hz) in the FFA and pSTS regions, respectively. C and D demonstrates the grand averaged waveforms for theta rhythm (4-8Hz) in the FFA and pSTS regions, respectively.

Figure 5. The relationships between the results of time domain and time-frequency domain in the FFA region. A and B depict the correlation results between time series and delta rhythm in the HC and LC condition, respectively.

Reference

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends in Cognitive Sciences*, 4(7), 267-278.

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- Babiloni, C., Pievani, M., Vecchio, F., Geroldi, C., Eusebi, F., Fracassi, C., . . . Frisoni, G. B. (2009). White-matter lesions along the cholinergic tracts are related to cortical sources of EEG rhythms in amnesic mild cognitive impairment. *Human Brain Mapping, 30*(5), 1431-1443.
- Baillet, S. (2017). Magnetoencephalography for brain electrophysiology and imaging. *Nature neuroscience, 20*(3), 327.
- Bates, A. T., Kiehl, K. A., Laurens, K. R., & Liddle, P. F. (2009). Low-frequency EEG oscillations associated with information processing in schizophrenia. *Schizophrenia research, 115*(2-3), 222-230.
- Beaudry, O., Roy-Charland, A., Perron, M., Cormier, I., & Tapp, R. (2014). Featural processing in recognition of emotional facial expressions. *Cognition and Emotion, 28*(3), 416-432.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological Studies of Face Perception in Humans. *Journal of Cognitive Neuroscience, 8*(6), 551-565.
- Bentin, S., & Deouell, L. Y. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology, 17*(1-3), 35-54.
- Bombari, D., Schmid, P. C., Schmid Mast, M., Birri, S., Mast, F. W., & Lobmaier, J. S. (2013). Emotion recognition: The role of featural and configural face information. *The Quarterly Journal of Experimental Psychology, 66*(12), 2426-2442.
- Bradley, M. M. (2009). Natural selective attention: Orienting and emotion. *Psychophysiology, 46*(1), 1-11.
- Bradley, M. M., & Lang, P. J. (2007). The International Affective Picture System (IAPS) in the study of emotion and attention. *Handbook of Emotion Elicitation and Assessment, 29-46*.
- Brooks, J. A., Chikazoe, J., Sadato, N., & Freeman, J. B. (2019). The neural representation of facial-emotion categories reflects conceptual structure. *Proceedings of the National Academy of Sciences, 116*(32), 15861-15870.
- Bruce, V., & Young, A. (1986). Understanding face recognition. *British journal of psychology, 77*(3), 305-327.
- Campanella, S., Hanoteau, C., Dépy, D., Rossion, B., Bruyer, R., Crommelinck, M., & Guérit, J. M. (2000). Right N170 modulation in a face discrimination task: An account for categorical perception of familiar faces. *Psychophysiology, 37*(6), 796-806.
- Camras, L. A. (1980). Children's understanding of facial expressions used during conflict encounters. *Child Development, 879-885*.
- Caravaglios, G., Costanzo, E., Palermo, F., & Muscoso, E. G. (2008). Decreased amplitude of auditory event-related delta responses in Alzheimer's disease. *International Journal of Psychophysiology, 70*(1), 23-32.
- Carretié, L., Martín-Loeches, M., Hinojosa, J. A., & Mercado, F. (2001). Emotion and attention interaction studied through event-related potentials. *Journal of cognitive neuroscience, 13*(8), 1109-1128.

-
- Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. (2000). Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. *Biological psychology*, *52*(2), 95-111.
- Darwin, C., & Prodger, P. (1998). *The expression of the emotions in man and animals*. Oxford University Press, USA.
- Pitcher, D. (2014). Facial expression recognition takes longer in the posterior superior temporal sulcus than in the occipital face area. *Journal of Neuroscience*, *34*(27), 9173-9177.
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of neuroscience methods*, *134*(1), 9-21.
- Dierks, T., Ihl, R., Frölich, L., & Maurer, K. (1993). Dementia of the alzheimer type: Effects on the spontaneous EEG described by dipole sources. *Psychiatry Research: Neuroimaging*, *50*(3), 151-162.
- Doegge, K., Kumar, M., Bates, A. T., Das, D., Boks, M. P. M., & Liddle, P. F. (2010). Time and frequency domain event-related electrical activity associated with response control in schizophrenia. *Clinical Neurophysiology*, *121*(10), 1760-1771.
- Dolan, R. J., Fletcher, P., Morris, J., Kapur, N., Deakin, J. F. W., & Frith, C. D. (1996). Neural activation during covert processing of positive emotional facial expressions. *Neuroimage*, *4*(3), 194-200.
- Ekman, P., & Friesen, W. V. (1986). A new pan-cultural facial expression of emotion. *Motivation and emotion*, *10*(2), 159-168.
- Ekman, P., & Friesen, W. V. (1971). Constants across cultures in the face and emotion. *Journal of personality and social psychology*, *17*(2), 124.
- Ekman, P., & Friesen, W. V. (1976). Measuring facial movement. *Environmental psychology and nonverbal behavior*, *1*(1), 56-75.
- Ekman, P., & Friesen, W. V. (1974). Detecting deception from the body or face. *Journal of personality and Social Psychology*, *29*(3), 288.
- Elfenbein, H. A., Mandal, M. K., Ambady, N., Harizuka, S., & Kumar, S. (2002). Cross-cultural patterns in emotion recognition: highlighting design and analytical techniques. *Emotion*, *2*(1), 75.
- Ergen, M., Marbach, S., Brand, A., Başar-Eroğlu, C., & Demiralp, T. (2008). P3 and delta band responses in visual oddball paradigm in schizophrenia. *Neuroscience letters*, *440*(3), 304-308.
- Ford, J. M., Roach, B. J., Hoffman, R. S., & Mathalon, D. H. (2008). The dependence of P300 amplitude on gamma synchrony breaks down in schizophrenia. *Brain research*, *1235*, 133-142.
- Fox, C. J., Hanif, H. M., Iaria, G., Duchaine, B. C., & Barton, J. J. (2011). Perceptual and anatomic patterns of selective deficits in facial identity and expression processing. *Neuropsychologia*, *49*(12), 3188-3200.
- Gagnon, M., Gosselin, P., Hudon-ven Der Buhs, I., Larocque, K., & Milliard, K. (2010). Children's recognition and discrimination of fear and disgust facial expressions. *Journal of Nonverbal Behavior*, *34*(1), 27-42.

-
- 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*(11), 1645-1654.
- Gosselin, P., & Simard, J. (1999). Children's knowledge of facial expressions of emotions: Distinguishing fear and surprise. *The Journal of genetic psychology*, *160*(2), 181-193.
- Güntekin, B., Saatçi, E., & Yener, G. (2008). Decrease of evoked delta, theta and alpha coherences in Alzheimer patients during a visual oddball paradigm. *Brain Research*, *1235*, 109-116.
- Hämäläinen, M. S., & Ilmoniemi, R. J. (1994). Interpreting magnetic fields of the brain: minimum norm estimates. *Medical & biological engineering & computing*, *32*(1), 35-42.
- Harry, B. B., Williams, M., Davis, C., & Kim, J. (2013). Emotional expressions evoke a differential response in the fusiform face area. *Frontiers in human neuroscience*, *7*, 692.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in cognitive sciences*, *4*(6), 223-233.
- Hinojosa, J. A., Mercado, F., & Carretié, L. (2015). N170 sensitivity to facial expression: A meta-analysis. *Neuroscience & Biobehavioral Reviews*, *55*, 498-509.
- Kawasaki, H., Tsuchiya, N., Kovach, C. K., Nourski, K. V., Oya, H., Howard, M. A., & Adolphs, R. (2012). Processing of facial emotion in the human fusiform gyrus. *Journal of cognitive neuroscience*, *24*(6), 1358-1370.
- 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*(1), 80.
- Hogan, M. J., Swanwick, G. R. J., Kaiser, J., Rowan, M., & Lawlor, B. (2003). Memory-related EEG power and coherence reductions in mild Alzheimer's disease. *International Journal of Psychophysiology*, *49*(2), 147-163.
- Huang, C., Wahlund, L. O., Dierks, T., Julin, P., Winblad, B., & Jelic, V. (2000). Discrimination of Alzheimer's disease and mild cognitive impairment by equivalent EEG sources: a cross-sectional and longitudinal study. *Clinical Neurophysiology*, *111*(11), 1961-1967.
- Huang, M. X., Mosher, J. C., & Leahy, R. M. (1999). A sensor-weighted overlapping-sphere head model and exhaustive head model comparison for MEG. *Physics in Medicine & Biology*, *44*(2), 423.
- Itier, R. J., Latinus, M., & Taylor, M. J. (2006). Face, eye and object early processing: What is the face specificity? *NeuroImage*, *29*(2), 667-676.
- Izard, C. E. (1994). Innate and universal facial expressions: evidence from developmental and cross-cultural research. *Psychol Bull*, *115*(2), 288-299.
- Jack, R. E., Blais, C., Scheepers, C., Schyns, P. G., & Caldara, R. (2009). Cultural Confusions Show that Facial Expressions Are Not Universal. *Current Biology*, *19*(18), 1543-1548.
- Jeffreys, D. A. (1996). Evoked Potential Studies of Face and Object Processing.

-
- Visual Cognition*, 3(1), 1-38.
- Jelic, V., Johansson, S. E., Almkvist, O., Shigeta, M., Julin, P., Nordberg, A., . . . Wahlund, L. O. (2000). Quantitative electroencephalography in mild cognitive impairment: longitudinal changes and possible prediction of Alzheimer's disease. *Neurobiology of Aging*, 21(4), 533-540.
- Kawasaki, H., Tsuchiya, N., Kovach, C. K., Nourski, K. V., Oya, H., Howard, M. A., & Adolphs, R. (2012). Processing of facial emotion in the human fusiform gyrus. *Journal of cognitive neuroscience*, 24(6), 1358-1370.
- Kessels, R. P. C., Montagne, B., Hendriks, A. W., Perrett, D. I., & de Haan, E. H. F. (2014). Assessment of perception of morphed facial expressions using the Emotion Recognition Task: Normative data from healthy participants aged 8–75. *Journal of Neuropsychology*, 8(1), 75-93.
- Kranczioch, C., Debener, S., & Engel, A. K. (2003). Event-related potential correlates of the attentional blink phenomenon. *Cognitive Brain Research*, 17(1), 177-187.
- Luck, S. J., & Hillyard, S. A. (2000). The operation of selective attention at multiple stages of processing: Evidence from human and monkey electrophysiology. *The new cognitive neurosciences*, 687-700.
- Pessoa, L., Japee, S., Sturman, D., & Ungerleider, L. G. (2005). Target visibility and visual awareness modulate amygdala responses to fearful faces. *Cerebral cortex*, 16(3), 366-375.
- Manera, V., Del Giudice, M., Grandi, E., & Colle, L. (2011). Individual differences in the recognition of enjoyment smiles: No role for perceptual-attentional factors and autistic-like traits. *Frontiers in psychology*, 2, 143.
- Matsumoto, D., & Hwang, H. S. (2011). Judgments of facial expressions of emotion in profile. *Emotion*, 11(5), 1223-1229.
- Matsumoto, D. (1992). American-Japanese cultural differences in the recognition of universal facial expressions. *Journal of cross-cultural psychology*, 23(1), 72-84.
- 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(44), 17435-17443.
- Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. *Proceedings of the National Academy of Sciences*, 99(17), 11458-11463.
- Pujol, J., Harrison, B. J., Ortiz, H., Deus, J., Soriano-Mas, C., López-Solà, M., ... & Cardoner, N. (2009). Influence of the fusiform gyrus on amygdala response to emotional faces in the non-clinical range of social anxiety. *Psychological Medicine*, 39(7), 1177-1187.
- Russell, J. A., & Bullock, M. (1986). On the dimensions preschoolers use to interpret facial expressions of emotion. *Developmental Psychology*, 22(1), 97-102.
- Russell, J. A., & Bullock, M. (1985). Multidimensional scaling of emotional facial expressions: similarity from preschoolers to adults. *Journal of Personality and Social Psychology*, 48(5), 1290.

-
- Said, C. P., Moore, C. D., Engell, A. D., Todorov, A., & Haxby, J. V. (2010a). Distributed representations of dynamic facial expressions in the superior temporal sulcus. *Journal of Vision*, *10*(5), 11-11.
- Said, C., Moore, C., Norman, K., Haxby, J., & Todorov, A. (2010b). Graded representations of emotional expressions in the left superior temporal sulcus. *Journal of Vision*, *10*(6), 11-11.
- Schmeichel, B. J., & Tang, D. (2014). The relationship between individual differences in executive functioning and emotion regulation: A comprehensive review. *The control within: Motivation and its regulation*, 133-152.
- Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Cacioppo, J. T., Ito, T., & Lang, P. J. (2000). Affective picture processing: the late positive potential is modulated by motivational relevance. *Psychophysiology*, *37*(2), 257-261.
- Schupp, H. T., Flaisch, T., Stockburger, J., & Junghöfer, M. (2006). Emotion and attention: event-related brain potential studies. In S. Anders, G. Ende, M. Junghofer, J. Kissler, & D. Wildgruber (Eds.), *Progress in Brain Research* (Vol. 156, pp. 31-51).
- Schupp, H. T., Stockburger, J., Codispoti, M., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2007). Selective visual attention to emotion. *Journal of neuroscience*, *27*(5), 1082-1089.
- Sormaz, M., Watson, D. M., Smith, W. A. P., Young, A. W., & Andrews, T. J. (2016). Modelling the perceptual similarity of facial expressions from image statistics and neural responses. *NeuroImage*, *129*, 64-71.
- Surguladze, S. A., Brammer, M. J., Young, A. W., Andrew, C., Travis, M. J., Williams, S. C., & Phillips, M. L. (2003). A preferential increase in the extrastriate response to signals of danger. *Neuroimage*, *19*(4), 1317-1328.
- Tadel, F., Baillet, S., Mosher, J. C., Pantazis, D., & Leahy, R. M. (2011). Brainstorm: a user-friendly application for MEG/EEG analysis. *Computational intelligence and neuroscience*, *2011*, 8.
- Tracy, J. L., & Robins, R. W. (2008). The automaticity of emotion recognition. *Emotion*, *8*(1), 81-95.
- Vassallo, S., Cooper, S. L., & Douglas, J. M. (2009). Visual scanning in the recognition of facial affect: Is there an observer sex difference?. *Journal of Vision*, *9*(3), 11-11.
- Verde, M. F., Macmillan, N. A., & Rotello, C. M. (2006). Measures of sensitivity based on a single hit rate and false alarm rate: The accuracy, precision, and robustness of d' , A_z , and A' . *Perception & psychophysics*, *68*(4), 643-654.
- 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*(3), 829-841.
- Vuilleumier, P., & Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging. *Neuropsychologia*, *45*(1), 174-194.
- Winston, J. S., O'doherty, J., & Dolan, R. J. (2003). Common and distinct neural

-
- responses during direct and incidental processing of multiple facial emotions. *Neuroimage*, 20(1), 84-97.
- Yener, G. G., Güntekin, B., Örken, D. N., Tülay, E., Forta, H., & Başar, E. (2012). Auditory delta event-related oscillatory responses are decreased in Alzheimer's disease. *Behavioural Neurology*, 25(1), 3-11.
- Young, A. W., Newcombe, F., Haan, E. H. D., Small, M., & Hay, D. C. (1993). Face perception after brain injury: Selective impairments affecting identity and expression. *Brain*, 116(4), 941-959.
- Zhao, K., Yan, W.-J., Chen, Y.-H., Zuo, X.-N., & Fu, X. (2013). Amygdala Volume Predicts Inter-Individual Differences in Fearful Face Recognition. *PLOS ONE*, 8(8), e74096.
- Zhao, K., Zhao, J., Zhang, M., Cui, Q., & Fu, X. (2017). Neural responses to rapid facial expressions of fear and surprise. *Frontiers in psychology*, 8, 761.
- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends in Cognitive Sciences*, 4(7), 267-278. doi:[https://doi.org/10.1016/S1364-6613\(00\)01501-1](https://doi.org/10.1016/S1364-6613(00)01501-1)
- Baillet, S. (2017). Magnetoencephalography for brain electrophysiology and imaging. *Nat Neurosci*, 20(3), 327-339. doi:10.1038/nn.4504
- Bates, A. T., Kiehl, K. A., Laurens, K. R., & Liddle, P. F. J. S. R. (2009). Low-frequency EEG oscillations associated with information processing in schizophrenia. *115*(2-3), 222-230.
- Beaudry, O., Roy-Charland, A., Perron, M., Cormier, I., & Tapp, R. (2014). Featural processing in recognition of emotional facial expressions. *Cognition and Emotion*, 28(3), 416-432. doi:10.1080/02699931.2013.833500
- Bradley, M. M. (2009). Natural selective attention: Orienting and emotion. *46*(1), 1-11. doi:10.1111/j.1469-8986.2008.00702.x
- Bradley, M. M., & Lang, P. J. (2007). The International Affective Picture System (IAPS) in the study of emotion and attention. *Handbook of Emotion Elicitation and Assessment*, 29-46.
- Brooks, J., Chikazoe, J., Sadato, N., & Freeman, J. (2019). The neural representation of facial-emotion categories reflects conceptual structure. *Proceedings of the National Academy of Sciences*, 116, 201816408. doi:10.1073/pnas.1816408116
- Bruce, V., & Young, A. J. B. J. o. P. (2011). Understanding face recognition. *77*(3), 305-327.
- Camras, L. A. J. C. D. (1980). Children's Understanding of Facial Expressions Used during Conflict Encounters. *51*(3), 879-885.
- Carretié, L., Martín-Loeches, M., Hinojosa, J. A., & Mercado, F. (2001). Emotion and attention interaction studied through event-related potentials. *13*(8), 1109.
- Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. J. B. P. (2000). Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. *52*(2), 95-111.

-
- Darwin, C. J. T. J. o. N., & Disease, M. (1978). The Expression of The Emotions in Man and Animals. *123*(1), 90.
- Delorme, A., & Makeig, S. J. J. N. M. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *134*(1), 9-21.
- Doege, K., Kumar, M., Bates, A. T., Das, D., Boks, M. P. M., & Liddle, P. F. J. C. N. (2010). Time and frequency domain event-related electrical activity associated with response control in schizophrenia. *121*(10), 1760-1771.
- Dolan, R. J., Fletcher, P., Morris, J., Kapur, N., Deakin, J. F. W., & Frith, C. D. J. N. (1996). Neural Activation during Covert Processing of Positive Emotional Facial Expressions. *4*(3 Pt 1), 194.
- Ekman, & Friesen, W. V., %J J Pers Soc Psychol. (1971). Constants across cultures in the face and emotion. *17*(2), 124-129.
- Ekman, & Friesen, W. V. J. J. o. p. S. P. (1974). Detecting deception from the body or face. *29*(3), 288.
- Ekman, Friesen, W. V. J. M., & Emotion. (1986). A new pan-cultural facial expression of emotion. *10*(2), 159-168. doi:10.1007/bf00992253
- Elfenbein, H. A., Mandal, M. K., Ambady, N., Harizuka, S., & Kumar, S. J. E. (2002). Cross-cultural patterns in emotion recognition: highlighting design and analytical techniques. *2*(1), 75.
- Ergen, M., Marbach, S., A, Basar-Eroglu, C., & Demiralp, T. J. N. L. (2008). P3 and delta band responses in visual oddball paradigm in schizophrenia. *440*(3), 304-308.
- Ford, J. M., Roach, B. J., Hoffman, R. S., & Mathalon, D. H. J. B. R. (2008). The dependence of P300 amplitude on gamma synchrony breaks down in schizophrenia. *1235*(none), 133-142.
- Gagnon, M., Gosselin, P., Hudon-ven der Buhs, I., Larocque, K., & Milliard, K. J. J. o. N. B. (2010). Children's Recognition and Discrimination of Fear and Disgust Facial Expressions. *34*(1), 27-42. doi:10.1007/s10919-009-0076-z
- Ganel, T., Valyear, K. F., Goshen-Gottstein, Y., & Goodale, M. A. J. N. (2005). The involvement of the "fusiform face area" in processing facial expression. *43*(11), 1645-1654.
- Gosselin, P., & Simard, J. J. J. o. G. P. (1999). Children's Knowledge of Facial Expressions of Emotions: Distinguishing Fear and Surprise. *160*(2), 181-193.
- Güntekin, B., Saatçi, E., & Yener, G. (2008). Decrease of evoked delta, theta and alpha coherences in Alzheimer patients during a visual oddball paradigm. *Brain Research*, *1235*, 109-116. doi:https://doi.org/10.1016/j.brainres.2008.06.028
- Hämäläinen, M. S., Ilmoniemi, R. J. J. M., Engineering, B., & Computing. (1994). Interpreting magnetic fields of the brain: minimum norm estimates. *32*(1), 35-42.
- Haxby, Hoffman, E. A., & Gobbini, M. I. J. T. i. C. S. (2000). The distributed human neural system for face perception. *4*(6), 223-233.
- Hiroto, K., Naotsugu, T., Kovach, C. K., Nourski, K. V., Hiroyuki, O., Howard, M. A.,

-
- & Ralph, A. J. J. o. C. N. (2012). Processing of facial emotion in the human fusiform gyrus. *24*(6), 1358-1370.
- Hoffman, E. A., & Haxby, J. V., %J Nature Neuroscience. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *3*(1), 80-84.
- Huang, M., Mosher, J. C., & Leahy, R. J. P. i. M. B. (1999). A sensor-weighted overlapping-sphere head model and exhaustive head model comparison for MEG. *44*(2), 423.
- Izard, C. E. (1994). Innate and universal facial expressions: evidence from developmental and cross-cultural research. *Psychol Bull*, *115*(2), 288-299. doi:10.1037/0033-2909.115.2.288
- Jack, R. E., Blais, C., Scheepers, C., Schyns, P. G., & Caldara, R. (2009). Cultural Confusions Show that Facial Expressions Are Not Universal. *Current Biology*, *19*(18), 1543-1548. doi:https://doi.org/10.1016/j.cub.2009.07.051
- Kawasaki, H., Tsuchiya, N., Kovach, C. K., Nourski, K. V., Oya, H., Howard, M. A., & Adolphs, R. (2012). Processing of Facial Emotion in the Human Fusiform Gyrus. *24*(6), 1358-1370. doi:10.1162/jocn_a_00175 %M 22185494
- Luiz, P., Shruti, J., David, S., & Ungerleider, L. G., %J Cerebral Cortex. (2006). Target visibility and visual awareness modulate amygdala responses to fearful faces. *16*(3), 366-375.
- Manera, V., Del, G. M., Grandi, E., & Colle, L. J. F. i. P. (2011). Individual Differences in the Recognition of Enjoyment Smiles: No Role for Perceptual-Attentional Factors and Autistic-Like Traits. *2*(4), 143.
- Matsumoto, D., & Hwang, H. S. (2011). Judgments of facial expressions of emotion in profile. *Emotion*, *11*(5), 1223-1229. doi:10.1037/a0024356
- Matsumoto, D. J. J. o. C.-C. P. (1992). American-Japanese Cultural Differences in the Recognition of Universal Facial Expressions. *23*(1), 72-84.
- Nicholas, F., Henson, R. N., Friston, K. J., & Calder, A. J., %J Journal of Neuroscience. (2013). Top-down control of visual responses to fear by the amygdala. *33*(44), 17435-17443.
- Pessoa, L., Mckenna, M., Gutierrez, E., & Ungerleider, L. G. J. P. N. A. S. U. S. A. (2002). Neural Processing of Emotional Faces Requires Attention. *99*(17), 11458-11463.
- Pujol, J., ., Harrison, B. J., Ortiz, H., ., Deus, J., ., Soriano-Mas, C., ., López-Solà, M., ., . . . Cardoner, N., . %J Psychological Medicine. (2009). Influence of the fusiform gyrus on amygdala response to emotional faces in the non-clinical range of social anxiety. *39*(7), 1177-1187.
- Russell, J. A., & Bullock, M. (1986). On the dimensions preschoolers use to interpret facial expressions of emotion. *Developmental Psychology*, *22*(1), 97-102. doi:10.1037/0012-1649.22.1.97
- Russell, J. A., Bullock, M. J. J. o. P., & Psychology, S. (1985). Multidimensional Scaling of Emotional Facial Expressions. Similarity From Preschoolers to Adults. *48*(5), 1290-1298.
- Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Cacioppo, J. T., Ito, T., & Lang, P. J.

-
- (2000). Affective picture processing: the late positive potential is modulated by motivational relevance. *Psychophysiology*, 37(2), 257-261. doi:10.1017/s0048577200001530
- Schupp, H. T., Jessica, S., Maurizio, C., Markus, J. F., Weike, A. I., & Hamm, A. O., %J Journal of Neuroscience. (2007). Selective visual attention to emotion. 27(5), 1082-1089.
- Surguladze, S. A., Brammer, M. J., Young, A. W., Andrew, C., Travis, M. J., Williams, S. C. R., & Phillips, M. L. J. N. (2003). A preferential increase in the extrastriate response to signals of danger. *19(4)*, 1317-1328.
- Tadel, F., Baillet, S., Mosher, J. C., Pantazis, D., Leahy, R. M. J. C. I., & Neuroscience. (2011). Brainstorm: a user-friendly application for MEG/EEG analysis. *2011(2011)*, 879716.
- Tracy, J. L., & Robins, R. W. (2008). The automaticity of emotion recognition. *Emotion*, 8(1), 81-95. doi:10.1037/1528-3542.8.1.81
- Vassallo, S., Cooper, S. L., & Douglas, J. M. (2009). Visual scanning in the recognition of facial affect: is there an observer sex difference? *J Vis*, 9(3), 11.11-10. doi:10.1167/9.3.11
- Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. J. N. (2001). Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *30(3)*, 0-841.
- Winston, J. S., O'Doherty, J., & Dolan, R. J. J. N. (2003). Common and distinct neural responses during direct and incidental processing of multiple facial emotions. *20(1)*, 84-97.
- Yener, G. G., Güntekin, B., DN, Ö., Tülay, E., Forta, H., & Başar, E. J. B. N. (2012). Auditory delta event-related oscillatory responses are decreased in Alzheimer's disease. *25(1)*, 3-11.
- Young, A. W., Newcombe, F., de Haan, E. H., Small, M., & Hay, D. C. J. B. A. J. o. N. (1993). Face perception after brain injury. Selective impairments affecting identity and expression. *116 (Pt 4)(3)*, 941.
- Zhao, K., Yan, W.-J., Chen, Y.-H., Zuo, X.-N., & Fu, X. (2013). Amygdala Volume Predicts Inter-Individual Differences in Fearful Face Recognition. *PLOS ONE*, 8(8), e74096. doi:10.1371/journal.pone.0074096
- Zhao, K., Zhao, J., Zhang, M., Cui, Q., & Fu, X. J. F. i. P. (2017). Neural Responses to Rapid Facial Expressions of Fear and Surprise. *8*, 1-8.