

**THE CONNECTION BETWEEN TRAIT ANXIETY AND THE
PROCESSING OF EMOTIONAL FACIAL EXPRESSIONS**
- An ERF study

Jonna Luopa & Teemu Rossi
Pro gradu
Department of Psychology
University of Jyväskylä
October 2019

UNIVERSITY OF JYVÄSKYLÄ

Department of Psychology

LUOPA, JONNA & ROSSI, TEEMU: The connection between trait anxiety and the processing of emotional facial expressions: An ERF study

Pro gradu, 38 p.

Supervisor: Tiina Parviainen

Psychology

October 2019

The aim of this study was first to investigate whether different negative and neutral facial expressions are processed differently and second to investigate whether trait anxiety affects this processing. 14 men, aged 20–54 years, viewed pictures of different negative and neutral facial expressions during a measurement of brain electric activation with MEG. The pictures were taken from the Karolinska Directed Emotional Faces (KDEF) set. After a random number of pictures, the participants were asked to identify the emotion the face was expressing by pressing a corresponding button. Trait anxiety was measured with Karolinska Scales of Personality (KSP) inventory. Occipital and parietal areas on three time-windows were chosen for further analysis. Peaks of activation were found in time-windows roughly corresponding to the M100, M170, EPN, VPP, M220 and the M300 or the LPP that have been used in previous studies. In the statistical analysis, only the M220 response was stronger to afraid faces compared to sad faces. In addition, the M220 response was stronger to afraid faces compared to neutral and angry faces but only on the right hemisphere. However, these effects were only approaching significance. No other differences between emotional and neutral expressions were found. Trait anxiety correlated positively with the strength of the M170, VPP and the M300 or the LPP responses to either emotional or neutral facial expressions, or both. Our study thus suggests that the evoked responses measured from the visual areas were not sensitive to different negative emotional expressions, and trait anxiety is associated with an early threat processing bias, enhanced structural encoding of the face and enhanced conscious processing of the face.

Keywords: trait anxiety, emotional face processing, MEG, ERF

Tutkimuksen tarkoituksena oli ensiksi selvittää, prosessoidaanko erilaisia negatiivisia sekä neutraaleja kasvonilmeitä eri tavalla, sekä toiseksi selvittää, vaikuttaako piirreahdistuneisuus tähän prosessointiin. 14 miehelle, iältään 20–54 vuotta, näytettiin MEG-laitteella tehdyn aivojen sähköisen aktivaation mittauksen aikana kuvia neutraaleista sekä erilaisista negatiivisista kasvonilmeistä. Kuvat otettiin Karolinska Directed Emotional Faces (KDEF) kuvapankista. Aina kun kuvia oli näytetty satunnainen määrä, osallistujia pyydettiin tunnistamaan kasvonilmeiden tunnetila painamalla tunnetilaa vastaavaa nappia ohjaimesta. Piirreahdistuneisuutta mitattiin Karolinska Scales of Personality (KSP) inventaariolla. Takaraivo- ja päälakilohkot valittiin tarkempaan tarkasteluun kolmessa eri aikaikkunassa. Aktivaatiohuiput kyseisissä aikaikkunoissa voisivat vastata herätepotentiaaleja M100, M170, EPN, VPP, M220 ja M300 tai LPP, joita on käytetty aiemmissa tutkimuksissa. Tilastollisissa analyyseissa vain M220-vaste oli voimakkaampi pelokkaiisiin ilmeisiin verrattuna surullisiin ilmeisiin. Lisäksi, M220-vaste oli voimakkaampi pelokkaiisiin ilmeisiin

verrattuna neutraaleihin sekä vihaisiin ilmeisiin, mutta vain oikeassa aivopuoliskossa. Nämä tulokset olivat kuitenkin ainoastaan suuntaa antavia. Muita eroja neutraalien sekä tunnepitoisten kasvonilmeiden välillä ei löytynyt. Piirreahdistuneisuus korreloi positiivisesti tunnepitoisten, neutraalien tai kaikkien kasvonilmeiden aiheuttamien M170-, VPP- ja M300- tai LPP-vasteiden voimakkuuden kanssa. Tutkimuksemme viittaa siihen, että visuaalisilta alueilta mitatut herätevasteet eivät ole sensitiivisiä eri negatiivisten tunnetilojen kasvonilmeille, ja että piirreahdistuneisuus on yhteydessä tehokkaampaan varhaiseen uhan prosessointiin, tehokkaampaan kasvojen rakenteelliseen prosessointiin sekä tehokkaampaan kasvojen tietoiseen prosessointiin.

Avainsanat: piirreahdistuneisuus, tunnepitoisten kasvonilmeiden prosessointi, MEG, ERF

TABLE OF CONTENTS

INTRODUCTION	1
Trait Anxiety and Negative Social Bias	2
Processing of Emotional Face Expressions.....	3
Trait Anxiety and Emotional Face Processing	7
Research Questions.....	10
METHODS.....	10
Participants.....	10
Magnetoencephalography (MEG).....	11
Procedure and Stimuli	12
Personality tests.....	14
Data analysis	15
RESULTS.....	19
Occipital area.....	19
Parietal area.....	19
DISCUSSION	21
Emotional face processing in the brain	21
Trait anxiety and emotional face processing	23
Limitations and Future Research Directions.....	26
Conclusion.....	27
REFERENCES:	27

INTRODUCTION

Anxiety is a common response to stressful situations. Because most of us experience varying degrees of anxiety in our daily lives, anxiety is not necessarily considered pathological. The symptoms of anxiety are diverse and can be divided into four different facets: physiological, cognitive, behavioral and emotional facets (Nolen-Hoeksema et al., 2009). According to Lönnqvist, Marttunen, Henriksson, Partonen, & Seppälä (2017) and Nolen-Hoeksema et al. (2009), physiological effects of anxiety include the typical “fight-or-flight” reactions including increased heart rate, blood pressure and muscle tension. Lönnqvist et al. and Nolen-Hoeksema et al. continue that the cognitive effects of anxiety usually include disproportionate fear of various subjective matters. For the behavioral effects, the same authors found that freezing and avoidance of anxiety-inducing matters are typical for anxiety. Deeply connected in the cognitive processes, the emotional effects of anxiety include the sense of dread, panic and terror (Lönnqvist et al., 2017; Nolen-Hoeksema et al., 2009). This kind of description of anxiety as an acute response to certain situations is common, and it describes the state of anxiety, also known as state anxiety (Endler & Okada, 1975). Anxiety can also be conceptualized as a personality trait known as trait anxiety, which can be understood as a vulnerability factor for state anxiety (Endler, Parker, Bagby, & Cox, 1991; af Klinteberg, Magnusson, & Schalling, 1986).

Facial expressions are important to social communication. They are produced by facial muscles that are controlled both automatically and voluntarily (Adolphs, 2002b). There are six different basic emotions that have their own unique facial expressions: happiness, fear, anger, sadness, surprise and disgust (Ekman & Friesen, 1971). These emotions are universally recognized (Ekman & Friesen, 1971).

Many psychiatric disorders are associated with poorer facial emotion recognition (e.g. Demenescu, Kortekaas, den Boer, & Aleman, 2010) which raises a question whether trait anxiety is likewise associated with distinct facial emotion recognition. Since trait anxiety has also been associated with attentional bias to threatening facial expressions (Mathews & MacLeod, 2005), it would be interesting to examine whether trait anxiety has any role in the brain-level processing of emotional faces.

To our knowledge, there are not many previous studies examining this subject. In addition, all the previous studies have used EEG (electroencephalography) as the brain activity measuring technique. MEG (magnetoencephalography) measures the magnetic field changes produced by brain activity from the scalp (Proudfoot, Woolrich, Nobre, & Turner, 2014) and although EEG and MEG both have an excellent temporal resolution, MEG has a better spatial resolution because magnetic fields are not as easily disturbed by the skull and the scalp as electric fields (in EEG) are (Baillet, 2017). Thus,

MEG was used in this study. The aim of this study is to bring coherence and diversity to the existing research concerning the connection between trait anxiety and emotional face processing.

Trait Anxiety and Negative Social Bias

The distinction between state and trait anxiety traces to the time before the Common Era (BCE), where Cicero distinguished between the two dimensions of anxiety (Endler, Magnusson, Ekehammar, & Okada, 1976; Eysenck, 1983). As with state anxiety, trait anxiety is also thought to be multidimensional – that is, there are many dimensions (or facets) of trait anxiety (Endler & Kocovski, 2001; af Klinteberg et al., 1986). The dimensions of trait anxiety vary within different trait anxiety measures (for Karolinska Scales of Personality see af Klinteberg et al., 1986 and for State-Trait Anxiety Inventory see Bados, Gómez-Benito, & Balaguer, 2010).

It is important to distinguish between trait anxiety and pathological forms of anxiety. High trait anxiety is not necessarily an anxiety disorder but there is a connection between trait anxiety and anxiety disorders. For example, Muris, Schmidt, Merckelbach, and Schouten (2001) found that trait anxiety is related to symptoms of social phobia and separation anxiety disorder. There is also an interesting connection between childhood trait anxiety and adult anxiety disorders: higher childhood trait anxiety is associated with higher odds of adult anxiety disorder (Mundy et al., 2015). However, other studies have found only a modest correlation between trait anxiety and BAI (Beck Anxiety Inventory), a measure of anxiety symptomatology (Schmidt, Lerew, & Jackson, 1997, 1999).

Some studies have also found brain-level similarities between trait anxiety and pathological forms of anxiety (e.g. Engels et al., 2007), especially when examining the connectivity of the brain (Lu, Yang, Chu, & Wu, 2018; Takagi et al., 2018). However, there are also studies that have found differences in the connectivity of the brain when comparing trait anxiety and pathological forms of anxiety (Montag, Reuter, Weber, Markett, & Schoene-Bake, 2012; Phan et al., 2009; Porta et al., 2017a, 2017b). Therefore, although there are common brain-level factors between trait anxiety and pathological forms of anxiety, it seems that is possible to differentiate between them using brain measures. In conclusion, trait anxiety is a unique concept with unique implications for brain functioning.

Many commonly used trait anxiety measures have a social aspect built inside them. For example, the Endler Multidimensional Anxiety Scales has four factors: Social Evaluation, Physical Danger, Ambiguous and Daily Routines (Endler et al., 1991). For the State-Trait Anxiety Inventory (STAI),

a commonly used unidimensional trait anxiety measure, there is some evidence that the measure is more related to anxiety vulnerability in social situations than for example in physical danger situations (Endler & Okada, 1975; Endler et al., 1991; Walsh, McNally, Skariah, Butt, & Eysenck, 2015). As vulnerability to anxiety in social situations seems to be a major part of the trait anxiety concept, it is reasonable to assume that level of trait anxiety has an impact on the perception of social stimuli.

There are some studies about the connection between trait anxiety and negative social biases. High trait anxiety is associated with increased attention to negative social-evaluative words in comparison to positive words (Brosschot, de Ruiter, & Kindt, 1999; Mansell, Ehlers, Clark, & Chen, 2002; Mathews & MacLeod, 2005). High trait anxiety is also associated with increased attentional bias to other kinds of negative stimuli, including threatening situations and faces (Hu & Dolcos, 2017; Koster, Verschuere, Crombez, & Van Damme, 2005; Mathews & MacLeod, 2005). Working memory might also play a part in negative biases as there is a study where negative biases associated with trait anxiety are apparent only during a high working memory load (Booth, Mackintosh, & Sharma, 2017).

The models for attentional biases in trait anxiety could explain the distinctive attentional shifting during threat processing. There are multiple models (Cisler & Koster, 2010), and all of them are concerned with the facilitated attention to threats in trait anxiety, as in the studies mentioned above. Williams, Watts, MacLeod, and Mathews (1988) model is the only model that is also concerned with attentional avoidance of threat in low trait anxious individuals (Cisler & Koster, 2010). In addition, a “vigilance-avoidance” pattern (Mogg, Mathews, & Weinman, 1987) has been theorized for trait anxiety where trait anxious individuals, at the beginning, attend to the threat and follow up with attentional avoidance. However, the existing research is inconsistent about the order and time in which vigilance and avoidance may happen (Bradley, Mogg, Falla, & Hamilton, 1998; Holmes, Nielsen, & Green, 2008; Koster et al., 2005; Lee & Knight, 2009; Vassilopoulos, 2005).

Since trait anxiety is associated with distinctive attentional shifting during social threats, trait anxiety could also shape the process of emotional face processing, especially in the case of threatening faces. In order to get a better understanding of the current research concerning the connection between trait anxiety and emotional face processing, the core mechanism of emotional face processing should first be discussed.

Processing of Emotional Face Expressions

There are two parallel routes where visual information, including information about facial expressions, is processed: the cortical and subcortical route (Adolphs, 2002b). The subcortical route goes from the retina via the superior colliculus and the pulvinar thalamus to the amygdala (Morris, Öhman, & Dolan, 1999). Cortical areas then receive input from the amygdala (Morris et al., 1999). The cortical route goes from the retina via the lateral geniculate thalamus to V1, V2 and other early visual cortical areas (Adolphs, 2002b; LeDoux, 1998). After that the amygdala and the occipitotemporal areas, including the superior temporal sulcus (STS) and fusiform face area (FFA), are activated and following that other cortical areas as well (Adolphs, 2002b; LeDoux, 1998). The subcortical route processes highly salient information, for example fearful faces, rapidly and automatically (LeDoux, 1998). In the cortical route, the information is processed in more detail but more slowly (LeDoux, 1998). The processing of facial expressions occurs in both hemispheres but is more lateralized to the right hemisphere (Adolphs, 2002b; Laurian, Bader, Lanares, & Oros, 1991; Sadeh, Podlipsky, Zhdanov, & Yovel, 2010).

Event-related potentials (ERP) in EEG studies or event-related fields (ERF) in MEG studies are measured brain responses to a stimulus and they reflect the temporal processing in the brain (Baillet, 2017). EEG and MEG are thus great tools for studying the temporal profile of emotional facial expression processing. Some of the ERP's related to face processing are general visually evoked responses while others are face specific. In general, early ERP's are thought to reflect structural encoding of the face whereas the late ERP's are thought to be sensitive to emotional information (Ashley, Vuilleumier, & Swick, 2004) although some studies have found emotional modulation on the early ERP components as well (e.g. Dima, Perry, Messaritaki, Zhang, & Singh, 2018). The ERP components related to emotional face processing include the P100, N170, vertex positive potential (VPP), early posterior negativity (EPN) and later ERP components such as the P300 and the late positive potential (LPP).

The first ERP component seen during the perception of faces is the P100 (in MEG measurements M100) measured from the occipital brain areas. The P100 is thought to originate from extrastriate visual areas and the occipitotemporal cortex (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002) but it has also been associated with the occipital face area (OFA) (Sadeh et al., 2010). Some studies suggest that the P100 is not sensitive to faces per se but to low level visual cues such as the light and contrasts of pictures (Allison, Puce, Spencer, & McCarthy, 1999; Rossion & Caharel, 2011). In contrast, some studies suggest that this ERP component is sensitive to faces (Liu, Harris, & Kanwisher, 2002; Rossion & Jacques, 2008). In addition to basic visual processing, the P100 is also associated with early attentional processing (Luck & Kappenman, 2012; Mangun & Buck, 1998). The P100 response has also been shown to be stronger to emotional versus neutral facial expressions (e.g.

Aguado et al., 2012; Batty & Taylor, 2003). It is thus unsettled whether the P100 reflects sensitivity to emotional information of the faces or to low level visual cues.

The N170 (M170 in MEG measurements) measured from the occipitotemporal cortex is the most recognized face specific ERP component and it is thought to reflect the structural encoding of the face (Bentin, Allison, Puce, Perez, & McCarthy, 1996). At the same latency, another ERP component, the VPP (vertex positive potential), occurs but there is no consensus on whether the VPP and the N170 originate from the same or different neural processes (Luo, Feng, He, Wang, & Luo, 2010). The N170 has been associated with the FFA, the OFA and the STS (Rossion & Jacques, 2012). Traditionally it has been thought not to be sensitive to emotions (Eimer & Holmes, 2002; Eimer, Holmes, & McGlone, 2003) but according to Hinojosa, Mercado and Carretié's (2015) meta-analysis the strength of the N170 response is affected by emotions.

Following the N170, an ERP component P200 that is maximal at parietal or occipitotemporal sites (Paulmann & Pell, 2009) is shown to be sensitive to emotional facial expressions and is thought to reflect evaluation of the emotional significance of a visual stimulus (Dennis & Chen, 2007; Eimer et al., 2003; Paulmann & Pell, 2009; Schutter, de Haan, & van Honk, 2004). It is also associated with attentional processing (Carretié, Martín-Loeches, Hinojosa, & Mercado, 2001). Its counterpart in MEG studies is the M220 (Itier, Herdman, George, Cheyne, & Taylor, 2006).

The early posterior negativity (EPN) at approximately 200-300 milliseconds after the stimulus onset is also affected by emotional facial expressions (Marinkovic & Halgren, 1998; Sato, Kochiyama, Yoshikawa, & Matsumura, 2001; Sawada, Sato, Uono, Kochiyama, & Toichi, 2014). It has been suggested that the EPN reflects more attentional resources directed implicitly to (Schupp, Junghöfer, Weike, & Hamm, 2003), more conscious awareness of (Sato et al., 2001) or rapid and conscious detection of emotional versus neutral stimulus (Sawada et al., 2014).

Later ERP components such as the parietal P300 (M300 in MEG measurements) and N300 are also sensitive to emotional pictures (Carretié, Iglesias, García, & Ballesteros, 1997; Schupp et al., 2004; Schutter et al., 2004). The P300 has been associated with attention, evaluation of the stimulus, memory and decision making (Campanella, Quinet, Bruyer, Crommelinck, & Guerit, 2002; Polich, 2007), while the N300 has been associated with emotional processing (Carretié et al., 1997). These late components are thought to reflect the shift to conscious processing of emotions (Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004). There is also an ERP component called the late positive potential (LPP) similar to the P300 but it extends beyond the P300 time-window (Hajcak, Weinberg, MacNamara, & Foti, 2012). The LPP is also sensitive to emotional facial expressions (Eimer et al., 2003; Krolak-Salmon, Fischer, Vighetto, & Manguiere, 2001). The LPP has been associated with the

encoding and storage of emotional stimuli, sustained attention to emotional stimulus and emotion regulation (Hajcak et al., 2012).

There are a few models that combine these ERP components and the processes they are thought to reflect. Luo et al. (2010) have suggested that facial expressions are processed in three stages. In the first stage negative and threatening facial expressions, such as fearful and angry, are automatically processed. The N100 and the P100 reflect this process. In the second stage, emotional facial expressions are separated from neutral expressions, which is reflected in the VPP and the N170 components. In the last stage different emotion facial expressions are separated from each other. The P300 and the N300 reflect processing in this stage. The idea that emotions are first separated from neutral facial expressions and then from each other is supported by other studies as well (e.g. Krolak-Salmon et al., 2001). In addition, Paulmann and Pell (2009) have suggested three phases to facial expression processing. First, configuration and some affective details are processed which is reflected in the P200. Second, the processing of the facial expressions' semantic value begins. This is reflected in the EPN. Finally, the full semantic value of the expression is detected based on the stored knowledge of that expression. This is reflected in a later ERP component N400.

In addition to these models, Adolphs (2002b) has suggested a model that combines temporal and spatial information about the processing of emotional facial expressions. It consists of three stages. In the first stage highly salient stimuli such as threatening facial expressions, for example fear and anger, are rapidly processed. This occurs approximately 120 milliseconds after the stimulus onset. It thus corresponds to the P100. Brain areas activated in this stage include the amygdala and the early visual cortical areas. In the second stage the occipitotemporal areas, including the STS and the FFA, but also other brain areas, such as the orbitofrontal cortex and the basal ganglia, are activated. Amygdala and the primary visual cortex are also activated again in this stage. A more detailed processing of the face occurs including the recognition of emotional expressions and identity of the person. This occurs approximately 170 milliseconds after the stimulus onset and thus corresponds to the N170. In the last stage in Adolphs' model top-down processing occurs and knowledge about the expression is integrated with the perception of the expression. This occurs approximately 300 milliseconds after the stimulus onset and thus corresponds to later ERP components such as the P300 and the LPP. The STS and the FFA are again activated but also other cortical areas such as the orbitofrontal cortex, the insula and the somatosensory cortex are activated. Adolphs suggests that there are feedback influences in multiple brain areas and that explains why some areas are activated in multiple stages. For example, amygdala and the orbitofrontal cortex have strong associations with each other (Amaral, 1992).

There is some evidence that different emotions are processed differently. Most of the evidence is from fMRI studies. Amygdala has especially been associated with the processing of fearful facial expressions (Murphy, Ninno-Smith, & Lawrence, 2003; Phan et al., 2002; Zhang et al., 2016) but it is also activated during the perception of other facial expressions (Adolphs, 2002a; Fusar-Poli et al., 2009; Yang et al., 2002) and faces per se (neutral expressions) (Posamentier & Abdi, 2003). The ACC and the orbitofrontal cortex have in turn been associated with the processing of angry facial expressions (Posamentier & Abdi, 2003). Some EEG studies also support the idea that fearful and angry facial expressions are processed differently from other emotional facial expressions. Angry faces elicit different P100 (Dima et al., 2018), N170 (Hinojosa et al., 2015) and the EPN (Balconi & Pozzoli, 2013; Schupp et al., 2004) responses than other emotional facial expressions. Fearful faces in turn elicit different N170 (Batty & Taylor, 2003; Hinojosa et al., 2015), P200 (Ashley et al., 2004), EPN (Balconi & Pozzoli, 2013) and the LPP (Krolak-Salmon et al., 2001) responses than other emotional facial expressions. However, there are also studies that have found different responses to be sensitive to emotional facial expressions compared to neutral facial expressions but have not found any differences between emotions (e.g. Eimer et al., 2003).

In summary, facial emotion recognition is a complex process. In the early phases coarse and automatic processing occurs and in the later phases more detailed and conscious processing takes place. However, there is also evidence that the processing of emotions can begin quite early, suggesting that emotional face processing occurs both automatically and consciously. This is also in line with the idea of cortical and subcortical routes.

Trait Anxiety and Emotional Face Processing

Facial emotion recognition problems are prominent in depression (Bistricky, Ingram, & Atchley, 2011; Demenescu et al., 2010) and in some anxiety disorders (Demenescu et al., 2010; Easter et al., 2005), including obsessive-compulsive disorder (Sprengelmeyer et al., 1997). For social anxiety, the studies are inconsistent. According to some studies high social anxiety symptoms and generalized social phobia are associated with poorer facial emotion recognition (Garner, Baldwin, Bradley & Mogg, 2009; Wieckowski et al., 2016) but according to other studies social anxiety is associated with better facial emotion recognition (Arrais et al., 2010; Hunter, Buckner, & Schmidt, 2009; Torro-Alves et al., 2016). In addition, Joormann and Gotlib (2006) did not find any differences between social phobia and control group in facial emotion recognition. Since trait anxiety has a social aspect, it would

be interesting to see if trait anxious individuals, in fact, could have a better or poorer facial emotion recognition ability. To our knowledge only two studies have investigated facial emotion recognition in trait anxiety. In the first study, Surcinelli, Codispoti, Montebanocci, Rossi, and Baldaro (2006) found that high trait anxiety group recognized fearful facial expressions better than low trait anxious group. However, the second study (Cooper, Rowe, & Penton-Voak, 2008), using faster emotional classification time, found no difference between high and low trait anxiety groups. Therefore, the current research about this subject is incoherent.

Since trait anxiety might impact facial emotion recognition it would be reasonable to assume that this effect could also be seen on a brain level. Trait anxiety is, for example, associated with increased amygdala reactivity to fear cues (Indovina, Robbins, Núñez-Elizalde, Dunn, & Bishop, 2011). Trait anxiety might thus also be associated with alterations in the temporal processing of emotional facial expressions. Most of the studies examining the effect of anxiety on temporal aspects of emotional face processing have focused on social anxiety (for review see Harrewijn, Schmidt, Westenberg, Tang, & van der Molen, 2017). However, some studies have focused on trait anxiety. These studies have examined the effect of trait anxiety on the strength of ERP components such as the P100, N170, VPP, P200, EPN and the LPP.

Most of the studies have found an effect of trait anxiety on the P100 response during emotional face perception. High trait anxiety group compared to low trait anxiety group has been shown to have stronger P100 responses elicited by fearful (Frenkel & Bar-Haim, 2011; Holmes et al., 2008), happy (Morel, George, Foucher, Chammat, & Dubal, 2014) and neutral faces (Frenkel & Bar-Haim, 2011). This anxiety effect on the P100 response has been found using subliminally shown fearful faces as well (Li, Zinbarg, Boehm and Paller, 2008; Williams et al., 2007). Altogether these findings suggest that the early processing of faces is enhanced in high trait anxious individuals but this enhancement is not limited to negative facial expressions. However, Walentowska and Wronka (2012) found high trait anxious participants to display weaker P100 responses elicited by subliminally shown fearful and neutral faces compared to low trait anxious participants. There are also studies that have not found any effects of trait anxiety on the P100 response (Chronaki et al., 2018; Eldar, Yankelevitch, Lamy, & Bar-Haim, 2010; Holmes, Nielsen, Tipper, & Green, 2009; Rossignol, Philippot, Douilliez, Crommelinck, & Campanella, 2005).

To our knowledge, none of the previous studies have found trait anxiety to affect the strength of the N170 elicited by emotional facial expressions (Chronaki et al., 2018; Morel et al., 2014; Rossignol et al., 2005; Walentowska & Wronka, 2012). This suggests that trait anxiety does not affect the structural encoding of the face. Also to our knowledge only two studies have examined the VPP. The other one did not find trait anxiety to have an effect on the VPP (Rossignol et al., 2005) whereas in

the other high trait anxious participants displayed weaker VPP responses to subliminally shown fearful faces than the low trait anxious participants (Williams et al., 2007).

Studies that have examined the effect of trait anxiety on the EPN during emotional facial perception are contradictory. There are studies that have found stronger EPN responses to angry (Fox, Derakshan, & Shoker, 2008), happy (Homes et al., 2008), fearful and neutral faces (Frenkel & Bar-Haim, 2011) in high trait anxious compared to low trait anxious participants. These studies suggest that trait anxiety is associated with greater allocation of attentional resources to faces. However, some studies suggest the opposite since they have found weaker EPN responses to happy (Holmes et al., 2009) and fearful faces (Holmes et al., 2008, 2009) in high trait anxious compared to low trait anxious participants. In addition, Walentowska and Wronka (2012) found that low trait anxious participants displayed stronger EPN responses to fearful compared to neutral faces but this difference between emotions was not significant in high trait anxious participants. There are also studies that have not found any effect of trait anxiety on the EPN (Li et al., 2008; Morel et al., 2014; Rossignol et al., 2005). Altogether more research is needed to draw any conclusions on the effect of trait anxiety on the EPN during emotional face perception.

To our knowledge, four studies have examined the effect of trait anxiety on the P200 component during emotional face perception and all of them found an effect. Three studies found the P200 response to be stronger to angry, happy, fearful or neutral faces in high trait anxious compared to low trait anxious participants (Bar-Haim et al., 2005; Eldar et al., 2010; Frenkel & Bar-Haim, 2011). These studies suggest that trait anxiety is associated with enhanced processing of emotional facial expressions but that this is not limited to threatening faces. However, Holmes et al. (2008) found high trait anxious participants to display weaker P200 responses to fearful faces than low trait anxious participants suggesting that trait anxiety could be associated with avoidance of threat.

Most of the studies that have examined the effect of trait anxiety on later ERP components during emotional face perception have focused on the LPP. Some studies have found stronger LPP responses to angry (Chronaki et al., 2018), fearful and happy faces (Holmes et al., 2009) in high trait anxious than in low trait anxious participants. This suggests that trait anxiety is associated with enhanced conscious processing of emotions from facial expressions. However, there are studies showing weaker LPP responses to fearful faces (Frenkel & Bar-Haim, 2011; Holmes et al., 2008) in high trait anxious compared to low trait anxious participants. This in turn suggests that trait anxiety is associated with diminished conscious processing of fear, which could support the idea that high trait anxious individuals avoid threat more than low trait anxious individuals. One study also found no effect of trait anxiety on the LPP during emotional face perception (Li et al., 2008). Again, more research is needed to draw conclusions.

In summary, not many studies have examined the effect of trait anxiety on the temporal aspects of emotional face perception. However, most of the studies done so far show that trait anxiety is associated with stronger P100 and P200 responses but not with modulation of the N170 component. In addition, most of the studies show that trait anxiety has an effect on the EPN and the LPP but they are not consistent on the direction of this effect (do anxious participants display stronger or weaker responses).

Research Questions

This study had two objectives. The first objective was to investigate whether different negative facial expressions (fearful, angry, sad) and neutral facial expressions evoke different responses, and whether there are differences between the two hemispheres in emotional facial expression processing. We had two hypotheses for this objective. Firstly, we expected that negative facial expressions would cause stronger evoked responses in the brain than neutral expressions, and the responses caused by different negative facial expressions would differ from each other. Secondly, there is some evidence that emotion processing, especially in the case of emotional facial expressions, is more lateralized to the right hemisphere. We expected to see this right hemisphere dominance in our measurements.

The second objective was to investigate whether trait anxiety is connected to the evoked responses caused by negative facial expressions, as in the earlier studies. For our hypothesis, we expected that the trait anxiety subscales of the Karolinska Scales of Personality (KSP) questionnaire would correlate positively with the strength of evoked responses caused by negative facial expressions.

METHODS

Participants

For the participant recruitment process, email lists from different educational institutions in Jyväskylä, Finland were used. 14 volunteers participated in this study. Exclusion criteria for the study were metal particles in body, any neurological or psychiatric conditions and central nervous system

agents that could affect the validity of the data. All of the participants were male, aged 20-54 years (mean = 30,6; median = 26; standard deviation = 11,1). All but three of the participants had graduated from or were studying in a university and all of the participants had at least completed comprehensive school. Most of the participants were either studying or working. All of the participants received a movie ticket as a reward for participating in the study. All of the participants gave an informed consent to participate in this study. The University of Jyväskylä Ethical Committee has approved this study.

Magnetoencephalography (MEG)

MEG-signal was measured with a whole-head system (Elekta Neuromag Oy, Helsinki, Finland) that has 306 channels. The channels consist of 204 planar gradiometers and 102 magnetometers. The measurements were conducted in a magnetically shielded room at the MEG Laboratory in the University of Jyväskylä.

Before the measurements, empty room data was measured for 4 minutes to estimate the intrinsic noise level. All magnetic materials were also removed from the participants before the experiment began.

To correct the effects of possible head movements, 5 Head Position Indicator (HPI) -coils were placed on the participants head. Two coils were placed behind earlobes, one on the forehead and two on the temples. After the coil placement, Isotrak 3D digitizer (Polhemus, USA) was used to digitize three anatomical landmarks of the head (nasion, left and right preauricular). Then the location of HPI-coils were digitized and a number of additional points were determined.

After the location of HPI coils was confirmed, in total 7 electrodes were placed to the participants body. Two of the electrodes were placed on the face – one close to the left cheekbone and second close to the right eyebrow. These electrodes measured eye movement and blinking (electro-oculogram, EOG). In addition, two electrodes that measured the heartbeat (electrocardiographic, ECG) were placed on the left shoulder and between the collarbones. Ground electrode was placed on the right collarbone. Finally, two GSR-electrodes (galvanic skin response) were placed on the root of non-dominant hand's thumb and little finger. However, the data from the GSR-electrodes was not used in this study.

Procedure and Stimuli

The participants were asked to sit in a chair with their head inside the helmet-shaped MEG-device and their hands on a table. Their dominant hand was placed on a response pad that was on the table. A screen was placed in front of the participant so that the distance between the eyes and the screen was approximately 105 cm. The participants were instructed to stay as still as possible during the experiment.

The Karolinska Directed Emotional Faces (KDEF) (Lundqvist, Flykt, & Öhman, 1998) was used as the emotional face stimuli set. From this set of pictures neutral expressions and three different emotional expressions were used: fearful, angry and sad (male and female) (see Figure 1). In total the participants saw 432 pictures in a random order. The pictures were presented with Presentation version 18 (build 6.9.2015) (Neurobehavioral Systems, Inc.) program. The pictures were 6 cm long and 4 cm wide and they were presented in the center of the screen. Each picture was shown for one second (1000 ms) and in between a black screen with a fixation point cross in the centre was shown for 1,5 seconds (1500 ms +/- 100 ms). The participants were instructed to keep their gaze on the fixation point even when the pictures were shown. After a random number of pictures, the participants were asked to answer what expression the previous picture was showing. The participants answered with the response pad that had four different colored buttons: each color represented different expression. The response options and the corresponding button colour were shown on the screen during every question. After the participant had pressed a button, next set of pictures were shown. This procedure is represented in Figure 2.

The experiment took approximately 15 minutes and there was a break halfway through. The participants got to determine the length of the break and pressed a button when they were ready to continue.

Because this study is a part of a bigger research project, the participants completed another experiment after this one. In that experiment, the participants listened to emotionally different tapes. Resting state activity was also measured before and after the whole experiment procedure.



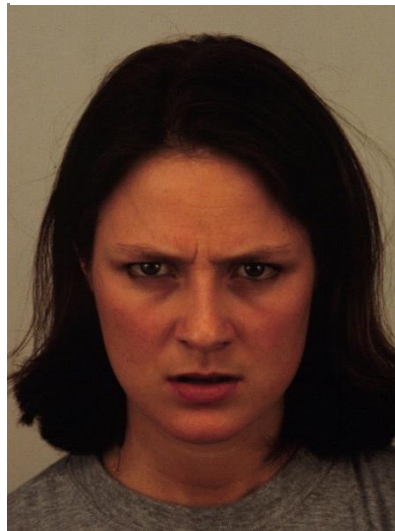
Afraid



Neutral



Sad



Angry

Figure 1. Examples of the facial expressions used in the experiment.

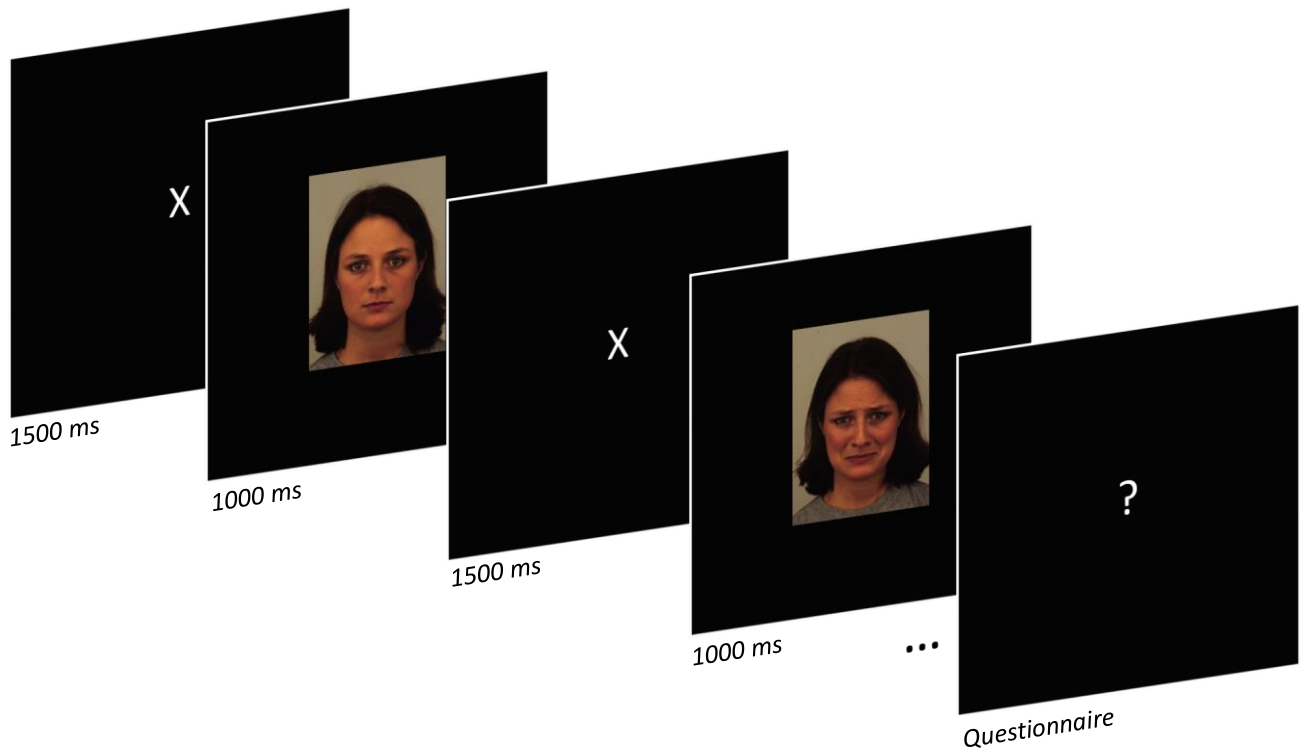


Figure 2. Sequence of events in facial emotion recognition task. After a random number of pictures, the participants were asked to recognize the emotion the previous picture was showing.

Personality tests

Karolinska Scales of Personality (KSP) (af Klinteberg et al., 1986) (for the Finnish version see Pulkkinen, Virtanen, af Klinteberg, & Magnusson, 2000) was used to measure trait anxiety. KSP is a self-report questionnaire that consists of 135 items that form 15 minor scales that can be further categorized into 4 major scales: extraversion, anxiety, aggression and conformity. Each item is answered to on a four-point Likert scale ranging from “does not apply to me” to “applies to me very well”. In this study, only the anxiety major scale and the five minor scales that it consists of were used. These minor scales are psychic anxiety (e.g. “My self-confidence is pretty bad”), somatic anxiety (e.g. “Sometimes my heart beats fast or irregularly without any apparent reason”), muscular tension (e.g. “My hands often shiver”), psychasthenia (e.g. “I get tired and stressed way too easily”)

and inhibition of aggression (e.g. “If I’m not treated appropriately in a restaurant, it’s difficult for me to point it out”). Each of these minor scales included 10 items.

Data analysis

During the MEG-measurement 1 kHz sampling rate was used. Low-pass filter was set to 330 Hz while high-pass filter was set to 0.1 Hz. For the offline filtering, first Xscan 3.0 software (Elekta Neuromag) was used to identify bad channels from the data, which were excluded from the pre-processing. Maxfilter 3.0 software (Elekta Neuromag) was used to pre-process the MEG data reducing external noise with spatiotemporal signal space separation (tSSS). The Maxfilter software was also used in conjunction with HPI-coils to correct the inaccurate data produced by head movements. After processing the data with the Maxfilter software, the data was imported with Meggie software (University of Jyväskylä), which is a graphical interface for MNE software used for processing MEG data.

First the data was filtered to the bandpass of our interest which was 0.01 - 40 Hz. Then the eye movement and heart rate artefacts were removed from the data with ICA (independent component analysis) with low pass filter 40.00Hz and transition band 0.50Hz. Filter length was 10.0 seconds. After that epochs for each emotion were created and averaged. The time frame for each epoch was from -200ms to 500ms. Epochs that contained amplitudes larger than 3000.0 fT/cm for gradiometers and larger than 4000.0 fT for magnetometers were excluded.

Root mean square (RMS) was calculated for each gradiometer pair. Then pools were created for each brain region (left and right frontal, left and right parietal, vertex, left and right temporal, left and right occipital) by averaging the RMS values from those regions. These were done with the MNE Python. We chose to focus on the occipital and parietal regions since according to whole head distribution of activation (see Figure 3) the ERF responses were the strongest on the occipital areas (see Figure 4) and there appeared to be more differences between emotions on the parietal regions.

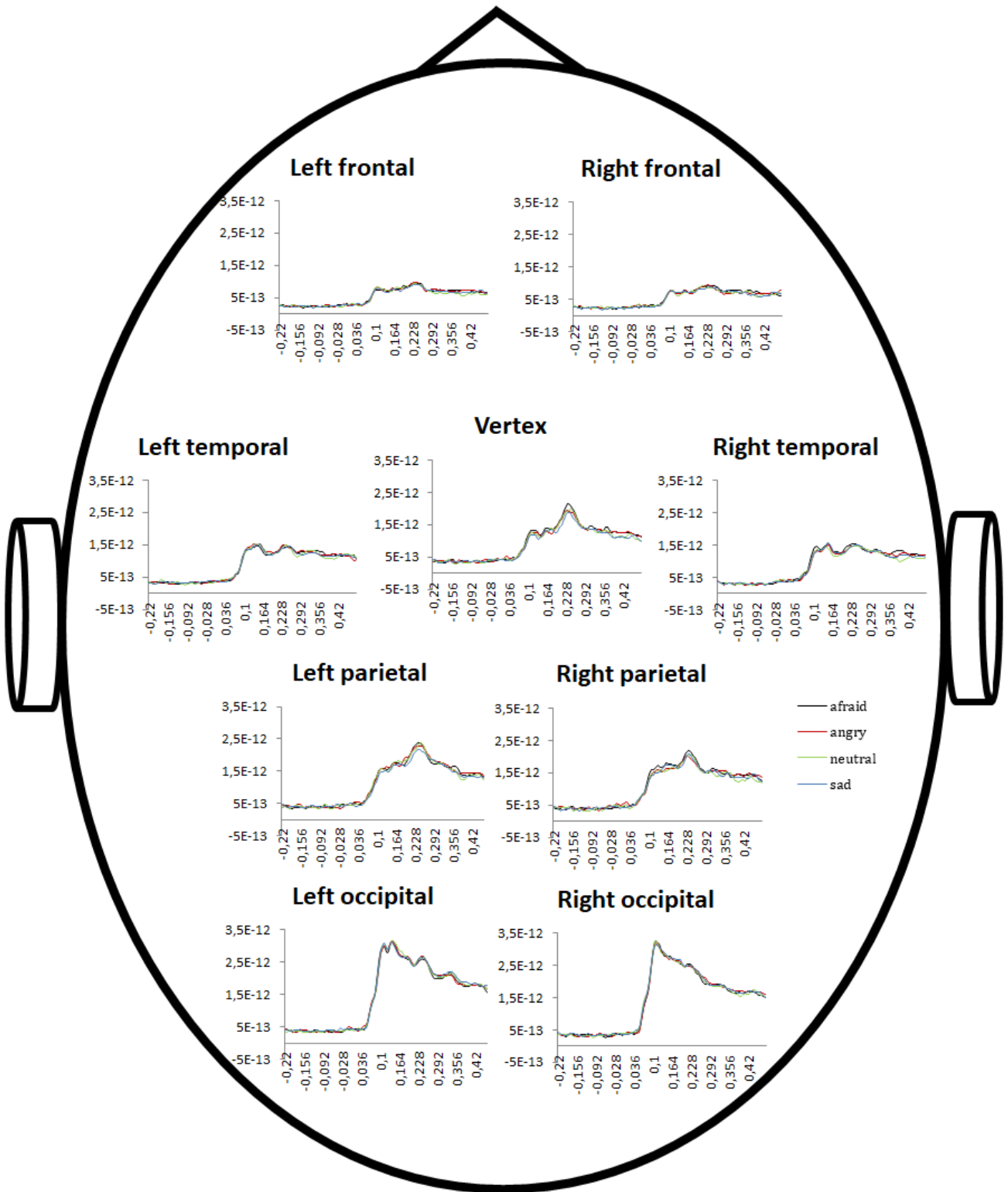


Figure 3. The whole head distribution of activation.

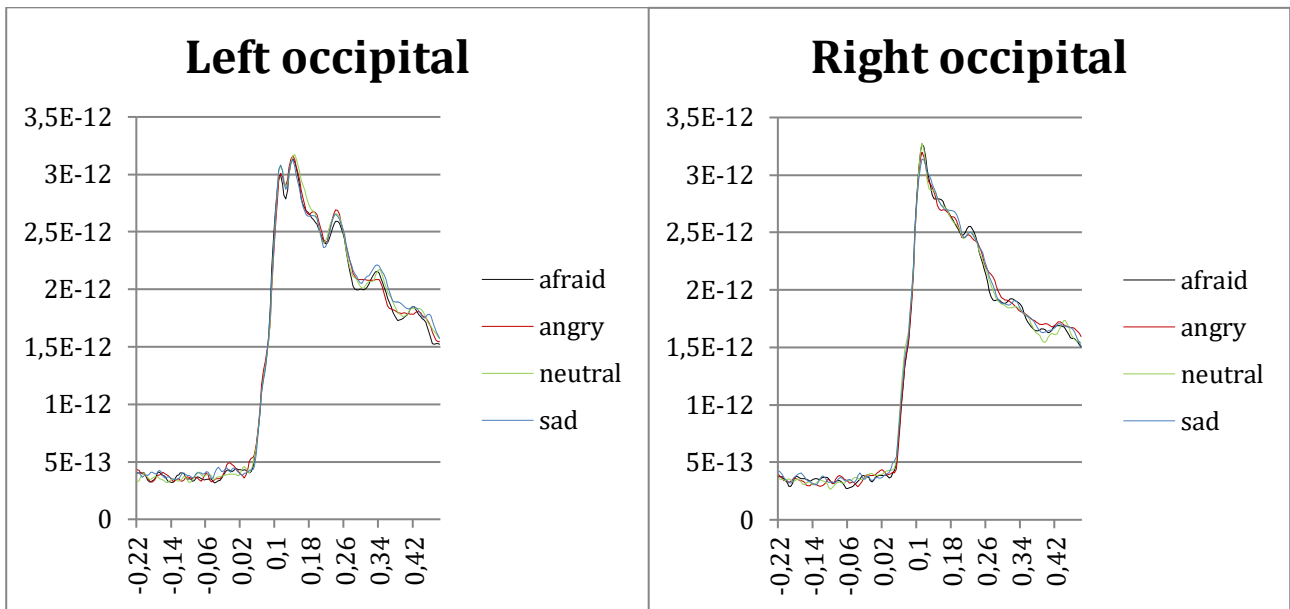


Figure 4. The grand averages of responses to different facial expressions in the occipital area.

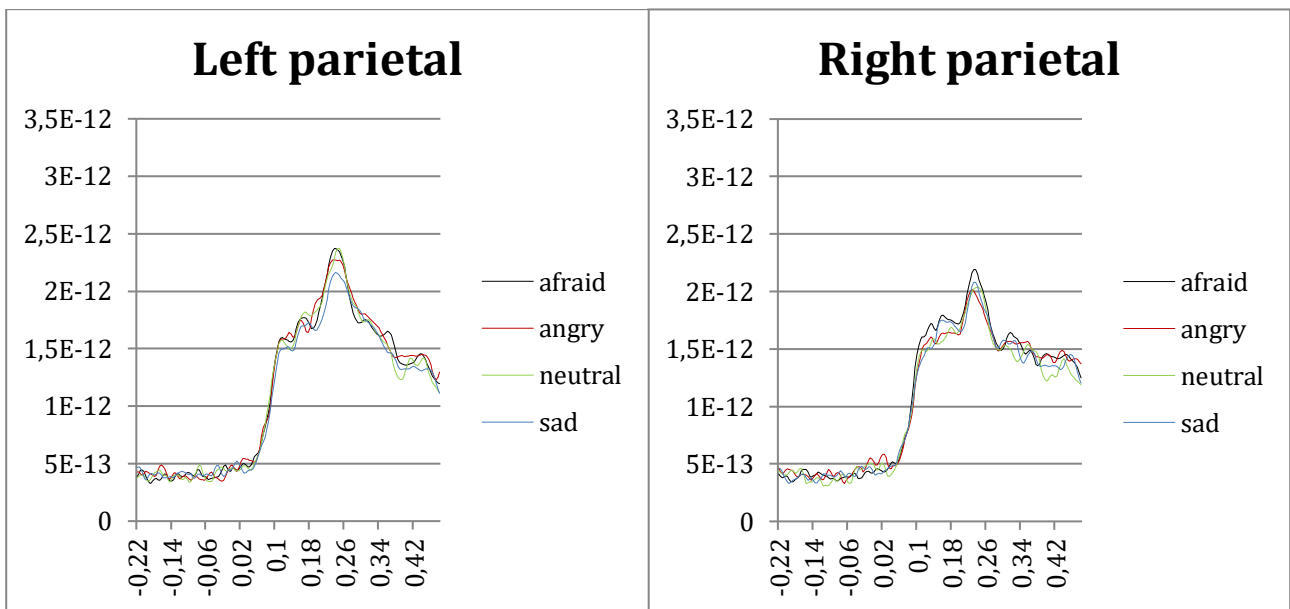


Figure 5. The grand averages of responses to different facial expressions in the parietal area.

Grand averages for each brain region and each emotion were calculated with Excel 2016. Based on the visual inspection of grand averages, time-windows of interest were chosen for occipital and

parietal areas. The first two time-windows were chosen based on the latency of the first two peaks. The third time-window was chosen to cover multiple ongoing small peaks. The time-windows for occipital areas were: 1) 68 - 132ms, 2) 132 - 212ms and 3) 216 - 400ms. These time-windows occur approximately at the same latency and area as the ERP or the ERF components P100/M100, N170/M170 and the EPN. The time-windows for parietal areas were: 1) 100 - 196ms, 2) 200 - 296ms and 3) 300 - 480ms. These time-windows occur approximately at the same latency and area as the ERP or the ERF components VPP, P200/M220 and P300/M300 or LPP. From the first two time-windows for each emotion, maximum values were calculated individually for each participant. If the maximum value calculated was not at the peak of the wave (e.g. part of a wave that peaked in the previous or the following time-window), peak value was searched by hand. There were three occasions where there were no clear peaks on the first or the second time-window. For those occasions, a mean value was calculated. Also two peak values (one for angry and one for sad faces) were 4 ms late for the first time-window and one peak value (for sad faces) was 4 ms late for the second time-window but we decided to include them into the previous time-window since the time differences were so small. The beginning of the next time-window was then postponed by 4 ms. From the last time-windows a mean for each emotion was calculated individually for each participant. Means instead of maximum values were used since contrary to earlier time windows, there were no notable peaks in the last time windows. These maximum and mean values were calculated for both occipital and parietal regions and then imported to SPSS.

The data from the KSP anxiety scales were analyzed with Excel 2016. Each minor scale (psychic anxiety, somatic anxiety, muscular tension, psychasthenia and inhibition of aggression) was scored independently and then summed up to form the score for the major scale of anxiety. The maximum for each minor scale was 40 points and the maximum for the major scale was 200 points.

Statistical analyses were done with IBM SPSS Statistics 24 program. To test the effects of hemisphere (left and right) and emotions (fear, anger, sadness and neutral) on visual processing, repeated measures variance analysis (ANOVA) was applied separately in the three time-windows. For every ANOVA, sphericity was assessed and Greenhouse-Geisser adjustment was made where appropriate. The association between the amplitudes of the ERF components for different facial expressions in both hemispheres and the anxiety scale points was examined using the Pearson correlation coefficient. Outliers were defined as values beyond 2.5 standard deviations from the mean. They formed only 0,5% of the data. These values were excluded. There were four outliers, one in anxiety subscale muscle tension, two among the amplitudes in the left parietal area elicited by fearful faces (in the first and the third time-window) and one among the amplitudes in the left occipital area elicited by angry faces in the first time-window. These values were excluded.

Because of the small participant sample, this study took a more liberal approach for the presentation of statistical results. It is harder to achieve statistical significance with a small sample, therefore results that were approaching significance ($p < 0.10$) were included.

RESULTS

Occipital area

In the first time-window (68-132 ms), that corresponds to the P100/M100, there was no significant main effect of emotion ($F(2.208;28.702) = 0.184$, $p = 0.853$) or hemisphere ($F(1,13) = 0.996$, $p = 0.336$) or interaction between emotion and hemisphere ($F(3,39) = 0.303$, $p = 0.823$). There were no significant correlations in this time-window.

In the second time-window (132-212 ms), that corresponds to the N170/M170 there was no significant main effect of emotion ($F(1.646;21.400) = 0.606$, $p = 0.524$) or hemisphere ($F(1,13) = 1.141$, $p = 0.305$) or interaction between emotion and hemisphere ($F(3,39) = 1.793$, $p = 0.164$). There was a significant correlation between psychasthenia and responses to angry faces ($r = 0.552$, $p < 0.05$) on the right hemisphere. The correlation between psychasthenia and responses to sad faces on the right hemisphere was approaching significance ($r = 0.503$, $p = 0.067$).

In the third time-window (216-400 ms), that corresponds to the EPN, there was no significant main effect of emotion ($F(3,39) = 0.668$, $p = 0.577$) or hemisphere ($F(1,13) = 0.974$, $p = 0.342$) or interaction between emotion and hemisphere ($F(3,39) = 0.692$, $p = 0.563$). The correlations between psychasthenia and responses to fearful ($r = 0.463$, $p = 0.095$), angry ($r = 0.500$, $p = 0.068$), neutral ($r = 0.471$, $p = 0.089$) and sad faces ($r = 0.467$, $p = 0.092$) on the right hemisphere were approaching significance.

All correlations in the occipital area were positive, which means that higher scores in the KSP anxiety scales were connected to larger evoked responses during the face stimuli.

Parietal area

In the first time-window (100-196 ms), that corresponds to the VPP, there was no significant main effect of emotion ($F(2,106;27.375) = 1.121, p = 0.343$) or hemisphere ($F(1,13) = 0.078, p = 0.785$) or interaction between emotion and hemisphere ($F(3,39) = 1.873, p = 0.150$). There were significant correlations between inhibition of aggression and responses to neutral faces on the right hemisphere ($r = 0.548, p < 0.05$) and responses to sad faces on both hemispheres (left: $r = 0.604, p < 0.05$; right: $r = 0.624, p < 0.05$). In addition, the correlations between inhibition of aggression and responses to angry faces on the right hemisphere ($r = 0.461, p = 0.097$), responses to neutral faces on the left hemisphere ($r = 0.466, p = 0.093$) and responses to fearful faces on both hemispheres (left: $r = 0.522, p = 0.067$; right: $r = 0.519, p = 0.057$) were approaching significance.

In the second time-window (200-296 ms), that corresponds to the P200/M220, the main effect of emotion ($F(3,39) = 2.273, p = 0.095$) was approaching significance. Post-hoc comparisons using the Bonferroni method revealed that responses elicited by fearful faces were stronger than those elicited by sad faces but this was only approaching significance ($p = 0.061$). There was no significant main effect of hemisphere ($F(1,13) = 1.348, p = 0.267$) but the interaction between emotion and hemisphere was approaching significance ($F(3,39) = 2.467, p = 0.076$). To further examine this interaction, we did repeated measures ANOVA separately to both hemispheres. There was no significant main effect of emotion on the left hemisphere ($F(3,39) = 2.039, p = 0.124$) but on the right hemisphere there was a main effect of emotion ($F(3,39) = 2.843, p = 0.050$). Post-hoc comparisons using the Bonferroni method revealed two differences that were approaching significance: fearful faces elicited stronger responses than angry ($p = 0.062$) and neutral faces ($p = 0.088$). There were no significant correlations.

In the third time-window (300-480 ms), that corresponds to the P300/M300 or the LPP, there was no significant main effect of emotion ($F(3,39) = 1.876, p = 0.150$) or hemisphere ($F(1,13) = 0.089, p = 0.770$) or interaction between emotion and hemisphere ($F(3,39) = 0.180, p = 0.909$). There were some significant correlations in this time-window. Psychasthenia correlated with responses to neutral (right: $r = 0.596, p < 0.05$, left: $r = 0.593, p < 0.05$) and sad (right: $r = 0.540, p < 0.05$, left: $r = 0.569, p < 0.05$) faces on both hemispheres and with responses to fearful ($r = 0.654, p < 0.05$) and angry faces ($r = 0.611, p < 0.05$) on the left hemisphere while anxiety major scale correlated with responses to neutral faces on the right hemisphere ($r = 0.582, p < 0.05$). In addition, the correlations between psychasthenia and responses to angry faces ($r = 0.526, p = 0.053$) and fearful faces on the right hemisphere ($r = 0.486, p = 0.078$) were approaching significance. The correlation between anxiety major scale and responses to sad faces on the right hemisphere was also approaching significance ($r = 0.486, p = 0.078$).

As on the occipital area, all correlations on the parietal area were positive, which again means that higher scores in the KSP anxiety scales were connected to larger evoked responses during the face stimuli.

DISCUSSION

This study had two objectives. The first objective was to investigate if the emotional face processing in the brain differs between different negative facial expressions and neutral facial expressions. The second objective was to investigate if trait anxiety is connected to evoked responses caused by negative and neutral facial expressions. Next, the results in the context of our research questions and hypotheses will be discussed.

Emotional face processing in the brain

Our first objective was to investigate whether neutral facial expressions and different negative facial expressions are processed differently in the brain. We hypothesized that negative facial expressions would cause stronger responses in the brain than neutral expressions, and the responses caused by different negative facial expressions would differ from each other. This was not the case in our study. There were a few approaching significant differences between the responses to emotional faces. Fearful faces caused stronger M220 responses compared to sad faces. In addition, fearful faces elicited stronger M220 responses than angry and neutral faces but only on the right hemisphere. Previous research has also found the P200 (ERP equivalent to the M220) to be sensitive to emotions. For instance, Paulmann and Pell (2009) found that the P200 response is stronger to emotional (angry, fearful and happy) compared to neutral faces. Since the P200 is thought to reflect the processing of the emotional significance of the stimulus and is associated with attentional processing, it is understandable that fearful faces elicit stronger response at this latency than sad or neutral faces. Fearful faces are more important to our survival than sad or neutral faces since they alert us of a possible threat. Thus fearful faces draw more attention than sad and neutral faces. Another explanation could be that fearful faces are more arousing than sad and neutral faces and thus elicit enhanced P200 and M220 responses. However, it is more difficult to explain why fearful faces elicited

stronger responses than angry faces at this latency. Angry facial expression might also be a sign of a potential threat and they are arousing as well. However, it has been suggested that fearful faces are more ambiguous cues of threat than angry faces (Whalen, 1998) and thus the processing of the emotional significance of fearful faces might require more resources.

Altogether, from our hypothesized negative expressions only fearful faces elicited different brain responses than neutral faces at the latency that is associated with attention and processing of the stimulus' emotional significance. Fearful faces also elicited stronger responses than the other negative expressions (angry and sad) at the same latency. This thus suggests that fearful faces draw more attention than the other facial expressions and supports the idea that fear is processed differently than other emotions (see e.g. Ashley et al., 2004; Murphy et al., 2003). However, it is important to remember that these results were only approaching significance. A bigger sample could change the results approaching significance to significant. However, there is also a possibility that the effect is not real and would not reach significance with a bigger sample.

There were no differences between emotions in any other time-windows suggesting that the evoked responses measured from the visual areas were not sensitive to different negative emotional expressions. This is partly in conflict with previous research since there are studies that have found ERP components (or corresponding ERF components) such as the P100, N170, EPN, VPP, P300 or the LPP to be sensitive to emotional versus neutral facial expressions (e.g. Ashley et al., 2004; Batty & Taylor, 2003; Eimer & Holmes, 2002; Eimer et al., 2003; Hinojosa et al., 2015; Sato et al., 2001). Especially the EPN and the LPP have been associated with emotional processing, which makes it surprising that we did not find any differences between emotional and neutral facial expressions at the corresponding latencies. This might be due to the small number of participants in our study or methodological differences between our study and previous studies. However, there are also studies that, like us, have not found emotional modulation on these components, especially on the N170 (e.g. Eimer & Holmes, 2002; Eimer et al., 2003). In addition, our results do not support the idea that anger is processed differently from other emotions (see e.g. Balconi & Pozzoli, 2013; Posamentier & Abdi, 2003).

Our second hypothesis was that right hemisphere would be dominant in the processing of emotional faces. This was only partly the case in our study since fearful faces elicited stronger M220 responses than angry and neutral faces but only on the right hemisphere. This is in line with previous research showing right hemisphere dominance in emotional face processing (e.g. Adolphs, 2002b). However, there were no other differences between hemispheres, which suggests that emotional facial expressions are processed in both hemispheres. There are a few possible explanations to why we did not find any other hemisphere differences. First, the number of our participants was quite small, which

could result in hemisphere differences not reaching statistical significance. Second, the gradiometers were pooled together with predefined areas, not based on where responses to faces occurred. This could have resulted in the responses of our interest being divided into two areas. The responses might have, for instance, occurred in occipitotemporal areas which could have resulted in the mean value for occipital areas being smaller than it would have been for occipitotemporal areas. This might also explain why we did not find differences between emotions in other time-windows except the one corresponding to the M220.

Trait anxiety and emotional face processing

Our second objective was to investigate the connection between trait anxiety and the evoked responses caused by negative facial expressions. Our hypothesis was that trait anxiety subscales correlate with responses caused by negative facial expressions. This was partly the case in our study since trait anxiety correlated positively with the strength of responses elicited by emotional facial expressions in three (out of six) time-windows. These correlations were especially seen in the later phases of processing, which suggests that trait anxiety might especially influence the top-down processing of emotional facial expressions.

Against our hypothesis, there was no correlation between trait anxiety and the strength of the M100 response. Most of the previous studies are in conflict with this (Frenkel & Bar-Haim, 2011; Holmes et al., 2008; Li et al., 2008; Morel et al., 2014; Walentowska & Wronka, 2012; Williams et al., 2007) but some have found similar results (Chronaki et al., 2018; Eldar et al., 2010; Holmes et al., 2009; Rossignol et al., 2005). However, a correlation between trait anxiety and the strength of the M170 response elicited by angry faces was found. This is in total conflict with previous research since none of the previous studies have found any effects of trait anxiety on the strength of the N170 response elicited by emotional facial expressions (Chronaki et al., 2018; Morel et al., 2014; Rossignol et al., 2005; Walentowska & Wronka, 2012). This thus raises the question, if the early (P100) response could occur a bit late in our study and display as a M170 response. This delay could be due to different methodology used in our study compared to previous studies that have found an effect of trait anxiety on the strength of the P100 response to emotional facial expressions. For instance, Holmes et al. (2008) used an implicit emotion recognition task while we used an explicit task and Li et al. (2008) showed the pictures only subliminally while we showed them for a longer period of time.

Nevertheless, both the P100 and the M170 are fairly early responses and angry faces are related to threat. Our study thus suggests that trait anxiety is associated with an early threat processing bias.

On the first parietal time-window (100 - 196 ms after the stimulus onset), that could correspond to the ERP component VPP, the trait anxiety subscale inhibition of aggression correlated positively with responses elicited by sad and neutral faces. In addition, inhibition of aggression correlated positively with responses elicited by other emotions as well, but these correlations were only approaching significance. Altogether, high score on inhibition of aggression was associated with enhanced processing of all the emotional expressions (especially sad) and neutral faces at this latency. This enhancement is occurring quite early, which suggests that inhibition of aggression is associated with enhanced early processing of facial expressions. The VPP is thought to reflect structural processing of the face, just like the N170 or the M170. Since in our study inhibition of aggression correlated with responses elicited by neutral faces as well as emotional faces, this could suggest that high inhibition of aggression and thus trait anxiety is associated with enhanced structural encoding of the face. However, this enhancement was not seen on the M170 component, which suggests that the brain responses in these corresponding time-windows and areas do not reflect the same process. This in turn supports the idea that our M170 response might reflect the same process as the M100 or the P100 response in the previous studies. To our knowledge, only two studies have examined the association between trait anxiety and the VPP response during emotional face perception and both of these are in conflict with our results. Williams et al. (2007) found trait anxiety to be associated with weaker VPP responses, while Rossignol et al. (2005) did not find any association between trait anxiety and the VPP during emotional face perception. Neither of these studies however used the same methodology as we did, since Williams et al. (2007) used subliminally shown pictures of faces and Rossignol et al. (2005) used an oddball paradigm.

There were more correlations in the third parietal time-window (300 - 480 ms after the stimulus onset) than in any other time-window. This time window could correspond to the ERF component M300 or the ERP component LPP. Trait anxiety correlated positively with responses elicited by neutral faces and every emotional expression at this latency. The M300 and the LPP are thought to reflect the conscious processing of emotions. Our results thus suggest that high trait anxiety is associated with enhanced conscious processing of not only emotional expressions but neutral faces as well. In support of this, there were similar correlations on the time-window that could correspond to the ERP component EPN, which is also thought to reflect conscious processing. These correlations however were only approaching significance. Top-down processing could explain this enhanced conscious processing of facial expressions in trait anxiety. Based on their previous experiences, thoughts and beliefs, high trait anxious individuals might be prone to consciously process faces more

thoroughly than non-anxious individuals. These results are especially interesting since an explicit emotion recognition task was used. Thus each participant had to process these emotional expressions consciously, not only those participants who scored high trait anxiety points. Our result thus suggests that trait anxiety is associated with enhanced conscious processing even when conscious processing is required by the task at hand. Our results are in line with Holmes' et al. (2009) and Chronaki's et al. (2018) studies showing high trait anxiety to be associated with stronger LPP responses to emotional faces. However there are also studies that on the contrary to our results have found high trait anxiety to be associated with weaker LPP responses (Frenkel & Bar-Haim, 2011; Holmes et al., 2008) or have not found any association (Li et al., 2008).

There were no correlations between trait anxiety and the strength of the M220 responses. This is in conflict with previous research, since to our knowledge each of the studies examining this subject has found trait anxiety to affect the strength of the P200 (ERP equivalent to the M220) responses to emotional facial expressions (Bar-Haim et al., 2005; Eldar et al., 2010; Frenkel & Bar-Haim, 2011; Holmes et al., 2008). However, the methodologies used in these studies are different than ours. Only in Frenkel and Bar-Haim's (2011) study the participants were asked to identify the emotion. However, in their study the participants had to recognize only whether the facial expression was fearful or not. In addition, in line with our study, previous studies have shown that social anxiety does not have an effect on the P200 response when the emotion recognition task is explicit (Harrewijn et al., 2017). This supports the idea that the conflicting results between our study and previous studies could be explained by methodological differences. Altogether our results on the M220 response suggest that fearful faces are processed more thoroughly than other emotional or neutral expressions at this latency but this is not affected by trait anxiety. However, since this is in conflict with previous research, more research on this area is needed.

Based on our statistically significant correlations between trait anxiety scales and brain amplitudes, it is possible that the psychasthenia scale is more functionally related to the neurobiological correlates of trait anxiety than the inhibition of aggression scale. This is due to psychasthenia scale, inhibition of aggression scale and major trait anxiety scale being the only scales with significant correlations to the brain responses, and significant major trait anxiety scale correlation appearing only in the same time-window and brain area as some of the significant psychasthenia correlations, in the third time-window of the parietal area. Inhibition of aggression scale conversely seems to be more functionally independent from the major trait anxiety scale, due to the significant correlations appearing solely in the first time-window of the parietal area. No other scales have significant correlations in this area and time-window. These results suggest that evoked responses to face stimuli and trait anxiety are connected by two mechanisms. Firstly, inhibition of

aggression is connected to evoked response in the time-window that corresponds to the ERP component VPP. Secondly, a major trait anxiety factor, including psychasthenia, is connected to the evoked responses in the time-windows that correspond to the M170, and the M300 or the LPP. In conclusion, during a face perception task, trait anxiety first manifests as larger parietal evoked responses to the faces which are connected to automatic, unconscious inhibition of aggression. Approximately at the same time, enhanced processing of faces could start to manifest, at first automatically (bottom-up) and then consciously (top-down). Because the previous research concerning the neurobiological correlates of trait anxiety subscales in the context of emotional face processing is nonexistent, this result is the first of its kind.

To sum up, trait anxiety was associated with stronger responses on time-windows and areas that could correspond to the M170, VPP and the P300 or the LPP. However, since we decided on our time-windows based solely on visual presentation of grand averages, our time-windows might not exactly correspond to these ERP and EFF components. In addition, the method of choosing the channels for examination might have influenced the obtained findings. Also since we used MEG in our study and EEG has been used in all of the previous studies on this subject, our results might not be exactly comparable with the previous studies. Another reason why our results might have differed from past research is that we used a different trait anxiety inventory (KSP) than the majority of previous research (STAI). Even though earlier research shows that some of the KSP anxiety scales do correlate with STAI (e.g. Oldenburg, Lundh, & Kivistö, 2002), we did not find a comprehensive analysis about the relatedness between the two trait anxiety inventories. In addition, in our study the participants were asked to identify the emotion the facial expression was showing. Our study thus examined explicit emotion recognition while an implicit emotion recognition task has been used in most of the previous studies. This might also have had an effect on the results since the task used can affect the processing of the emotional face (Fusar-Poli et al., 2009).

Limitations and Future Research Directions

This study had some limitations, and firstly the sample of participants will be discussed. The sample size was somewhat low ($n = 14$) and because of the low participant number, a correlational analysis was used instead of composing a high and a low trait anxiety group as in the majority of previous research. This is important to note when combining research about this subject. In addition, all participants were males. Since gender can affect the activation of brain areas during a facial emotion

perception task (Fusar-Poli et al., 2009; Orozco & Ehlers, 1998), caution should be exercised when generalizing the results to females. Most of the participants also had a university-level education, which is connected to distinct processing of facial expressions when compared with lower level of education (Demenescu et al., 2014). Secondly, this study did not incorporate source modeling of the MEG signals. Source modeling would have given us more accurate locations of the MEG signals, but in this study we were concerned with broader brain regions for the investigation of preliminary effects and correlations. Future research should consider incorporating source modeling of the MEG signals for more accurate results. Thirdly, state anxiety was not controlled. This could have affected the results since trait and state anxiety are connected and the experiment could have induced state anxiety.

Conclusion

In line with our hypothesis, fearful faces elicited stronger M220 responses than sad, angry and neutral faces although these differences were only approaching significance. Against our hypothesis, no differences between emotional or neutral facial expressions were found in any other ERF components. In addition, there were no great differences between hemispheres, which was against our hypothesis. Our results thus suggest that the evoked responses measured from the visual areas were not sensitive to different negative emotional expressions, and the emotional expressions are for the most part processed in both hemispheres but could be more lateralized to the right hemisphere.

In line with our hypothesis, trait anxiety correlated positively with the strength of the M170, VPP and the M300 or the LPP responses to emotional or neutral facial expressions. These results thus suggest that trait anxiety is associated with an early threat processing bias, enhanced structural encoding of the face and enhanced conscious processing of emotional facial expressions and faces per se. However, since there are studies that are in conflict with our results, more research is needed to draw conclusions on how trait anxiety affects the processing of emotional facial expressions.

REFERENCES:

Adolphs, R. (2002a). Neural systems for recognizing emotion. *Current Opinion in Neurobiology*, 12(2), 169–177. [https://doi-org.ezproxy.jyu.fi/10.1016/S0959-4388\(02\)00301-X](https://doi-org.ezproxy.jyu.fi/10.1016/S0959-4388(02)00301-X)

- Adolphs, R. (2002b). Recognizing emotion from facial expressions: Psychological and neurological mechanisms. *Behavioral and Cognitive Neuroscience Reviews*, 1(1), 21–62. <https://doi-org.ezproxy.jyu.fi/10.1177/1534582302001001003>
- Aguado, L., Valdés-Conroy, B., Rodríguez, S., Román, F. J., Diéguez-Risco, T., & Fernández-Cahill, M. (2012). Modulation of early perceptual processing by emotional expression and acquired valence of faces: An ERP study. *Journal of Psychophysiology*, 26(1), 29–41. <https://doi-org.ezproxy.jyu.fi/10.1027/0269-8803/a000065>
- Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. (1999). Electrophysiological studies of human face perception I: Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex*, 9(5), 415–430. <https://doi-org.ezproxy.jyu.fi/10.1093/cercor/9.5.415>
- Amaral, D. G., Price, J. L., Pitkanen, A., & Carmichael, S. T. (1992). Anatomical organization of the primate amygdaloid complex. In J. P. Aggleton (Ed.), *The amygdala: Neurobiological aspects of emotion, memory, and mental dysfunction* (pp. 1-66). New York: Wiley-Liss.
- Arrais, K. C., Machado-de-Sousa, J. P., Trzesniak, C., Santos Filho, A., Ferrari, M. C. F., Osório, F. L., ... & Hallak, J. E. C. (2010). Social anxiety disorder women easily recognize fearful, sad and happy faces: the influence of gender. *Journal of Psychiatric Research*, 44(8), 535-540. <https://doi.org/10.1016/j.jpsychires.2009.11.003>
- Ashley, V., Vuilleumier, P., Swick, D. (2004). Time-course and specificity of event-related potentials to emotional expressions. *Neuroreport* 2004; 15:211–215. <https://doi.org/10.1097/01.wnr.0000091411.19795.f5>
- Bados, A., Gómez-Benito, J., & Balaguer, G. (2010). The state-trait anxiety inventory, trait version: does it really measure anxiety?. *Journal of personality assessment*, 92(6), 560-567. <https://doi.org/10.1080/00223891.2010.513295>
- Baillet, S. (2017). Magnetoencephalography for brain electrophysiology and imaging. *Nature Neuroscience*, 20(3), 327–339. <https://doi-org.ezproxy.jyu.fi/10.1038/nn.4504>
- Balconi, M., & Pozzoli, U. (2003). Face-selective processing and the effect of pleasant and unpleasant emotional expressions on ERP correlates. *International Journal of Psychophysiology*, 49(1), 67–74. [https://doi-org.ezproxy.jyu.fi/10.1016/S0167-8760\(03\)00081-3](https://doi-org.ezproxy.jyu.fi/10.1016/S0167-8760(03)00081-3)
- Bar-Haim, Y., Lamy, D., & Glickman, S. (2005). Attentional bias in anxiety: A behavioral and ERP study. *Brain and Cognition*, 59(1), 11–22. <https://doi-org.ezproxy.jyu.fi/10.1016/j.bandc.2005.03.005>
- Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research*, 17(3), 613–620. [https://doi-org.ezproxy.jyu.fi/10.1016/S0926-6410\(03\)00174-5](https://doi-org.ezproxy.jyu.fi/10.1016/S0926-6410(03)00174-5)

- 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. <https://doi-org.ezproxy.jyu.fi/10.1162/jocn.1996.8.6.551>
- Bistricky, S. L., Ingram, R. E., & Atchley, R. A. (2011). Facial affect processing and depression susceptibility: cognitive biases and cognitive neuroscience. *Psychological Bulletin*, 137(6), 998. <https://doi.org/10.1037/a0025348>
- Booth, R. W., Mackintosh, B., & Sharma, D. (2017). Working memory regulates trait anxiety-related threat processing biases. *Emotion*, 17(4), 616. <https://doi.org/10.1037/emo0000264>
- Bradley, B. P., Mogg, K., Falla, S. J., & Hamilton, L. R. (1998). Attentional bias for threatening facial expressions in anxiety: Manipulation of stimulus duration. *Cognition & Emotion*, 12(6), 737–753. <http://doi.org/10.1080/026999398379411>
- Brosschot, J. F., de Ruiter, C., & Kindt, M. (1999). Processing bias in anxious subjects and repressors, measured by emotional Stroop interference and attentional allocation. *Personality and Individual Differences*, 26(5), 777–793. [https://doi.org/10.1016/S0191-8869\(98\)00173-1](https://doi.org/10.1016/S0191-8869(98)00173-1)
- Campanella, S., Quinet, P., Bruyer, R., Crommelinck, M., & Guerit, J.-M. (2002). Categorical perception of happiness and fear facial expressions: An ERP study. *Journal of Cognitive Neuroscience*, 14(2), 210–227. <https://doi-org.ezproxy.jyu.fi/10.1162/089892902317236858>
- Carretié, L., Iglesias, J., García, T., & Ballesteros, M. (1997). N300, P300 and the emotional processing of visual stimuli. *Electroencephalography & Clinical Neurophysiology*, 103(2), 298–303. [https://doi-org.ezproxy.jyu.fi/10.1016/S0013-4694\(96\)96565-7](https://doi-org.ezproxy.jyu.fi/10.1016/S0013-4694(96)96565-7)
- 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. <https://doi-org.ezproxy.jyu.fi/10.1162/089892901753294400>
- Chronaki, G., Broyd, S. J., Garner, M., Benikos, N., Thompson, M. J. J., Sonuga-Barke, E. J. S., & Hadwin, J. A. (2018). The moderating effect of self-reported state and trait anxiety on the late positive potential to emotional faces in 6–11-year-old children. *Frontiers in Psychology*, 9. <https://doi-org.ezproxy.jyu.fi/10.3389/fpsyg.2018.00125>
- Cisler, J. M., & Koster, E. H. (2010). Mechanisms of attentional biases towards threat in anxiety disorders: An integrative review. *Clinical psychology review*, 30(2), 203–216. <https://doi.org/10.1016/j.cpr.2009.11.003>
- Cooper, R. M., Rowe, A. C., & Penton-Voak, I. S. (2008). The role of trait anxiety in the recognition of emotional facial expressions. *Journal of Anxiety Disorders*, 22(7), 1120–1127.

<https://doi.org/10.1016/j.janxdis.2007.11.010>

Demeneşcu, L. R., Kortekaas, R., den Boer, J. A., & Aleman, A. (2010). Impaired attribution of emotion to facial expressions in anxiety and major depression. *PloS one*, 5(12), e15058.

<https://doi.org/10.1371/journal.pone.0015058>

Demeneşcu, L. R., Stan, A., Kortekaas, R., van der Wee, N. J., Veltman, D. J., & Aleman, A. (2014). On the connection between level of education and the neural circuitry of emotion perception. *Frontiers in human neuroscience*, 8, 866.

<https://doi.org/10.3389/fnhum.2014.00866>

Dennis, T. A., & Chen, C.-C. (2007). Neurophysiological mechanisms in the emotional modulation of attention: The interplay between threat sensitivity and attentional control. *Biological Psychology*, 76(1–2), 1–10. <https://doi-org.ezproxy.jyu.fi/10.1016/j.biopsycho.2007.05.001>

Dima, D. C., Perry, G., Messaritaki, E., Zhang, J., & Singh, K. D. (2018). Spatiotemporal dynamics in human visual cortex rapidly encode the emotional content of faces. *Human Brain Mapping*, 39(10), 3993–4006. <https://doi-org.ezproxy.jyu.fi/10.1002/hbm.24226>

Di Russo, F., Martínez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human brain mapping*, 15(2), 95–111. <https://doi-org.ezproxy.jyu.fi/10.1002/hbm.10010>

Easter, J., McClure, E. B., Monk, C. S., Dhanani, M., Hodgdon, H., Leibenluft, E., ... & Ernst, M. (2005). Emotion recognition deficits in pediatric anxiety disorders: implications for amygdala research. *Journal of Child & Adolescent Psychopharmacology*, 15(4), 563–570. <https://doi.org/10.1089/cap.2005.15.563>

Eimer, M., and Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport* 13, 427–431. <https://doi.org/10.1097/00001756-200203250-00013>

Eimer, M., Holmes, A., & McGlone, F. P. (2003). The role of spatial attention in the processing of facial expression: An ERP study of rapid brain responses to six basic emotions. *Cognitive, Affective & Behavioral Neuroscience*, 3(2), 97–110. <https://doi-org.ezproxy.jyu.fi/10.3758/CABN.3.2.97>

Ekman, P., & Friesen, W. V. (1971). Constants across cultures in the face and emotion. *Journal of Personality and Social Psychology*, 17(2), 124–129. <https://doi-org.ezproxy.jyu.fi/10.1037/h0030377>

Eldar, S., Yankelevitch, R., Lamy, D., & Bar-Haim, Y. (2010). Enhanced neural reactivity and selective attention to threat in anxiety. *Biological Psychology*, 85(2), 252–257. <https://doi-org.ezproxy.jyu.fi/10.1016/j.biopsycho.2010.07.010>

- Endler, N. S., & Okada, M. (1975). A multidimensional measure of trait anxiety: The SR Inventory of General Trait Anxiousness. *Journal of Consulting and Clinical Psychology, 43*(3), 319. <http://doi.org/10.1037/h0076643>
- Endler, N. S., Magnusson, D., Ekehammar, B., & Okada, M. (1976). The multidimensionality of state and trait anxiety. *Scandinavian Journal of Psychology, 17*(1), 81-96. <https://doi-org.ezproxy.jyu.fi/10.1111/j.1467-9450.1976.tb00215.x>
- Endler, N. S., Parker, J. D., Bagby, R. M., & Cox, B. J. (1991). Multidimensionality of state and trait anxiety: Factor structure of the Endler Multidimensional Anxiety Scales. *Journal of Personality and social psychology, 60*(6), 919. <http://doi.org/10.1037/0022-3514.60.6.919>
- Endler, N. S., & Kocovski, N. L. (2001). State and trait anxiety revisited. *Journal of anxiety disorders, 15*(3), 231-245. [https://doi.org/10.1016/S0887-6185\(01\)00060-3](https://doi.org/10.1016/S0887-6185(01)00060-3)
- Engels, A. S., Heller, W., Mohanty, A., Herrington, J. D., Banich, M. T., Webb, A. G., & Miller, G. A. (2007). Specificity of regional brain activity in anxiety types during emotion processing. *Psychophysiology, 44*(3), 352-363. <https://doi.org/10.1111/j.1469-8986.2007.00518.x>
- Eysenck, H. J. (1983). Cicero and the state-trait theory of anxiety: Another case of delayed recognition. *American Psychologist, 38*(1), 114. <http://doi.org/10.1037/0003-066X.38.1.114>
- Fox, E., Derakshan, N., & Shoker, L. (2008). Trait anxiety modulates the electrophysiological indices of rapid spatial orienting towards angry faces. *NeuroReport: For Rapid Communication of Neuroscience Research, 19*(3), 259–263. <https://doi-org.ezproxy.jyu.fi/10.1097/WNR.0b013e3282f53d2a>
- Frenkel, T. I., & Bar-Haim, Y. (2011). Neural activation during the processing of ambiguous fearful facial expressions: An ERP study in anxious and nonanxious individuals. *Biological Psychology, 88*(2–3), 188–195. <https://doi-org.ezproxy.jyu.fi/10.1016/j.biopsycho.2011.08.001>
- 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: Japan, 34*(6), 418–432.
- Garner, M., Baldwin, D. S., Bradley, B. P., & Mogg, K. (2009). Impaired identification of fearful faces in Generalised Social Phobia. *Journal of Affective Disorders, 115*(3), 460-465. <https://doi.org/10.1016/j.jad.2008.10.020>
- Hajcak, G., Weinberg, A., MacNamara, A., & Foti, D. (2012). ERPs and the study of emotion. In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford handbook of event-related potential components*. (pp. 441–472). New York, NY: Oxford University Press. <https://doi.org/10.1093/oxfordhb/9780195374148.013.0222>

- Harrewijn, A., Schmidt, L. A., Westenberg, P. M., Tang, A., & van der Molen, M. J. W. (2017). Electrocortical measures of information processing biases in social anxiety disorder: A review. *Biological Psychology*, 129, 324–348. <https://doi-org.ezproxy.jyu.fi/10.1016/j.biopsycho.2017.09.013>
- Hinojosa, J. A., Mercado, F., & Carretié, L. (2015). N170 sensitivity to facial expression: A meta-analysis. *Neuroscience and Biobehavioral Reviews*, 55, 498–509. <https://doi-org.ezproxy.jyu.fi/10.1016/j.neubiorev.2015.06.002>
- Holmes, A., Nielsen, M. K., & Green, S. (2008). Effects of anxiety on the processing of fearful and happy faces: an event-related potential study. *Biological psychology*, 77(2), 159-173. <https://doi.org/10.1016/j.biopsycho.2007.10.003>
- Holmes, A., Nielsen, M. K., Tipper, S., & Green, S. (2009). An electrophysiological investigation into the automaticity of emotional face processing in high versus low trait anxious individuals. *Cognitive, Affective & Behavioral Neuroscience*, 9(3), 323–334. <https://doi-org.ezproxy.jyu.fi/10.3758/CABN.9.3.323>
- Hu, Y., & Dolcos, S. (2017). Trait anxiety mediates the link between inferior frontal cortex volume and negative affective bias in healthy adults. *Social cognitive and affective neuroscience*, 12(5), 775-782. <https://dx.doi.org/10.1093%2Fscan%2Fnsx008>
- Hunter, L. R., Buckner, J. D., & Schmidt, N. B. (2009). Interpreting facial expressions: The influence of social anxiety, emotional valence, and race. *Journal of Anxiety Disorders*, 23(4), 482-488. <https://dx.doi.org/10.1016%2Fj.janxdis.2008.10.004>
- Indovina, I., Robbins, T. W., Núñez-Elizalde, A. O., Dunn, B. D., & Bishop, S. J. (2011). Fear-conditioning mechanisms associated with trait vulnerability to anxiety in humans. *Neuron*, 69(3), 563-571. <https://doi.org/10.1016/j.neuron.2010.12.034>
- Itier, R. J., Herdman, A. T., George, N., Cheyne, D., & Taylor, M. J. (2006). Inversion and contrast-reversal effects on face processing assessed by MEG. *Brain Research*, 1115(1), 108–120. <https://doi-org.ezproxy.jyu.fi/10.1016/j.brainres.2006.07.072>
- Joormann, J., & Gotlib, I. H. (2006). Is this happiness I see? Biases in the identification of emotional facial expressions in depression and social phobia. *Journal of abnormal psychology*, 115(4), 705. <https://doi.org/10.1037/0021-843X.115.4.705>
- af Klinteberg, B., Magnusson, D., & Schalling, D. (1986). Self-report assessment of personality traits: Data from the KSP inventory on a representative sample of normal male and female subjects within a developmental project. Department of psychology, University of Stockholm.

- Koster, E. H., Verschuere, B., Crombez, G., & Van Damme, S. (2005). Time-course of attention for threatening pictures in high and low trait anxiety. *Behaviour research and therapy*, 43(8), 1087-1098. <https://doi.org/10.1016/j.brat.2004.08.004>
- Krolak-Salmon, P., Fischer, C., Vighetto, A., & Mauguière, F. (2001). Processing of facial emotional expression; Spatio-temporal data as assessed by scalp event-related potentials. *European Journal of Neuroscience*, 13(5), 987–994. <https://doi-org.ezproxy.jyu.fi/10.1046/j.0953-816x.2001.01454.x>
- Laurian, S., Bader, M., Lanares, J., & Oros, L. (1991). Topography of event-related potentials elicited by visual emotional stimuli. *International Journal of Psychophysiology*, 10(3), 231–238. [https://doi-org.ezproxy.jyu.fi/10.1016/0167-8760\(91\)90033-T](https://doi-org.ezproxy.jyu.fi/10.1016/0167-8760(91)90033-T)
- LeDoux, J. (1998). *The emotional brain: the mysterious underpinnings of emotional life*. New York: Simon and Schuster.
- Lee, L. O., & Knight, B. G. (2009). Attentional bias for threat in older adults: moderation of the positivity bias by trait anxiety and stimulus modality. *Psychology and aging*, 24(3), 741. <https://doi.org/10.1037/a0016409>
- Li, W., Zinbarg, R. E., Boehm, S. G., & Paller, K. A. (2008). Neural and behavioral evidence for affective priming from unconsciously perceived emotional facial expressions and the influence of trait anxiety. *Journal of Cognitive Neuroscience*, 20(1), 95–107. <https://doi-org.ezproxy.jyu.fi/10.1162/jocn.2008.20006>
- Liddell, B. J., Williams, L. M., Rathjen, J., Shevrin, H., & Gordon, E. (2004). A Temporal Dissociation of Subliminal versus Supraliminal Fear Perception: An Event-related Potential Study. *Journal of Cognitive Neuroscience*, 16(3), 479–486. <https://doi-org.ezproxy.jyu.fi/10.1162/089892904322926809>
- Liu, J., Harris, A., & Kanwisher, N. (2002). Stages of processing in face perception: An MEG study. *Nature Neuroscience*, 5(9), 910–916. <https://doi-org.ezproxy.jyu.fi/10.1038/nn909>
- Lu, M., Yang, C., Chu, T., & Wu, S. (2018). Cerebral White Matter Changes in Young Healthy Individuals With High Trait Anxiety: A Tract-Based Spatial Statistics Study. *Frontiers in neurology*, 9. <https://dx.doi.org/10.3389%2Ffneur.2018.00704>
- Luck, S. J., & Kappenman, E. S. (2012). ERP components and selective attention. In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford handbook of event-related potential components*. (pp. 295–327). New York, NY: Oxford University Press. <https://doi.org/10.1093/oxfordhb/9780195374148.013.0144>

- Luo, W., Feng, W., He, W., Wang, N.-Y., & Luo, Y.-J. (2010). Three stages of facial expression processing: ERP study with rapid serial visual presentation. *NeuroImage*, 49(2), 1857–1867. <https://doi-org.ezproxy.jyu.fi/10.1016/j.neuroimage.2009.09.018>
- Lundqvist, D., Flykt, A. and Öhman, A. 1998. The Karolinska Directed Emotional Faces (KDEF), Stockholm: Department of Neurosciences Karolinska Hospital.
- Lönnqvist, J., Marttunen, M., Henriksson, M., Partonen, T. & Seppälä, O. (2017). *Psykiatria*. [Helsinki]: Kustannus Oy Duodecim.
- Mangun, G. R., & Buck, L. A. (1998). Sustained visual-spatial attention produces costs and benefits in response time and evoked neural activity. *Neuropsychologia*, 36(3), 189–200. [https://doi-org.ezproxy.jyu.fi/10.1016/S0028-3932\(97\)00123-1](https://doi-org.ezproxy.jyu.fi/10.1016/S0028-3932(97)00123-1)
- Mansell, W., Ehlers, A., Clark, D., & Chen, Y. P. (2002). Attention to positive and negative social-evaluative words: Investigating the effects of social anxiety, trait anxiety and social threat. *Anxiety, Stress & Coping*, 15(1), 19-29. <https://doi.org/10.1080/10615800290007263>
- Marinkovic, K., & Halgren, E. (1998). Human brain potentials related to the emotional expression, repetition, and gender of faces. *Psychobiology*, 26(4), 348–356. <https://doi.org/10.3758/BF03330621>
- Mathews, A., & MacLeod, C. (2005). Cognitive vulnerability to emotional disorders. *Annu. Rev. Clin. Psychol.*, 1, 167-195. <https://doi.org/10.1146/annurev.clinpsy.1.102803.143916>
- Mogg, K., Mathews, A., & Weinman, J. (1987). Memory bias in clinical anxiety. *Journal of abnormal psychology*, 96(2), 94. <http://dx.doi.org/10.1037/0021-843X.96.2.94>
- Montag, C., Reuter, M., Weber, B., Markett, S., & Schoene-Bake, J. C. (2012). Individual differences in trait anxiety are associated with white matter tract integrity in the left temporal lobe in healthy males but not females. *Neuroscience*, 217, 77-83. <https://doi.org/10.1016/j.neuroscience.2012.05.017>
- Morel, S., George, N., Foucher, A., Chammat, M., & Dubal, S. (2014). ERP evidence for an early emotional bias towards happy faces in trait anxiety. *Biological Psychology*, 99, 183–192. <https://doi-org.ezproxy.jyu.fi/10.1016/j.biopsycho.2014.03.011>
- Morris, J. S., Öhman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating “unseen” fear. *Proceedings of the National Academy of Sciences* Feb 1999, 96 (4) 1680-1685. <https://doi.org/10.1073/pnas.96.4.1680>

- Mundy, E. A., Weber, M., Rauch, S. L., Killgore, W. D., Simon, N. M., Pollack, M. H., & Rosso, I. M. (2015). Adult anxiety disorders in relation to trait anxiety and perceived stress in childhood. *Psychological reports, 117*(2), 473-489.
<https://doi.org/10.2466/02.10.PR0.117c17z6>
- Muris, P., Schmidt, H., Merckelbach, H., & Schouten, E. (2001). Anxiety sensitivity in adolescents: factor structure and relationships to trait anxiety and symptoms of anxiety disorders and depression. *Behaviour research and therapy, 39*(1), 89-100.
[http://dx.doi.org/10.1016/S0005-7967\(99\)00179-5](http://dx.doi.org/10.1016/S0005-7967(99)00179-5)
- Murphy, F. C., Nimmo-Smith, I., & Lawrence, A. D. (2003). Functional neuroanatomy of emotions: A meta-analysis. *Cognitive, Affective & Behavioral Neuroscience, 3*(3), 207–233. <https://doi-org.ezproxy.jyu.fi/10.3758/CABN.3.3.207>
- Nolen-Hoeksema, S., Fredrickson, B., Wagenaar, W. A., Loftus, G. R., Atkinson, R. L. & Hilgard, E. R. (2009). *Atkinson & Hilgard's introduction to psychology* (15th ed.). Andover: Wadsworth/Cengage Learning.
- Oldenburg, C., Lundh, L. G., & Kivistö, P. (2002). Explicit and implicit memory, trait anxiety, and repressive coping style. *Personality and Individual Differences, 32*(1), 107-119.
[https://doi.org/10.1016/S0191-8869\(01\)00009-5](https://doi.org/10.1016/S0191-8869(01)00009-5)
- Orozco, S., & Ehlers, C. L. (1998). Gender differences in electrophysiological responses to facial stimuli. *Biological Psychiatry, 44*(4), 281–289. [https://doi-org.ezproxy.jyu.fi/10.1016/S0006-3223\(97\)00487-3](https://doi-org.ezproxy.jyu.fi/10.1016/S0006-3223(97)00487-3)
- Paulmann, S., & Pell, M. D. (2009). Facial expression decoding as a function of emotional meaning status: ERP evidence. *NeuroReport: For Rapid Communication of Neuroscience Research, 20*(18), 1603–1608. <https://doi-org.ezproxy.jyu.fi/10.1097/WNR.0b013e3283320e3f>
- Phan, K. L., Orlichenko, A., Boyd, E., Angstadt, M., Coccaro, E. F., Liberzon, I., & Arfanakis, K. (2009). Preliminary evidence of white matter abnormality in the uncinate fasciculus in generalized social anxiety disorder. *Biological psychiatry, 66*(7), 691-694.
<http://dx.doi.org/10.1016/j.biopsych.2009.02.028>
- Phan, K. L., Wager, T., Taylor, S. F., & Liberzon, I. (2002). Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage, 16*(2), 331–348.
<https://doi.org/10.1006/nimg.2002.1087>
- Philippot, P., & Douilliez, C. (2005). Social phobics do not misinterpret facial expression of emotion. *Behaviour Research and Therapy, 43*(5), 639-652.
<http://dx.doi.org/10.1016/j.brat.2004.05.005>

- Polich, J. (2007). Updating p300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, 118(10), 2128–2148. <https://doi-org.ezproxy.jyu.fi/10.1016/j.clinph.2007.04.019>
- Porta, D., Goldberg, X., Martínez-Zalacaín, I., González, I., Fullana, M., Harrison, B. J., ... & Via, E. (2017a). 121. From Healthy to Pathological Anxiety: Testing the Prefronto-Subcortical Circuit in High Anxiety-Trait and Generalized Anxiety Disorder. *Biological Psychiatry*, 81(10), S51. <https://doi.org/10.1016/j.biopsych.2017.02.133>
- Porta, D., Goldberg, X., Martínez-Zalacaín, I., González, I., Fullana, M., Pujol, J., ... & Cardoner, N. (2017b). The prefrontal-amygdala circuit in trait anxiety and generalized anxiety disorder. Testing the boundaries between healthy and pathological worries. *Age (years)*, 23(4.73), 21-61. [http://doi.org/10.1016/S0924-977X\(17\)31754-6](http://doi.org/10.1016/S0924-977X(17)31754-6)
- Posamentier, M.T., & Abdi, H.. (2003). Processing faces and facial expressions. *Neuropsychology Review*, 13 (3) (2003), pp. 113-143. <https://doi-org.ezproxy.jyu.fi/10.1023/A:1025519712569>
- Proudfoot, M., Woolrich, M.W., Nobre, A.C. & Turner, M.R. (2014). *PractNeurol*. 14:336–343. doi: <http://dx.doi.org/10.1136/practneurol-2013-000768>
- Pulkkinen, L., Virtanen, T., Klinteberg, B. A., & Magnusson, D. (2000). Child behaviour and adult personality: Comparisons between criminality groups in finland and sweden. *Criminal Behaviour and Mental Health : CBMH*, 10(3), 155. doi: <http://dx.doi.org/10.1002/cbm.354>
- Rossignol, M., Philippot, P., Douilliez, C., Crommelinck, M., & Campanella, S. (2005). The perception of fearful and happy facial expression is modulated by anxiety: an event-related potential study. *Neuroscience letters*, 377(2), 115-120. <https://doi.org/10.1016/j.neulet.2004.11.091>
- Rossion, B., & Caharel, S. (2011). ERP evidence for the speed of face categorization in the human brain: Disentangling the contribution of low-level visual cues from face perception. *Vision Research*, 51(12), 1297–1311. <https://doi-org.ezproxy.jyu.fi/10.1016/j.visres.2011.04.003>
- Rossion, B. & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *NeuroImage*, 39 (2008), pp. 1959-1979. <https://doi.org/10.1016/j.neuroimage.2007.10.011>
- Rossion, B., & Jacques, C. (2012). The N170: Understanding the time course of face perception in the human brain. In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford handbook of event-related potential components*. (pp. 115–141). New York, NY: Oxford University Press. <https://doi.org/10.1093/oxfordhb/9780195374148.013.0064>
- 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(10), 1490–1501. <https://doi-org.ezproxy.jyu.fi/10.1002/hbm.20952>

- Sato, W., Kochiyama, T., Yoshikawa, S., & Matsumura, M. (2001). Emotional expression boosts early visual processing of the face: ERP recording and its decomposition by independent component analysis. *NeuroReport: For Rapid Communication of Neuroscience Research*, 12(4), 709–714. <https://doi-org.ezproxy.jyu.fi/10.1097/00001756-200103260-00019>
- Sawada, R., Sato, W., Uono, S., Kochiyama, T., & Toichi, M. (2014). Electrophysiological correlates of the efficient detection of emotional facial expressions. *Brain research*, 1560, 60-72. <https://doi.org/10.1016/j.brainres.2014.02.046>
- Schmidt, N. B., Lerew, D. R., & Jackson, R. J. (1997). The role of anxiety sensitivity in the pathogenesis of panic: Prospective evaluation of spontaneous panic attacks during acute stress. *Journal of abnormal psychology*, 106(3), 355. <http://dx.doi.org/10.1037/0021-843X.106.3.355>
- Schmidt, N. B., Lerew, D. R., & Jackson, R. J. (1999). Prospective evaluation of anxiety sensitivity in the pathogenesis of panic: replication and extension. *Journal of abnormal psychology*, 108(3), 532. <http://dx.doi.org/10.1037/0021-843X.108.3.532>
- Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2003). Emotional facilitation of sensory processing in the visual cortex. *Psychological Science*, 14(1), 7–13. <https://doi-org.ezproxy.jyu.fi/10.1111/1467-9280.01411>
- Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2004). The selective processing of briefly presented affective pictures: An ERP analysis. *Psychophysiology*, 41(3), 441–449. <https://doi-org.ezproxy.jyu.fi/10.1111/j.1469-8986.2004.00174.x>
- Schutter, D. J. L. G., de Haan, E. H. F., & van Honk, J. (2004). Functionally dissociated aspects in anterior and posterior electrocortical processing of facial threat. *International Journal of Psychophysiology*, 53(1), 29–36. <https://doi-org.ezproxy.jyu.fi/10.1016/j.ijpsycho.2004.01.003>
- Sprengelmeyer, R., Young, A. W., Pundt, I., Sprengelmeyer, A., Calder, A. J., Berrios, G., ... & Przuntek, H. (1997). Disgust implicated in obsessive–compulsive disorder. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 264(1389), 1767-1773. <https://dx.doi.org/10.1098%2Frsph.1997.0245>
- Surcinelli, P., Codispoti, M., Montebanocci, O., Rossi, N., & Baldaro, B. (2006). Facial emotion recognition in trait anxiety. *Journal of anxiety disorders*, 20(1), 110-117. <https://doi.org/10.1016/j.janxdis.2004.11.010>
- Takagi, Y., Sakai, Y., Abe, Y., Nishida, S., Harrison, B. J., Martinez-Zalacain, I., ... & Tanaka, S. C. (2018). A common brain network among state, trait, and pathological anxiety from whole-brain functional connectivity. *NeuroImage*, 172, 506-516. <https://doi.org/10.1016/j.neuroimage.2018.01.080>

- Torro-Alves, N., Bezerra, I. A. D. O., Rodrigues, M. R., Machado-de-Sousa, J. P., Osório, F. D. L., & Crippa, J. A. (2016). Facial emotion recognition in social anxiety: The influence of dynamic information. *Psychology & Neuroscience*, 9(1), 1. <http://doi.org/10.1037/pne0000042>
- Vassilopoulos, S. P. (2005). Social anxiety and the vigilance-avoidance pattern of attentional processing. *Behavioural and Cognitive Psychotherapy*, 33(1), 13-24. <http://doi.org/10.1017/S1352465804001730>
- Walentowska, W., & Wronka, E. (2012). Trait anxiety and involuntary processing of facial emotions. *International Journal of Psychophysiology*, 85(1), 27–36. <https://doi-org.ezproxy.jyu.fi/10.1016/j.ijpsycho.2011.12.004>
- Walsh, J. J., McNally, M. A., Skariah, A., Butt, A. A., & Eysenck, M. W. (2015). Interpretive bias, repressive coping, and trait anxiety. *Anxiety, Stress, & Coping*, 28(6), 617-633. <https://doi.org/10.1080/10615806.2015.1007047>
- Whalen, P. J. (1998). Fear, vigilance, and ambiguity: Initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science*, 7(6), 177–188. <https://doi-org.ezproxy.jyu.fi/10.1111/1467-8721.ep10836912>
- Wieckowski, A. T., Coffman, M. C., Kim-Spoon, J., White, S. W., Richey, J. A., & Ollendick, T. H. (2016). Impaired fear recognition and social anxiety symptoms in adolescence. *Journal of child and family studies*, 25(11), 3381-3386. <https://doi.org/10.1007/s10826-016-0491-9>
- Williams, L. M., Kemp, A. H., Felmingham, K., Liddell, B. J., Palmer, D. M., & Bryant, R. A. (2007). Neural biases to covert and overt signals of fear: Dissociation by trait anxiety and depression. *Journal of Cognitive Neuroscience*, 19(10), 1595–1608. <https://doi-org.ezproxy.jyu.fi/10.1162/jocn.2007.19.10.1595>
- Williams, J. M. G., Watts, F. N., MacLeod, C., & Mathews, A. (1988). *Cognitive psychology and emotional disorders*. John Wiley & Sons.
- Yang, T. T., Menon, V., Eliez, S., Blasey, C., White, C. D., Reid, A. J., Gotlib, I. H., & Reiss, A. L. (2002). Amygdalar activation associated with positive and negative facial expressions. *NeuroReport: For Rapid Communication of Neuroscience Research*, 13(14), 1737–1741. <https://doi-org.ezproxy.jyu.fi/10.1097/00001756-200210070-00009>
- Zhang, H., Japee, S., Nolan, R., Chu, C., Liu, N., & Ungerleider, L. G. (2016). Face-selective regions differ in their ability to classify facial expressions. *NeuroImage*, 130, 77–90. <https://doi-org.ezproxy.jyu.fi/10.1016/j.neuroimage.2016.01.045>