FACING EMOTIONAL FACES

THE NATURE OF AUTOMATICITY OF FACIAL EMOTION PROCESSING STUDIED WITH ERPS

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Contents

Chapter 1.

GENERAL INTRODUCTION: EMOTIONAL EXPRESSION PROCESSING – EXPERIMENTAL APPROACH

1.1. Facial emotion processing and event-related brain potentials

Faces are perhaps the most important object category in visual perception, as they frequently convey behaviourally, socially, and emotionally relevant information which is critical for the adaptive control of action. Given this undisputed significance of faces, it is not surprising that the study of human face processing has been for a long time one of the most active research areas in the visual cognition. In the recent years, numerous new insights into the mechanisms and neural processes which underlie the ability to perceive and recognize faces have come from studies investigating face processing with clinical and experimental neuroscientific methods. Among them, functional resonance imaging (fMRI) with its good spatial resolution, as well as magnetoencephalography (MEG), and both scalp and intracranial recordings of electroencephalography (EEG) with their satisfying temporal resolution have been in common use.

The main rationale for this effort is the fact that emotional functioning determines important evolutionary adaptations involved in the control of behaviour in complex social environments. Among sources of social information, emotional faces are salient stimuli conveying essential nonverbal signals. For that reason they are assumed to be the best direct indicator of current affective dispositions and attitudes, both positive and negative. Specifically, due to their biological and social significance, information about emotional states derived from faces should be processed very rapidly to be available for the immediate regulation of behaviour. From the other point of view, however, negative consequences of rapid face categorization may be the tendencies to form stereotypes and prejudices.

There is general consensus that faces are processed preferentially among various visual stimuli, which can be reflected in distinct patterns of brain activity (Bentin et al., 1996; Ishai et al., 2005; Kanwisher et al., 1997). There are also results suggesting that face processing engages broadly distributed and highly specialized neural network. The initial perceptual analysis of faces activates the inferior occipital cortex (the occipital face area, OFA; Rossion et al., 2003a) and the lateral fusiform gyrus (the fusiform face area, FFA; Kanwisher et al., 1997), where the invariant aspects of faces are elaborated enabling later identity recognition. Simultaneously, a region around the superior temporal sulcus (STS) is involved in the analyses of the changeable face features, such as facial expression, eye and mouth movements (Allison et al., 2000). Moreover, electrophysiological findings indicate that face exposition produces a specific ERP component, the N170 (Bentin et al., 1996; Itier and Taylor, 2004). Importantly, findings from studies, where neural generators of the N170 or its counterpart detected with MEG (M170) have been identified, indicate that the fusiform gyrus (Halgren et al., 2000; Itier et al., 2006; Rossion et al., 1999; Rossion et al., 2003b), as well as the superior temporal gyrus (Itier et al., 2007; Itier and Taylor, 2004) are their possible sources.

Recent studies have indicated that a stimulus can be categorized as a face much earlier than other objects (Liu et al., 2002). Some psychophysiological studies also suggest that emotional information from faces can be registered and discriminated very rapidly. Responses measured over occipital regions differentiate negative expressions from positive ones starting from 100 milliseconds after stimulus onset (Pourtois et al., 2004). Notably, however, when brain responses to emotional faces were compared to responses to neutral ones, a differential effect has been observed with slightly longer latencies. Larger amplitudes of the N170 component of the ERP have been recorded to faces when compared to non-face objects. The onset of the face effect has been observed remarkably early, between 140-200 milliseconds post-stimulus from occipito-temporal locations (Batty and Taylor, 2003; Bentin et al., 1996; Eimer, 2000; Itier and Taylor, 2004). Similarly, the M170, the magnetic counterpart of the N170 scalp potential, is also face-sensitive, as revealed by Halgren et al. (2000). Evidence supporting face-specific mechanisms has been provided by studies showing that stimulus inversion disrupts the processing of faces more than other objects, which has been termed as the face inversion effect (Yin, 1969). It has been revealed by numerous ERP studies that the face-sensitive N170 is strongly influenced by the face inversion. In comparison to upright presentations, when faces are presented upside-down the N170 latency is significantly delayed, and its amplitude may be larger, however only if subject is engaged in an explicit face discrimination task (Rossion et al., 1999).

There are also a number of studies in which the amplitude of N170 recorded in response to emotional faces has been found to be larger than for neutral faces (Batty and Taylor, 2003; Blau et al., 2007; Miyoshi et al., 2004; Rigato et al., 2010; Vlamings et al., 2009). At later stages, authors have reported increased activity of the visual system elicited by facial emotions in comparison to neutral ones. This effect has been termed as the Early Posterior Negativity (EPN; Sato et al., 2001; Schupp et al., 2004b). Enhanced negativity elicited by emotional expressions was obtained about 200 milliseconds after stimulus onset. Recently, it has been suggested that the EPN reflects the activation of temporo-parieto-occipital areas engaged in the visual information processing, when stimuli of high evolutionary significance are presented (Schupp et al., 2003, 2004a).

In other studies, enhanced fronto-central positivity was elicited starting from 150 milliseconds post-stimulus by the exposition of emotional faces as compared to neutral ones (Eimer and Holmes, 2002; Eimer et al., 2003; Holmes et al., 2003, 2006). What is also important, analogous emotional expression effects, reflected in the fronto-central positivity, have been found for six basic emotions (Eimer et al., 2003). Finally, although some researchers treat this as a kind of controversy, early ERP components reflecting visual processing, like the occipital P1 component recorded around 100 milliseconds after stimulus onset, can also be expression-sensitive (Holmes et al., 2008, 2009; Pourtois et al., 2005).

Numerous emotion-specific effects have been obtained in experiments with relatively long, supraliminal face presentations. However, affectively salient facial stimuli can capture attention and evoke specific electrophysiological responses even without reaching the level of conscious awareness. It has been suggested that subliminal processing of expressive facial cues may be mediated *via* a 'short' retino-thalamic-amygdalar neural pathway (Pessoa, 2005). Nevertheless, some emotional expression effects can be eliminated when attention is directed away from the location of peripherally presented emotional faces, which indicates that attention can effectively modulate the processing of facial emotions at early stages. These results are consistent with some neuroimaging studies reporting different responses of the visual areas specialized in face processing, as well as the amygdala, to faces signalling emotions as compared to neutral expressions (Pessoa et al., 2002b). Such differentiation has not been observed when attention was directed towards other objects with different spatial location.

To summarize, facial emotional expressions are salient stimuli, which significantly influence human brain activity. Their processing is rapid, as some emotional expression effects have been consequently obtained starting from 100 milliseconds post-stimulus. Moreover, due to the possible links between some subcortical structures and the posterior cortical areas, facial emotions can evoke similar brain responses in case of both subliminal and supraliminal presentations. Another important factor, irrespective of the duration of facial stimuli presentation, is undoubtedly the influence of the attentional processes. All these points will be the issue of further dissertation in a light of the privileged processing of facial emotional expressions.

1.2. The influence of individual differences on the emotional face perception

It has been known for a long time that some clinical conditions are distinctively linked with the processing of affective information. The most evident example can be found in the anxious or depressed patients, and their particular processing of stimuli with a negative valence (Williams et al., 1988). However, it has been recently realized that also subclinical personality- or temperament-related traits can influence the type of information which captures subject's attention. Individuals, who score high on the anxiety scales, are generally drawn towards negative information (MacLeod and Mathews, 1988; MacLeod et al., 1986). In the experimental manner, highly anxious individuals are more likely to orient towards negative facial emotions (Bradley et al., 1998; Fox, 2002; Mogg and Bradley, 1999), and are slower in disengaging attention from negative expressions (Fox et al., 2001).

The general consensus comes both from electrophysiological and neuroimaging studies that emotionally salient faces have a special status in capturing visual attention, even involuntarily. However, still little is known about the neural correlates of the emotionally-rooted temperamental traits influencing information processing from the perspective of the subjects. Specifically, it has been suggested that the cognitive system of anxious individuals, characterized by the state or trait of apprehension, may be distinctively sensitive and may bias the processing of threat-related stimuli. Whalen (1998) suggests that fearful stimuli in comparison to angry ones evoke stronger brain responses due to their ambiguity. In the light of anxiety-related hypervigilance, perception of stimuli requiring more information to be interpreted may result in stronger activation of the anxious individuals. Generally, to study this issue more thoroughly, both clinical populations (displaying diverse anxiety disorders) and subclinical subjects (reporting high levels of trait anxiety in the State-Trait Anxiety Inventory; Spielberger et al., 1983) have been employed. It has been assumed that in high-anxious individuals threat-related information can rapidly capture attention (Bar-Haim et al., 2007; Mathews and Mackintosh, 1998; Mathews and MacLeod, 2002) even without conscious processing of the stimuli (Mogg and Bradley, 1998). Numerous neuroimaging studies confirm these results showing increased amygdala activity in highly trait anxious individuals during unconscious processing of fearful stimuli (Bishop, 2007; Etkin et al., 2004) when compared with low-anxious individuals. Consistent with these results, Ewbank et al. (2009) have obtained a significant positive correlation between the level of anxiety and the left amygdala activity in response to fearful expressions in condition when they were task-irrelevant and, due to attentional modulation, their processing was involuntary. Furthermore, early attentional orienting to threatening stimuli in high-anxious individuals has been shown in numerous electrophysiological studies suggesting privileged threat evaluation at initial stages (Fox et al., 2008; Li et al., 2005). Therefore, anxiety-related effects can be observed starting about 100 milliseconds after stimulus onset, which is consistent with the hypothesis that high level of anxiety can be linked with hypervigilant processing of emotional information. However, in one of the recent ERP studies in anxious individuals, which has aimed to examine the automaticity in facial emotion processing in tasks with different cognitive load (Holmes et al., 2009), authors have revealed that while the EPN differentiation was more apparent within low-anxious group, the P1 modulation was not influenced by the level of anxiety.

To review, it should be suggested that a complete investigation of cognitive and neural mechanisms involved in the expression recognition should take individual differences, like trait anxiety, into account. Specifically, their role in the understanding of specific sensitivity towards emotional information should help in shaping a construct of the privileged processing of facial emotions, which will be an important point of this dissertation.

1.3. The idea of automaticity and prioritization of emotional expression processing

Emotions help to shape information gathering, such that motivationally relevant items receive heightened attention (Lang and Davis, 2006). The processing of emotional stimuli is often proposed to take place in an automatic fashion, which is to happen independently of top-down factors (such as attention and awareness) and irrespective of the internal dispositions of the perceiver (personality or temperament-related individual differences). More generally, although the construct of automaticity is operationalized in quite different ways across studies in cognitive and social psychology, it can be characterized as involving processing occurring independently of the availability of resources, not affected by intentions and strategies, and not necessarily tied to conscious processing (Jonides, 1981; Posner and Snyder, 1975). A reformulated and complex definition of the automaticity has also been proposed by Palermo and Rhodes (2007), where the idea of rapid, unconscious, mandatory, and capacity-free processes has been presented. From a more clinical perspective, cognitive models of anxiety also assume the existence of a prioritized and largely automatic threat-processing system, and propose that anxiety is characterized by attentional bias that favours the processing of threat cues. These biases are proposed to be associated with individual differences in clinical anxiety susceptibility (Bishop, 2007; Mogg and Bradley, 1998).

In the recent years, a host of experimental paradigms have documented ways in which the processing of emotion-laden stimuli is prioritized. These include detection, search, interference, masking, and attentional blink procedures. For instance, negative arousing pictures capture and hold attention, impairing participants' ability to perform a simple task on a subsequent target stimulus in a rapid stream of visual stimuli (Most el al., 2005). Emotional state can also influence attention. Whereas negative emotions appear to narrow thought and action repertoires, positive emotions broaden them as well as the scope of attention (Fredrickson and Branigan, 2005). Consistent with this notion, a recent neuroimaging study showed that positive and negative states had opposing influences over perceptual encoding in early visual cortices, with positive states broadening and negative states narrowing the field of attention (Schmitz et al., 2009). The mechanisms underlying affective prioritization continue to be the target of the research, but are generally believed to be related to increased sensory processing to affective stimuli. Bradley and colleagues (2003) have reported more extensive visual cortex activity when participants viewed emotional compared to neutral pictures. Later, Padmala and Pessoa (2008) showed a close link between improvements in behavioural performance and trial-by-trial responses in the early visual cortex, including primary visual cortex, during the processing of affectively significant visual objects. Increased cortical responses in the visual cortex to affective stimuli may be due to the modulatory signals from the amygdala, which is consistent with the existence of efferent projections reaching many levels of the visual cortex (Amaral et al., 1992). Indeed, patients with the amygdala lesions failed to exhibit differential responses in the visual cortex when viewing emotional faces (Vuilleumier et al., 2004).

In the investigation of the automaticity of facial emotion processing, the lack of being consciously aware of the presented stimuli is probably one of the most prominent issues for examination. Conscious awareness may be disrupted by some neuropsychological disorders of vision, like prosopagnosia, which is a specific impairment of face recognition (Hecaen and Angelergues, 1962). Experimentally and in healthy subjects, the state of unconsciousness can be simulated by very brief and backward masked stimuli presentations. Both healthy subjects and prosopagnosic patients appear to be able to encode some facial information without conscious awareness. Experimental evidence that facial threat is privileged in the processing comes mostly from studies where backward masking procedure has been used. With this technique, Whalen et al. (1998) have found stronger activity of the amygdala to fearful faces relative to happy ones. From the other hand, results obtained by Pessoa et al. (2006) suggest that the amygdala activity in response to fearful faces is probably related to the objectively assessed visibility of masked stimuli. In recent ERP studies authors report fear-specific patterns of brain activity in response to subliminal processing of backward masked facial stimuli (Eimer et al., 2008; Kiss and Eimer, 2008). Both experiments, conducted by the same group of researchers, have revealed no effects recorded in the time window of the N170 component. In contrast, Pegna et al. (2008) have found that subliminally presented fearful faces elicited larger N170 amplitudes than non-fearful (happy and neutral) faces. What should be noticed, this early effect has been obtained in a task demanding active detection of fearful faces, which can be related to voluntary attention involvement. Nevertheless, although all these experiments successfully explore the topic of subliminal processing of facial emotions, at least one imperfection can be found in the experimental procedures, which is the type of the mask. Eimer et al. (2008) and Pegna et al. (2008) used images of neutral faces as the masking stimuli. Kiss and Eimer (2008) used scrambled neutral faces, although the images probably still resulted in oval-shaped and face-similar masking objects. In this context it should be emphasised that the probability that brain responses to subliminally presented faces can interfere with responses to masking facial stimuli is relatively high and may serve to disrupt the analyses.

On the contrary to the reports confirming facial emotion processing during subliminal face presentations and without reaching the conscious awareness, some recent studies suggest instead that affective processing is, in many circumstances, under the control of attention. Attentional mechanisms bias information processing in the brain and lead to a selective perception of a small part of the enormous amount of stimulation continuously coming to our senses. There is some evidence that emotional expression effect observed at early stages of the face processing starting 120-180 milliseconds after stimulus onset can be eliminated or highly attenuated when attention is not voluntarily engaged in the recognition of facial emotions. This kind of modulation of the emotional expression effect can be obtained when attention is directed away from faces (Eimer and Holmes, 2007). Similar effect of attention can be observed even if faces are presented within the foveal vision. Specifically, recent neuroimaging studies have reported different responses to emotional and neutral faces in case of the fusiform gyrus and the amygdala (Pessoa et al., 2002a). Importantly, this differentiation has been observed only when attention was explicitly engaged in the recognition of facial emotion and has not been observed when attention was directed away from faces, and was focused on the other objects with different spatial location. Therefore, it can be assumed that early emotional expression effects, reflected in the modulation of P1 and N170 components, can be determined by the top-down attentional modulation resulting in differential activation of the brain structures crucial for face processing. Some recent ERP studies have also shown attention effects on early stages of the other visual features processing, such as colour or form (Anllo-Vento et al., 1998; Han et al., 2000; Mouchetant-Rostaing et al., 2000; Taylor, 2002). These findings are consistent with a mechanism of gating or 'sensory gain control' of the early visual processing via descending neural influences from higher brain areas (Beck and Kastner, 2009; Hillyard et al., 1998; Kastner and Ungerleider, 2001; Pessoa et al., 2002a). Several neuroimaging studies have shown that differential neural response have been observed when subjects directed attention to a specific visual feature (colour, form) in comparison to a condition where different feature of the same object was attended (Kastner and Ungerleider, 2000).

1.4. The main aim of the thesis

Faces and facial emotional expressions are undoubtedly critical sources in gaining emotional information, thus their processing should be prioritized for an immediate regulation of behaviour and distribution of effective social interactions. Numerous experimental evidence from behavioural, electrophysiological, and neuroimaging studies suggest that their processing can be regarded in terms of prioritization or automaticity. Therefore, emotional expression processing can be operationalized in terms of rapid, involuntary, and unconscious processing (Palermo and Rhodes, 2007). With the inclusion of the individual differences, other researchers have indicated that at least some models of anxiety also assume the existence of a prioritized and largely automatic facial emotion (threat) processing system (Bishop, 2007).

However, in a light of the discrepancies in the experimental findings presented above, the idea of the entire automaticity – a notion that is very often invoked in the context of affective processing – may be indefensible. In agreement with the quotation of Moors and De Houwer (2006, p.321): *every process is uncontrolled, efficient, unconscious, and fast, to some degree*, every process can and should be treated as an automatic one, however, only to some extent. This suggests that the construct of the automaticity can not only be understood in terms of a simple dichotomy (automatic versus controlled processes). To fully explore the nature of the automaticity, the frameworks for understanding the continuous nature of cognitive and affective processing are highly recommended.

The main aim of this dissertation is to present a sequence of experimental results on the nature of automaticity of emotional expression processing. Following the operational definitions presented by Posner and Snyder (1975), and by Palermo and Rhodes (2007), emotional expression processing will be investigated in terms of its rapid, involuntary (mandatory), unconscious, and dependant on the individual differences nature. To achieve this, a combination of behavioural and electrophysiological measures, together with the questionnaire will be used. Specifically, the most prominent will be the use of scalp-recorded event-related brain potentials (ERPs), which will ideally serve to track the temporal aspects of facial emotion processing. Direct investigation of particular ERP components (early and late) will enable further description of the continuous nature of facial emotion automaticity at different stages of processing.

1.5. The main questions of the thesis

Emotional stimuli comprise a privileged stimulus category that is prioritized in their processing, which takes place in an obligatory fashion, independent of attention and conscious awareness. From the perspective of the perceiver, high level of trait anxiety is also often linked with the emotional expression processing in an automatic manner.

As there has been an ongoing debate on the automaticity of facial emotion processing, and in the literature this issue has been broadly discussed, the main issue of this dissertation concentrates around the extent of the automaticity, and conditions under which it can be observed. Importantly, using the ERP method, which tracks fast changes in evoked brain activity, the specific effort will be put into answering the following questions:

1. If the automaticity of facial affect processing is understood in terms of rapid, involuntary and unconscious processing, can all these aspects be confirmed? It is expected that this can be achieved using particular experimental procedures, which concentrates around non-spatial attentional manipulations and backward masking of the subliminally presented facial emotions.

2. Is emotional expression processing always automatic? If it is not, when (at which stage) it is, and what external factors can influence emotional expression processing? As it has been suggested in the literature, some of the ERP components can be under the influence of attention, whereas the other ones reflect rather unintentional expression processing. Using ERP method, can the temporal characteristics of automatic facial emotion processing be outlined?

3. Can internal dispositions of the perceiver modulate one’s facial emotion processing, and is this influence always the same? This question will be tested in a light of the experimental facts revealing that trait anxiety can modulate facial emotion perception and processing.

4. As a final point, can all these results modify the defintion of automatic facial emotion processing? Is the dichotomic characteristic of the automaticity still valid? If not, how can it be redefined?

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Chapter 2.

THE INFLUENCE OF ATTENTION ON THE EMOTIONAL EXPRESSION PROCESSING

This chapter is based on the modified version of Wronka, E., and Walentowska, W. (2011). Attention modulates emotional expression processing. *Psychophysiology, 48,* 1047-1056.

2.1. Abstract

To investigate the time course of emotional expression processing, we recorded ERPs to facial stimuli. The first task was to discriminate emotional expressions. Enhanced negativity of the face-specific N170 was elicited by emotional as opposed to neutral faces, followed by the occipital negativity (240-340 ms post-stimulus). The second task was to classify face gender. Here, N170 was unaffected by the emotional expression. However, emotional expression effect was expressed in the anterior positivity (160-250 ms post-stimulus) and subsequent occipital negativity (240-340 ms post-stimulus). Results support the thesis that structural encoding relevant to gender recognition and simultaneous expression analysis are independent processes. Attention modulates facial emotion processing 140-185 ms post-stimulus. Involuntary differentiation of facial expression was observed later (160-340 ms post-stimulus), what suggests unintentional attention capture.

2.2. Introduction

Emotional reaction indicates important evolutionary adaptations critically involved in the control of behavior in complex environment. Identification of brain structures relevant to perception and analysis of emotionally significant information requires the application of several complementary methods, such as single cell recordings, functional brain imaging or neuropsychological investigation of focal brain damages. These studies have revealed a complex interconnected network of brain structures responsible for the analysis of emotional events. The network includes higher order sensory cortices, where perceptual representation of emotionally relevant stimuli is formed, together with the amygdala, the orbitofrontal cortex and the ventral striatum, where sensory representations appear to be classified in terms of their emotional significance. In other structures, including the somatosensory cortex, the anterior cingulate and the medial prefrontal cortex, conscious representations of emotional states are generated. As the final outcomes, they can be used to control the behavior in social situations and to plan the future actions.

Facial emotional expressions are particularly salient stimuli for transferring important nonverbal signals to others. For that reason, emotional expressions are the best direct indicators of affective dispositions and attitudes. There is growing evidence suggesting that brain regions generally engaged in the processing of emotional information are also activated during the processing of facial emotions. Their initial perceptual analysis takes place in the inferior occipital cortex ('the occipital face area', OFA; Rossion, Caldara, Seghier, Schuller, Lazeyras, & Mayer, 2003a) and in the lateral fusiform gyrus ('the fusiform face area', FFA; Kanwisher, McDermott, & Chun, 1997) for invariant aspects of faces which determine face identity (Haxby, Hoffman, & Gobbini, 2000). The superior temporal sulcus (STS) is involved in the processing of changeable aspects of faces, such as facial expression, eye and mouth movements (Allison, Puce, & McCarthy, 2000). A rapid evaluation of the emotional and motivational significance of facial expression appears to be mediated by the amygdala and the orbitofrontal cortex (Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998), while structures such as the anterior cingulate, the prefrontal cortex and somatosensory areas are linked with forming conscious representations of facial emotional expressions (Adolphs, 2003).

Due to the biological and social significance of facial emotions, information about emotional states derived from faces should be processed very rapidly to be available for an immediate regulation of behavior. Recent ERP and MEG studies have indicated that stimulus can be categorized as a face much earlier than other objects (Liu, Harris, & Kanwisher, 2002), including animals' faces (Rousselet, Macé, & Fabre-Thorpe, 2003). Psychophysiological studies also suggest that emotional information from faces can be registered and discriminated very rapidly. Responses measured over occipital regions differentiate negative expressions from positive ones starting from 100 ms after stimulus onset (Pourtois, Grandjean, Sander, & Vuilleumier, 2004). Notably, however, when brain responses to emotional faces were compared to responses to neutral ones, a differential effect has been observed with slightly longer latencies. The onset of the emotional expression effect was still remarkably early ranging from 120 to 180 ms post-stimulus in different experiments. There are a number of studies in which modulation of the face-specific N170 component has been observed (Batty & Taylor, 2003; Blau, Maurer, Tottenham, & McCandliss, 2007; Miyoshi, Katayama, & Morotomi, 2004; Rigato, Farroni, & Johnson, 2010; Vlamings, Goffaux, & Kemner, 2009). The amplitude of N170 recorded in response to emotional faces has been found to be increased as compared to ERPs obtained for neutral faces. What is also worth noting, the results from studies where source localization techniques have been used to identify neural generators of N170 or its counterpart detected with MEG (M170) suggest that both the fusiform gyri (Halgren, Raij, Marinkovic, Jousmaki, & Hari, 2000; Itier, Herdman, George, Cheyne, & Taylor, 2006; Rossion, Campanella, Gomez, Delinte, Debatisse, Liard, Dubois, Bruyer, Crommelinck, & Guerit, 1999; Rossion, Joyce, Cottrell, & Tarr, 2003b), as well as region around the superior temporal sulcus (Itier, Alain, Sedore, & McIntosh, 2007; Itier & Taylor, 2004) are their possible primary sources.

In other studies the enhanced fronto-central positivity was elicited by the exposition of emotional faces as compared to neutral ones (Eimer & Holmes, 2002; Eimer, Holmes, & McGlone, 2003; Holmes, Kiss, & Eimer, 2006; Holmes, Vuilleumier, & Eimer, 2003). What is also important, analogous emotional expression effects, reflected in the fronto-central positivity, have been found for six basic emotions (Eimer, Holmes, & McGlone, 2003). Moreover, emotional expression effect was eliminated when attention was directed away from the location of peripherally presented emotional faces, which indicates that attention can effectively modulate the processing of facial emotions at early stages. These results are consistent with previous neuroimaging studies reporting different responses of visual areas specialized in face processing, as well as the amygdala, to faces signaling emotions as compared to neutral expressions (Pessoa, McKeena, Guterrez, & Ungerleider, 2002). Such differentiation has not been observed when attention was directed towards other objects with different spatial location.

Other authors have also reported that activity of visual system can be influenced by the emotional expression. This effect can be reflected in the Early Posterior Negativity (Sato, Kochiyama, Yoshikawa, & Matsumura, 2001; Schupp, Öhman, Junghöfer, Weike, Stockburger, & Hamm, 2004b). In this case, the enhanced negativity elicited by emotional expressions was obtained about 200 ms after stimulus onset. It has been recently suggested that the EPN component reflects activation of temporo-parieto-occipital areas engaged in visual information processing when stimuli of high evolutionary significance are presented (Schupp, Junghöfer, Weike, & Hamm, 2003a; Schupp, Junghöfer, Weike, & Hamm, 2004a).

Given these findings, it can be assumed that facial emotions are detected very rapidly and brain responses to emotional expressions are noticeably different from ERPs elicited by neutral faces. However, emotional expressions effects differ substantially between studies and this phenomenon can be related to diverse experimental procedures. While some authors explicitly instructed the subjects to attend presented faces and to discriminate emotional expressions (Leppänen, Kaupinnen, Peltola, & Hietanen, 2007), others asked participants to attend facial stimuli and to identify face gender (Sato et al., 2001) or to discriminate faces from non-faces (Batty & Taylor, 2003). Emotional expression effects have also been obtained from studies where no specific response was required (Miyoshi, Katayama, & Morotomi, 2004; Schupp et al., 2004b). Thus, it can be suggested that attention was differently engaged in perception of emotional expression in all these studies. Due to this, it should be clarified to what extent attention can modulate the processing of facial expressions and at which stage of face processing the attentional impact can be observed. Direct comparison of brain activity recorded when attention is unequivocally allocated to expression processing and when it is not focused on expression itself, but is actively engaged in other face-related task may help to disentangle the role of attention in face processing.

The effect of facial emotions has been recently tested in tasks demanding allocation of attention to different spatial locations, usually towards faces or other objects (Eimer & Holmes, 2002;

Eimer, Holmes, & McGlone, 2003; Holmes, Kiss, & Eimer, 2006; Holmes, Vuilleumier, & Eimer, 2003). However, in all these studies brain activity measured in conditions demanding allocation of attention to face processing was compared to data obtained from tasks requiring allocation of attention to the processing of non-face objects, presented in different spatial location. Thus, experimental manipulation of space-based attention was implemented together with manipulation of object-based attention. For that reason, it is not clear how these specific experimental manipulations can influence emotional expression recognition. Specifically, it is not obvious if attentional modulation similar to this observed in numerous previous studies (Eimer & Holmes, 2002; Eimer, Holmes, & McGlone, 2003; Holmes, Vuilleumier, & Eimer, 2003) can be observed when attention would not be spatially manipulated.

The current study was designed to test the hypothesis that non-spatial attention can effectively modulate the processing of facial emotions. Our aim was to investigate the effects of attentional influences on the processing of emotional and neutral faces in expression-relevant and expression-irrelevant task. We recorded ERPs in response to faces presented centrally on the computer screen in two different tasks. In the first one we asked our subjects to differentiate facial expressions (Face Expression Task), while the second task was to identify face gender (Face Gender Task). Thus, attention was directed towards facial features relevant to expression recognition in our first task and it was directed towards facial features crucial for gender recognition in the second one.

We expected that experimental manipulation would result in different patterns of behavioral responses. Specifically, in Face Expression Task we predicted faster average reaction times and lower error rates measured in response to emotional stimuli when compared to neutral faces. It has been previously shown that expression of happiness (Eimer, Holmes, & McGlone, 2003) or anger (Hansen & Hansen, 1988) is categorized faster than emotional neutrality. Due to dissimilar attention engagement, emotional expression effect would be completely absent in Face Gender Task.

We also expected that if brain structures involved in the analyses of invariant aspects of faces (identity recognition) and changeable facial features (expression identification) are anatomically separated and engaged in independent processes, attention would differently influence their activity reflected in ERP responses. For that reason, each emotional expression effect observed in our Face Expression Task and absent in Face Gender Task would be related to voluntary attentional impact. On the other hand, all emotional expression effects obtained in both tasks would be related to involuntary differentiation of facial emotions. Specifically, we predicted that emotional expression detection would influence ERPs at relatively early latencies, within time window of the face-specific N170 component. Then, this effect would be associated with voluntary, top-down modulation of visual areas involved in the face processing (FFA, STS). Analogous effects have been observed in several studies on attention (Pessoa, Kastner, & Ungerleider, 2002). At the same time attending face gender would result in dissimilar attentional modulation. Therefore, in Face Gender Task we did not expect any differences in the amplitude of N170 component elicited by emotional and neutral faces. Additionally, we predicted that faces with emotional expressions would modulate ERP waveforms over frontal sites within time range of 160-250 ms post-stimulus. Attentional modulation of this early component has been previously reported (Eimer & Holmes, 2002; Eimer, Holmes, & McGlone, 2003; Holmes, Kiss, & Eimer, 2006; Holmes, Vuilleumier, & Eimer, 2003). Finally, we expected that emotional expression effect reflected in the Early Posterior Negativity (EPN) would be present beyond 200 ms after stimulus onset over occipital electrodes in both conditions, which is consistent with recent reports (Sato et al., 2001; Schupp et al., 2004b).

2.3. Methods

2.3.1. Participants

Twenty nine healthy subjects participated in this study after giving informed consent. Seven subjects had to be excluded because of excessive eye blinks or muscle artifacts, so that 22 subjects (12 females and 10 males; mean age: 20.76, SD=1.58) remained in the sample. All subjects were right-handed and had normal or corrected to normal vision, and were free of neurological or psychiatric history. They received course credits for their participation.

2.3.2. Stimuli

Black and white photographs of faces of eight different individuals (4 females & 4 males) were used as the stimuli. All faces were taken from a standard set of Pictures of Facial Affect (POFA; Ekman & Friesen, 1976). Facial expressions were angry, happy or neutral, resulting in a total of 24 different facial stimuli.

2.3.3. Procedure

Subjects were seated in a dimly lit, sound-attenuated and electrically shielded cabin. A computer screen was placed at a viewing distance of 70 cm. Two task conditions were run, each consisting of four successive experimental blocks. In Face Expression Task participants were instructed to monitor the centrally presented faces, and to respond as quickly and accurately as possible with a right-hand button press whenever the neutral expression was displayed and with a left-hand button press whenever the face was emotional. In Face Gender Task participants were instructed to monitor the centrally presented faces, and to respond as quickly and accurately as possible with a right-hand button press whenever the male face was shown and with a left-hand button press whenever the face was female. Subjects were also instructed to maintain central eye fixation during the trials. In order to control lateral bias in motor response, left- and right-hand responses were counterbalanced across subjects. Moreover, half of our subjects started with Face Expression Task, while the other half started with Face Gender Task.

Each trial began with a 500-ms presentation of the fixation cross. Seven hundred and fifty milliseconds after the offset of the fixation cross, the face was presented for 300 ms. In each trial one face was presented at the fixation covering (2.5x3.5 visual angle). The interval between subject's response and the beginning of the next trial was 1200 ms. Both tasks consisted of 320 trials in each of them (160 presentations of faces with neutral expression, 80 presentations of happy faces and 80 presentations of angry faces), resulting in 640 trials in the whole experiment. The particular neutral face was presented 20 times in Face Gender Task and 20 times in Face Expression Task. Each happy and each angry face was presented 10 times in each task. In half of the trials female faces were presented and in the remaining half male faces were shown. Faces with different expressions were presented in random order in both tasks.

2.3.4. ERP procedures and data analysis

The EEG was recorded using BioSemi ActiveTwo system with Ag–AgCl electrodes from 32 monopolar locations (AF3, AF4, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO7, PO3, PO4, PO8, O1, Oz, O2), according to the 10–20 system. Two additional electrodes, common mode sense (CMS) active electrode and driven right leg (DRL) passive electrode, were used as reference and ground electrodes, respectively; cf. www.biosemi.com/faq/cms&drl.htm. All cephalic electrodes were placed on the scalp using the Electro-Cap. Two additional electrodes were placed at both mastoids and were also referred to CMS active electrode. The horizontal and vertical EOG were monitored by 4 electrodes, placed above and below the right eye and in the external canthi of both eyes. The EEG was acquired at a sampling rate of 512 Hz. Output data were subsequently transferred to and stored in a computer for analyses. The EEG data was off-line filtered with bandpass 0.016-70 Hz (24 dB) and sampled for 1.0 sec trial (100 ms prior to the stimulus onset and 900 ms after the stimulus onset) using BrainVision software. Finally, data were corrected for eye-movement artifacts (Gratton, Coles, & Donchin, 1983) and re-referenced to linked mastoids. Using CMS electrode, located over the left hemisphere at C1 location, it was very likely to obtain strong laterality effects and therefore it was reasonable to re-reference all electrodes to linked mastoids, as it is suggested by BioSemi company; www.biosemi.com/faq/cms&drl.htm. Trials with various artifacts were rejected, with a criterion of ±70 μV.

Key-press onset times were measured for each correct response and only artifact-free EEG obtained in response to correctly identified stimuli was averaged. Separate averages were computed for all combinations of task (face expression vs. face gender) and facial expression (emotional vs. neutral), resulting in four average waveforms for each electrode and each participant. The average number of trials considered for the analyses was: M=134.86, SD=17.37 & M=136.54, SD=13.62 for neutral & emotional trials in Face Expression Task, respectively and M=124.09, SD=22.84 & M=125.09, SD=21.57 for neutral & emotional trials in Face Gender Task, respectively.

The N170 component was defined as the largest negative-going peak within 140-185 ms after stimulus onset. The Anterior Positivity (AP) and the Early Posterior Negativity (EPN) components were defined as the mean voltage within 160-250 ms and 240-340 ms after stimulus onset, respectively. The amplitudes of these components were calculated relative to the pre-stimulus baseline. Analyses of the effects on the N170 component were restricted to parieto-occipital electrodes (P07, PO3, PO4, PO8). PO7 & PO8 electrodes were chosen due to the fact that at these locations N170 amplitude has been found to be maximal (Bentin & Deouell, 2000; Jacques & Rossion, 2004; Sagiv & Bentin, 2001; Yovel, Levy, Grabowecky, & Paller, 2003). The N170 amplitude was also measured at PO3 & PO4 electrodes, located closely to posterior part of the superior temporal gyrus, the possible neural source of the N170 component (Itier et al., 2007; Itier & Taylor, 2004). Analyses of the effects on the AP component were performed at fronto-central electrodes (F3, FC1, Fz, FC2, F4), in agreement with previous findings (Eimer, Holmes, & McGlone, 2003). Analyses of the effects on the EPN component were performed at occipital electrodes (O1, Oz, O2) also following previous findings (Schupp, Junghöfer, Weike, & Hamm, 2003b; Schupp et al., 2004a; 2004b).

Behavioral results, RTs and error rates, were analyzed using repeated-measures analysis of variance (ANOVA), examining the effects of within-subject factors of EXPRESSION (emotional vs. neutral) and TASK (Face Expression vs. Face Gender). Amplitude of the N170 component was analyzed using repeated-measures analysis of variance (ANOVA), testing the effects of within-subjects factors of electrode location over HEMISPHERE (left vs. right), EXPRESSION (emotional vs. neutral) and TASK (Face Expression vs. Face Gender). Amplitudes of the AP and EPN components were tested with repeated-measures analysis of variance (ANOVA), examining the effects of within-subjects factors of EXPRESSION (emotional vs. neutral) and TASK (Face Expression vs. Face Gender).

2.4. Results

2.4.1. Behavioral results

Correct responses were faster in Face Gender Task (500.92 ms) than in Face Expression Task (613.99 ms) and this difference was highly significant [main effect of task: F(1,21)=52.77, p<.001]. At the same time the effect of expression was also found [F(1,21)=22.34, p<.001], as well as significant effect of task x expression interaction [F(1,21)=22.38, p<.001]. These results suggest different strength of the expression effect in each task. To test such conclusion, we compared RTs obtained for neutral and emotional faces separately in each task. In Face Expression Task faster reactions were measured in response to emotional faces (576.51 ms) when compared to neutral faces (655.47 ms) and significant effect of expression was found [F(1,21)=23.08, p<.001]. However, such effect was not observed in Face Gender Task [F(1,21)=0.31, p>.1].

For error rates, incorrect responses were more frequent in Face Expression Task (9.45 %) than in Face Gender Task (2.90 %) [main effect of task: F(1,21)=37.39, p<.001]. The main effect of expression was moderate [F(1,21)=3.71, p=.068], while the effect of task x expression interaction was significant [F(1,21)=5.26, p=.032]. Again, these results let us suggest that the strength of emotional expression effect was incomparable between tasks. Thus, we compared error rates measured for both expressions separately in each task. In Face Expression Task higher error rates were observed for trials with neutral faces (12.07 %) in comparison to emotional faces (6.82 %) and significant effect of expression was obtained [F(1,21)=4.55, p=.045]. The same comparison in Face Gender Task brought us no significant results [F(1,21)=0.13, p>.1].

In Face Gender Task no significant effects of emotional expression were obtained neither for RTs, nor for error rates (F<1), which indicates that facial emotional expression did not interfere with face gender identification performance.

2.4.2. Electrophysiological results

Emotional expression effect was absent at early stages in Face Gender Task. ERPs elicited by emotional faces started to differ from ERPs recorded to neutral trials about 160 ms post-stimulus at fronto-central locations. This effect remained present for the next 180 ms interval, as it is shown in Figure 2.1. Emotional expression effect was also evident between 240-340 ms after face onset at occipital sites. In contrast to this, when the task was to discriminate facial expressions (in Face Expression Task), the enhanced negativity was obtained at parieto-occipital locations. This emotional expression effect started 140 ms post-stimulus, overlapping with N170 component (see Figure 2.2). Moderate expression effect reflected in the enhanced anterior positivity was also present under this condition between 160-250 ms after face presentation (AP component). Finally, exposition of emotional faces elicited the enhanced occipital negativity when compared to neutral trials (EPN, 240-340 ms post-stimulus). This effect was comparable in both tasks (see also Figure 2.3).

2.4.2.1. N170 component

The amplitudes of N170 component were initially assessed with a three-factor (task x expression x hemisphere) ANOVA. Results obtained from the analyses suggest that the amplitude measured over the right hemisphere (M=-1.09 μV, SD=7.27) was larger than the amplitude recorded over the left hemisphere (M=2.15 μV, SD=5.70) [main effect of hemisphere: F(1,21)=19.66, p<.001]. This difference is illustrated in Figures 2.1 & 2.2, which show ERP responses to neutral and emotional faces at parieto-occipital electrodes (PO7, PO3, PO4, PO8) separately for each task. Analyses of the main effect of task [F(1,21)=2.47, p=.131], as well as the main effect of expression [F(1,21)=0.46, p=.505] brought no significant findings. These results suggest that the pattern of brain activity involved in generation of the N170 was comparable in both tasks and for both expressions (when tested across tasks). None of two-way interactions [task x expression: F(1,21)=0.47, p=.498; task x hemisphere: F(1,21)=2.30, p=.144; expression x hemisphere: F(1,21)=2.93, p=.102] were found to be significant. At the same time significant effect of a three-way interaction was found [F(1,21)=6.72, p=.017]. For that reason, we performed separate two-factor analyses (expression x hemisphere) for each task.

The main effect of hemisphere was still significant in both analyses [F(1,21)=21.29, p<.001 & F(1,21)=16.29, p=.001 for Face Expression Task and Face Gender Task, respectively]. Higher amplitudes of the face-specific N170 component were measured for electrodes located on the right side (M=-0.78 μV, SD=7.47; M=-1.40 μV, SD=7.09 for Face Expression Task and Face Gender Task, respectively) in comparison to the left hemisphere (M=2.70 μV, SD=5.96; M=1.59 μV, SD=5.39 for Face Expression Task and Face Gender Task, respectively) and this effect was similar in both tasks. The main effect of expression [F(1,21)=0.11, p=.918], as well as the interaction between expression and hemisphere [F(1,21)=0.57, p=.814] did not reach the level of significance when tested in Face Gender Task. In other words, the amplitudes of N170 component recorded in response to emotional and neutral faces were comparable in this task. When data obtained in Face Expression Task were taken under consideration, significant expression x hemisphere interaction was found [F(1,21)=8.20, p=.009], while the main effect of expression was still not significant [F(1,21)=1.13, p=,300]. However, we also found that the amplitude of N170 measured over the right hemisphere and elicited by emotional faces (M= -1.13 μV, SD=7.49) was higher [F(1,21)=5.60, p=.028] when compared to the same component recorded in response to neutral stimuli (M= -0.42 μV, SD=7.53). We did not obtain any significant differences [F(1,21)=0.34, p=.563] in the amplitude of N170 recorded over the left hemisphere and elicited by emotional faces (M=2.79 μV, SD=5.97) in comparison to neutral stimuli (M=2.62 μV, SD=6.03).

To summarize, emotional expression did not influence ERP responses measured within the N170 latency window in Face Gender Task. In contrast, in Face Expression Task negative shift within the N170 latency was observed for emotional faces when compared to neutral stimuli, but only over the right hemisphere. Considering the fact that this effect was restricted to explicit facial expression recognition, it probably reflects voluntary attentional modulation.

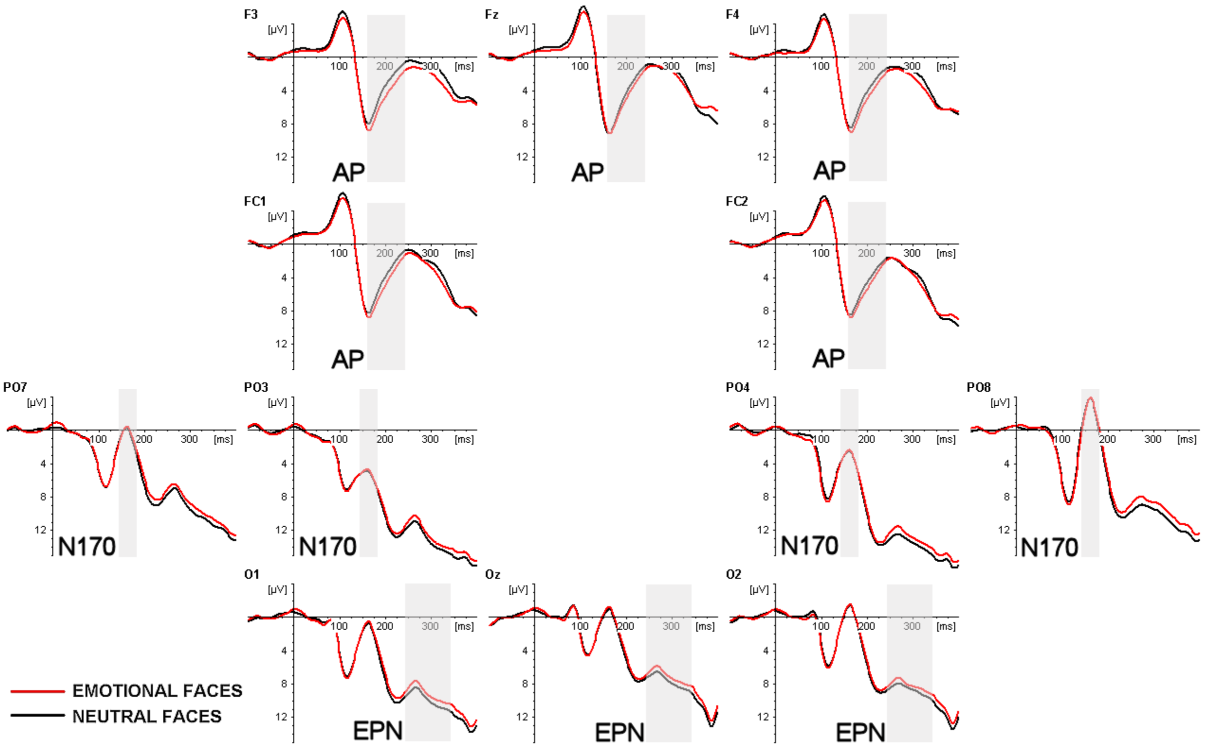

Figure 2.1. Grand average ERPs obtained at fronto-central (FC1, F3, Fz, F4, FC2), parieto-occipital (PO7, P03, PO4, PO8), and occipital (O1, Oz, O2) electrodes in Face Gender Task in response to stimuli containing either emotional (red lines) or neutral faces (black lines). Time windows for the region of interest are highlighted at corresponding electrodes: Anterior Positivity (AP, 160-250 ms post-stimulus), N170 (140-185 ms post-stimulus), and Early Posterior Negativity (EPN, 240-340 ms post-stimulus).

2.4.2.2. Anterior Positivity (AP)

Mean amplitudes obtained between 160-250 ms after stimulus onset were initially assessed with a two -factor (task x expression) ANOVA. This analysis was performed for mean amplitudes measured at fronto-central electrodes (F3, FC1, Fz, FC2, F4). Here, the enhanced positivity was observed in response to emotional faces (M=7.79 µV, SD=6.38) when compared to neutral stimuli (M=6.94 µV, SD=6.25) and the main effect of expression was found to be significant [F(1,21)=12.97, p=.002]. This effect is illustrated in Figures 2.1 & 2.2, representing ERPs in response to neutral and emotional faces at fronto-central electrodes separately in each task. At the same time non-significant result was obtained for the main effect of task [F(1,21)=1.34, p=.260] suggesting that differential attention engagement did not produce distinct pattern of brain activity. The effect of a two-way interaction (task x expression [F(1,21)=0.23, p=.635] was found to be non-significant neither. This let us suggest that emotional expression effect measured in both tasks did not differ significantly. To verify this findings, we performed separate analyses for each task. We found that the enhanced positivity in response to emotional faces (M=8.27 µV, SD=6.32 & M=7.30 µV, SD=6.07 for emotional & neutral trials, respectively) was observed in Face Gender Task [F(1,21)=9.19, p=.006]. Similar difference was also obtained in Face Expression Task. In this case observed positivity was attenuated (M=7.32 μV, SD=6.42 & M=6.58 μV, SD=6.42 for emotional & neutral trials, respectively), but not completely eliminated [F(1,21)=4.29, p=.051]. Similar pattern of results was also obtained for the subsequent time window (250 -340 ms post-stimulus). Here, the enhanced positivity in response to emotional faces was still observed in Face Gender Task (M=6.03 μV, SD=7.04 & M=5.29 μV, SD=6.96 for emotional & neutral trials, respectively). However, the effect was substantially reduced and did not reach the level of significance [F(1,22)=3.62, p=.071]. The same was true for Face Expression Task, where the AP component was reduced (M=5.81 μV, SD=7.32 & M=5.13 μV, SD=7.24 for emotional & neutral trials, respectively) [F(1,22)=3.14, p=.091].

Thus, it seems that emotional expression effect observed at fronto-central locations and reflected in the Anterior Positivity was comparable when attention was engaged in face gender discrimination and when it was explicitly allocated to expression recognition. Due to this, it can be concluded that the AP component reflects brain activity related to unintentional attention engagement in processing of stimuli with high biological and social relevance.

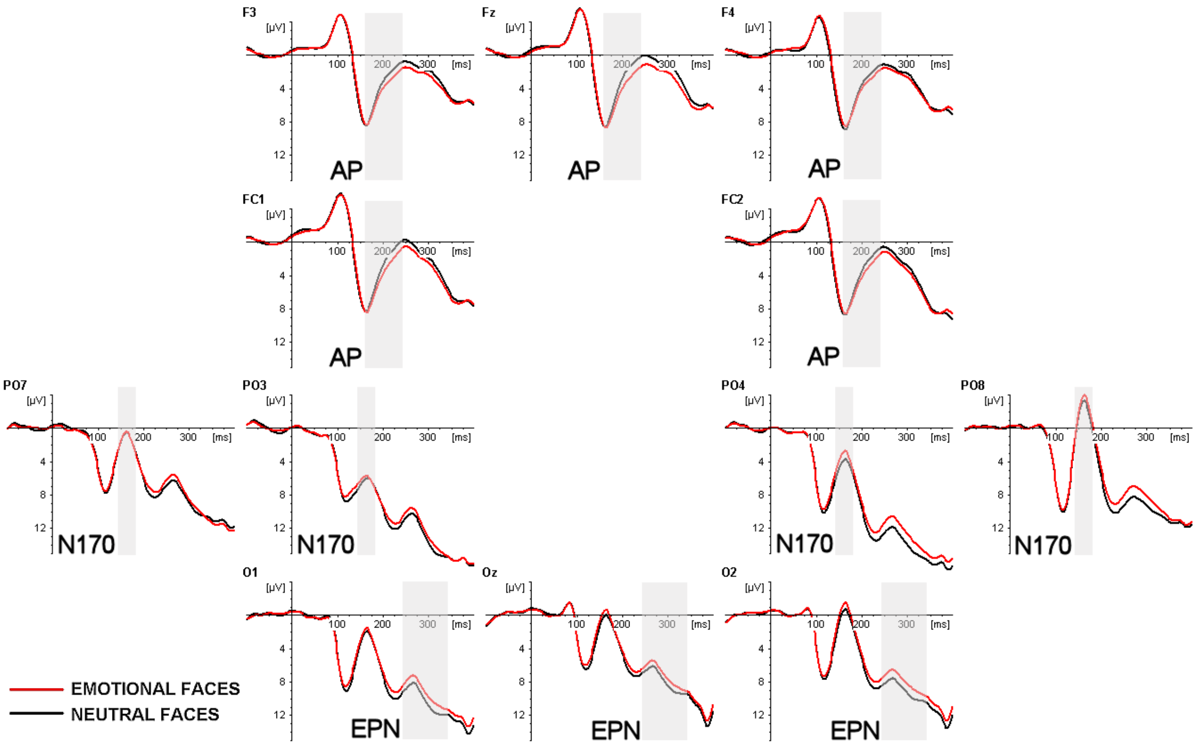

Figure 2.2. Grand average ERPs obtained at fronto-central (FC1, F3, Fz, F4, FC2), parieto-occipital (PO7, P03, PO4, PO8), and occipital (O1, Oz, O2) electrodes in Face Expression Task in response to stimuli containing either emotional (red lines) or neutral faces (black lines). Time windows for the region of interest are highlighted at corresponding electrodes: Anterior Positivity (AP, 160-250 ms post-stimulus), N170 (140-185 ms post-stimulus), and Early Posterior Negativity (EPN, 240-340 ms post-stimulus).

2.4.2.3. Early Posterior Negativity (EPN)

Mean amplitudes obtained for the latency window of 240-340 ms after stimulus onset were initially assessed with a two-factor (task x expression) ANOVA. This analysis was performed for mean amplitudes measured at occipital electrodes (O1, Oz, O2), where highly significant main effect of emotional expression was found [F(1,21)=41.94, p<.0001]. The enhanced negativity was obtained in response to emotional faces (M=7.93 μV, SD=4.49) when compared to neutral stimuli (M=8.63 μV, SD=4.37). This fact is further illustrated in Figures 2.1 & 2.2, which show ERPs in response to neutral and emotional faces at occipital electrodes separately in each task. At the same time non-significant results were obtained for the main effect of task [F(1,21)=0.08, p=.775], as well as for a two-way interaction (task x expression [F(1,21)=0.97, p=.335]. Thus, it can be assumed that the only factor influencing brain activity, reflected in the EPN component, was the emotional expression. What also should be emphasized, the enhanced negativity measured in response to emotional faces was evident in each task when tested separately [F(1,21)=24.30, p<.0001 & F(1,21)=9.63, p=.005 for Face Expression Task & Face Gender Task, respectively].

These results let us suggest that the modulation of visual cortices elicited by emotional expression is not determined exclusively by voluntary attention. It rather reflects a process that can be triggered by involuntary attention capture.

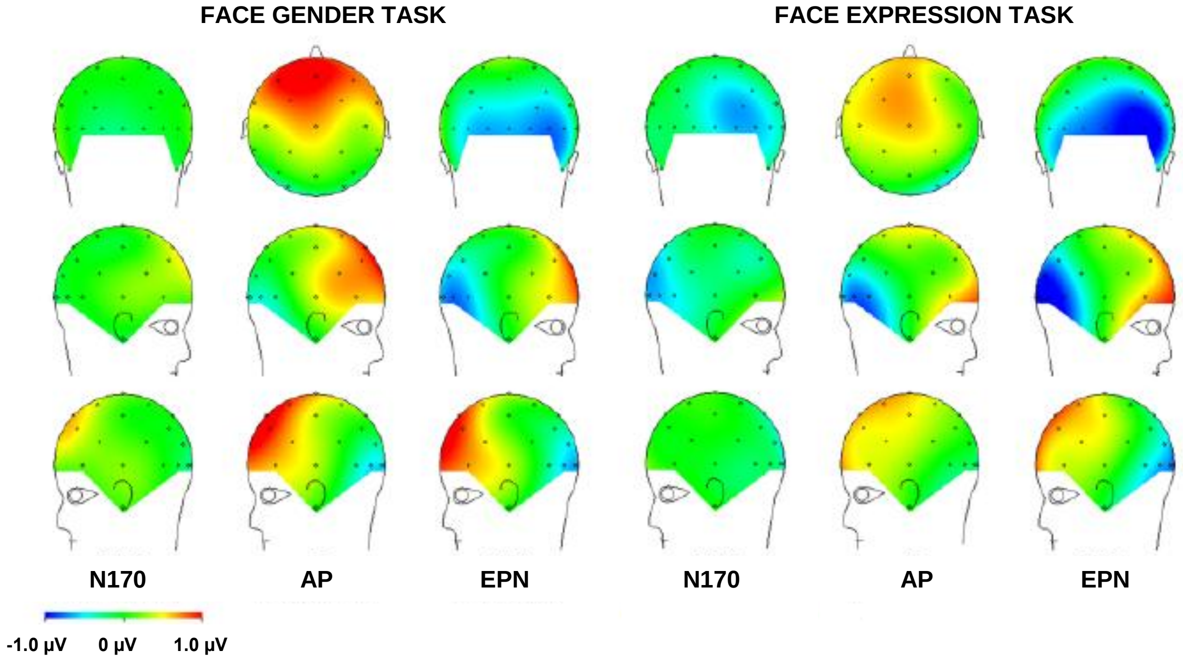

Figure 2.3. Topographical maps representing voltage differences between brain activity elicited by emotional and neutral faces in Face Gender Task and Face Expression Task in time intervals for N170 (140-185 ms post-stimulus), Anterior Positivity (AP, 160-250 ms post-stimulus), and Early Posterior Negativity (EPN, 240-340 ms post-stimulus).

2.5. Discussion

The aim of the current study was to investigate the role of non-spatial attention in emotional expression processing. We expected that if attention is able to modulate facial emotion detection, then ERP responses to emotional and neutral faces recorded when attention was directed towards facial features relevant to facial emotion recognition would differ from those obtained when attention was focused on facial features crucial for gender recognition. We also assumed that emotional expression effects observed exclusively in our Face Expression Task would be related to voluntary attentional modulation, while the effects apparent in both tasks would be related to unintentional attention engagement.

Results obtained in our study suggest that both types of effects can be observed in parallel. Specifically, negative shift within the latency of the face-specific N170 component was observed at parieto-occipital locations for emotional faces when compared to neutral stimuli. Due to the fact that this effect was restricted only to condition when attention was explicitly engaged in expression recognition, it can be suggested that it reflects voluntary attentional impact. Nevertheless, our results support also the thesis that emotional expression has an ability to engage attention involuntarily, which was reflected in the enhanced fronto-central positivity (160-250 ms post-stimulus) in response to emotional faces when compared to neutral ones. This expression effect was evident despite the differences in experimental instructions, in both tasks. It was followed by the enhanced negativity, elicited by emotional faces and recorded over occipital sites 240-340 ms post-stimulus. Similarly, expression-related modulation was observed in both experimental conditions.

When facial expression was attended (in Face Expression Task), emotional faces elicited enhanced amplitude of the N170 component. The effect obtained in our experiment is consistent with previous findings highlighting the differences in the amplitude of N170 between emotional and neutral faces (Batty & Taylor, 2003; Blau et al., 2007; Miyoshi, Katayama, & Morotomi, 2004; Rigato, Farroni, & Johnson, 2010; Vlamings, Goffaux, & Kemner, 2009). Moreover, consistent effect has been additionally observed by Sprengelmeyer and Jentzsch (2006) reporting modulation of the N170 amplitude in response to faces varying in expression intensity. We did not observe a similar expression effect in our Face Gender Task. What is important in this context, in both tasks identical facial stimuli were presented at fixation and the only significant difference was the experimental instruction. Thus, we can conclude that emotional expression effect obtained at the N170 latency in Face Expression Task is related to the influence of attention that was explicitly directed towards facial features relevant to emotion recognition. However, such modulatory impact was not present in Face Gender Task, when attention was directed towards facial features important for identity recognition (gender of the face in our study).

Registered effect was evident for the right and almost absent for the left side of the brain. This difference can be related to previously reported functional lateralization of face processing (Yovel et al., 2003). Recent electrophysiological studies have demonstrated that the amplitude of face-sensitive N170 recorded over the right hemisphere significantly exceeds its left-side counterpart (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Campanella, Hanoteau, Dépy, Rossion, Bruyer, Crommenlinck, & Guérit, 2000; Rossion et al., 2003b; Yovel et al., 2003). Similarly, human neuroimaging studies have consistently revealed larger face-sensitive regions over the right rather than the left hemisphere for centrally presented faces (Kanwisher, McDermott, & Chun, 1997; Kanwisher & Yovel, 2006). Moreover, a right hemisphere advantage in perception and interpretation of emotional expression has been found (Adolphs, Damasio, Tranel, & Damasio, 1996).

Later phase of emotional expression effect was observed between 160-250 ms post-stimulus over the frontal cortex. In this case, we obtained slowly emerging enhanced positivity (Anterior Positivity, AP) elicited in Face Expression Task for trials containing emotional faces relative to trials with neutral faces. This ERP effect is similar to results obtained in numerous previous studies (Ashley, Vuilleumier, & Swick, 2004; Eimer & Holmes, 2002; Eimer, Holmes, & McGlone, 2003; Holmes, Kiss, & Eimer, 2006; Holmes, Vuilleumier, & Eimer, 2003). What is also important, analogous effect was observed in Face Gender Task, where the enhanced positivity was evident between 160-340 ms after face onset. It was even more pronounced in comparison to the modulation obtained in Face Expression Task. The fact that these two effects emerged with comparable latencies at fronto-central areas implies that they probably represent similar psychological process of early involuntary response to emotional signals. However, this finding is in contrast to previous results demonstrating an absence of emotional expression effects when attention was directed away from the location of presented face (Eimer, Holmes, & McGlone, 2003; Holmes, Vuilleumier, & Eimer, 2003). Importantly, the main difference between the present experiment and earlier studies is that in our experiment faces were presented centrally within foveal vision, rather than in the periphery of the visual field. For that reason, we speculate that the absence of differential responses to emotional faces probably results from specific experimental procedure (facial stimuli were presented outside the foveal vision, thus attention was directed towards location significantly different than the face position). Results from at least one recent study support this assumption (Holmes, Kiss, & Eimer, 2006). In this study centrally presented fearful and neutral faces were flanked by a pair of peripheral lines. The enhanced fronto-central positivity elicited by emotional expressions, but only when attention was focused on facial stimuli, has been observed. However, the initial phase of this early emotional expression effect was preserved when attention was directed away from faces and was focused on line pairs. Taken together, results reported by Holmes and colleagues (2006), as well as the data from the present experiment suggest that early processing of facial emotions expressed in the fronto-central positivity is involuntary and largely unaffected by attention.

Emotional faces elicited enlarged negativity between 240-340 ms post-stimulus over occipital sites when compared to neutral stimuli. This differential response, dubbed as the Early Posterior Negativity (EPN), was observed in both conditions of our study. Lack of any task x expression interactions suggests that the modulation of visual cortices elicited by emotional expression is not exclusively determined by voluntary attention, but rather represents processes triggered by involuntary attention capture. The effect observed in the present study is consistent with previous experiments reporting bilaterally pronounced relative negativity over temporo-occipital areas, recorded in response to emotionally relevant stimuli when compared to neutral ones. For example, the EPN component has been observed for emotional pictures from the IAPS (Lang, Bradley, & Cuthbert, 1999). Specifically, Schupp et al. (2004a) have reported increased negativity within 280-320 ms post-stimulus only in response to emotional (pleasant and unpleasant) pictures in comparison to neutral images. Previously, similar findings have also been reported by this group (Schupp et al., 2003a; 2003b). Results from recent fMRI studies have revealed that presentation of positive and negative images (but not neutral ones) from the IAPS evoked stronger activity in posterior visual areas (Junghöfer, Schupp, Stark, & Vaitl, 2005). Modulation of temporo-occipital activity has also been observed in case of facial stimuli. Sato et al. (2001) have found increased negativity within 240-300 ms after stimulus onset in response to pictures with positive and negative facial expressions when compared to neutral facial images. Schupp et al. (2004b) have reported augmented EPN amplitudes to threatening faces in relation to friendly and neutral ones. In this case emotional expression effect was mostly pronounced around 280 ms post-stimulus. Additionally, negative shift in ERPs recorded in response to high-intensity when compared to low-intensity fearful expressions has been observed by Leppänen et al. (2007). All these findings suggest that emotionally relevant stimuli are capable of preferentially activating posterior brain areas which can be associated with fine sensory analyses performed by human visual system. However, the effect is not specifically related to the face processing since it has been detected for other types of emotional stimuli as well.

To conclude the main findings, results from the present study have shown that facial emotions can influence ERP responses at three different stages of information processing. These different effects are related to diverse psychological processes. Firstly, attention voluntarily engaged in emotional expression processing can effectively influence brain activity within the extrastriate cortex. Thus, it can promote its rapid detection and recognition. This top-down modulation has been observed as early as 140-185 ms post-stimulus. Secondly, emotional expression can trigger unintentional attention capture, which has been expressed in the fronto-central positivity starting from 160 ms after face presentation, even if attention was directed towards facial features relevant to gender recognition. However, as it has been explained above, this early response can be diminished when face is presented outside the foveal vision or attention is allocated to distant spatial location. Thus, early frontal positivity probably depends on effective processing of facial stimuli within human visual system. Thirdly, when attention is captured by the emotional face, it is able to modulate the activity of posterior brain areas involved in sensory analyses. Attentional modulation of visual areas can promote precise processing of information gained by the system. This effect has been reflected in increased negativity observed between 240-340 ms after face onset. It have also been triggered involuntarily, as it could have been observed irrespective of the experimental instruction in our study.

The results from conducted research show that at some stages attention effectively influences processing of facial emotional expressions. Beyond others, some theoretical implications arise from these findings. Using unique experimental procedure we have successfully managed to make one step further towards clarifying the role of attention in facial stimuli processing. Answering all questions in this ongoing debate may help to apply this knowledge for practical purposes, e.g. in clinical practice. At least some psychiatric or neurological disorders, such as autism, social phobia or clinical level of anxiety are characterized by the impaired processing of facial emotions in everyday life. However, it still remains unclear whether these deficits involve low-level attentional impairments and/or abnormal high-level cognitive processing together with affective reactivity. Therefore, a deeper understanding of how attention shapes human cognition and interacts with emotional functioning may help in better diagnose and treatment of numerous affective disorders.

One of the possible limitations of our study is undoubtedly the fact that it was narrowly designed to compare emotional and neutral stimuli. Therefore, due to the unequal number of angry, happy and neutral faces, it has not been optimized to determine if diverse facial emotions (angry and happy ones) may lead to different effects in ERP recordings. Going further, it is still unknown whether possible effects would be limited only to angry and happy faces, or similar results could be obtained for other expressions (e.g. fear, disgust).

Following that, at least two important areas for future research can be distinguished. Firstly, as it was mentioned above, effects of diverse emotional expressions (both positive and negative ones) should be investigated more thoroughly. Secondly, additional techniques should be employed to extend the insight into the sources of scalp-recorded potentials. It is established in the literature that ERPs are well-suited to excellently provide with information about the time course of the processes of interest. However, their most pronounced disadvantage is poor spatial resolution. For that reason, it would be useful in the future studies to combine electrophysiological recordings together with source localization methods (e.g. Low Resolution Electromagnetic Tomography, LORETA) or to conduct the experiment using neuroimaging techniques, like fMRI.

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Chapter 3.

THE INFLUENCE OF AWARENESS ON THE EMOTIONAL EXPRESSION PROCESSING

This chapter is based on the modified version of Walentowska, W., and Wronka, E. (submitted). ERP correlates of subliminal processing of facial emotions.

3.1. Abstract

There is growing evidence that facial emotional expression can trigger specific brain responses even when it is presented subliminally. To investigate this issue more thoroughly, ERPs in response to briefly presented and backward masked faces and non-face objects were recorded. N170 component was found to be larger when recorded in trials with faces in comparison to non-face stimuli. Moreover, a significant difference in the N170 was observed as the effect of face inversion, while no such differentiation was obtained for non-face objects. Additionally, ERPs to fearful and neutral faces were compared. While the N170 component was not affected by facial emotion, the negative shift specific for fearful stimuli (the Early Posterior Negativity, EPN) was recorded only when faces were presented in their upright orientation, and was not observed when faces were inverted. Our findings highlight that faces, even in the absence of conscious awareness and attention, are processed differently than other stimuli (the N170 effect). However, as revealed by the EPN component, involuntary differentiation of facial expression is determined by the structural analysis of face features, disrupted as the effect of face inversion.

3.2. Introduction

Emotional facial expressions are particularly salient stimuli conveying important nonverbal signals to others. For that reason, they are assumed to be the best direct indicator of the current affective dispositions and attitudes. Due to its biological and social significance, emotional information derived from faces should be processed very rapidly to be available for an immediate regulation of behavior. Recent studies suggest that facial emotional information processing is assumed to be rapid, unconscious, involuntary and capacity-free (Palermo & Rhodes, 2007).

Research on the brain structures relevant to perception and analysis of emotionally significant information has been conducted with the application of several complementary methods, such as electrophysiological recordings, functional brain imaging or neuropsychological investigation of focal brain damage. Recent findings suggest a separate brain module critically involved in face processing, located in the fusiform gyrus and in the superior temporal gyrus (Allison, Puce, & McCarthy, 2000; Haxby, Hoffman, & Gobbini, 2000). Moreover, brain regions generally engaged in the processing of faces are strongly activated during the processing of facial emotions. The initial perceptual analysis takes place in the inferior occipital cortex (Rossion et al., 2003), and in the lateral fusiform gyrus (Kanwisher, McDermott, & Chun, 1997) for invariant aspects of faces which determine face identity (Haxby, Hoffman, & Gobbini, 2000). The superior temporal sulcus is involved in the processing of changeable aspects of faces, such as facial expression, eye and mouth movements (Allison, Puce, & McCarthy, 2000). It has been moreover suggested that the amygdala and the orbitofrontal cortex mediate a rapid, preattentive evaluation of the emotional and motivational significance of facial expression (Sprengelmeyer et al., 1998), while the anterior cingulate, the prefrontal cortex and somatosensory areas are linked with forming conscious representations of facial emotional expressions (Adolphs, 2003).

Previous studies have indicated that a stimulus can be categorized as a face much earlier than other objects (Liu, Harris, & Kanwisher, 2002). Psychophysiological studies also suggest that emotional information from faces can be registered and discriminated very rapidly. Responses measured over occipital regions differentiate negative expressions from positive ones starting from 100 ms after stimulus onset (Pourtois et al., 2004). Notably, however, when brain responses to emotional faces were compared to responses to neutral ones, a differential effect has been observed with slightly longer latencies. Larger amplitudes between 140-200 ms poststimulus from occipito-temporal locations have been regularly obtained to faces when compared to non-face objects. The onset of this face effect, reflected in the differentiation of the N170 component, has been observed by numerous researchers (Batty & Taylor, 2003; Bentin et al., 1996; Eimer, 2000; Eimer & Kiss, 2010; Itier & Taylor, 2004a). Similarly, M170, the magnetic counterpart of the N170 scalp potential, is also face-sensitive, as revealed by Halgren et al. (2000). Evidence supporting face-specific mechanisms has been provided by studies showing that stimulus inversion disrupts the processing of faces more than other objects, which has been termed as the face inversion effect (Yin, 1969). It has been revealed by numerous ERP studies that the face-sensitive N170 is strongly influenced by face inversion. In comparison to upright presentations, when faces are presented upside-down the N170 latency is significantly delayed, and its amplitude may be larger (Eimer, 2000), however only if subjects are engaged in an explicit face discrimination task (Rossion et al., 1999).

The onset of emotional expression effect investigated with ERPs can be observed remarkably early. There are also a number of studies in which the amplitude of N170 recorded in response to emotional faces has been found to be more pronounced than for neutral faces (Batty & Taylor, 2003; Blau et al., 2007; Miyoshi, Katayama, & Morotomi, 2004; Rigato, Farroni, & Johnson, 2010; Vlamings, Goffaux, & Kemner, 2009). However, in our previous study (Wronka & Walentowska, 2011), the N170 modulation has been obtained exclusively in a task demanding emotional expression categorization, which suggests voluntary facial emotion processing at this stage of analysis. At later stages, authors have reported increased activity of the visual system elicited by facial emotions in comparison to neutral faces. This effect has been termed the Early Posterior Negativity (EPN; Sato et al., 2001; Schupp et al., 2004b; Wronka & Walentowska, 2011). In this case, the enhanced negativity elicited by emotional expressions was obtained about 200 ms after the stimulus onset. Recently, it has been suggested that the EPN reflects the activation of temporo-parieto-occipital areas engaged in the visual information processing, when stimuli of high evolutionary significance are presented (Schupp et al., 2003, 2004a).

Numerous emotion-specific effects have been obtained in experiments with relatively long, supraliminal face presentations. However, consistently with privileged processing of expressive facial cues, facial emotional stimuli can capture attention and evoke specific electrophysiological responses even without reaching the level of conscious awareness. It has been suggested that subliminal processing of expressive facial cues may be mediated *via* a ‘short’ retino-thalamic-amygdalar neural pathway (see Pessoa, 2005 for discussion). Experimental evidence that facial threat is privileged in the processing comes mostly from studies where backward masking procedure has been used. With this technique, Whalen et al. (1998) have found stronger activity of the amygdala to fearful faces relative to happy ones. From the other hand, results obtained by Pessoa et al. (2006) suggest that the amygdala activity in response to fearful faces is probably related to the objectively assessed visibility of masked stimuli. However, fMRI technique with its rather low millisecond resolution does not provide information about the temporal characteristics of information processing. This can be obtained using electrophysiological recordings. In recent ERP studies authors report fear-specific patterns of brain activity in response to subliminal processing of backward masked facial stimuli (Eimer, Kiss, & Holmes, 2008; Kiss & Eimer, 2008). Both experiments have revealed no effects recorded in the time window of the N170 component. In contrast, Pegna and co-authors (2008) have found that subliminally presented fearful faces elicited larger N170 amplitudes than non-fearful (happy and neutral) faces. What should be noticed, this early effect has been obtained in a task demanding active detection of fearful faces, which can be related to voluntary attention involvement. Nevertheless, although all these experiments explore the topic of unconscious processing of facial emotions, at least one limitation can be found in the experimental procedures, which is the type of the mask. Images of neutral faces as the masking stimuli have been used by Eimer with colleagues (2008), and Pegna with co-authors (2008). Kiss and Eimer (2008) used scrambled neutral faces, although the images probably still were face-similar masking objects. Therefore, there is a high probability that brain activity elicited by subliminally presented faces can interfere with brain responses to masking facial stimuli, which may serve to disrupt the analyses.

The current study was designed to investigate the differences between brain responses to subliminally presented faces and non-face objects. This issue has been extensively studied using supraliminally displayed stimuli, and the systematic face effect within the latency of N170 component has been observed. However, the open question is whether similar pattern of results can be obtained with very rapid stimuli exposition. Results from our previous experiment have shown that the N170 is sensitive to the stimulus category: larger amplitudes for subliminally presented and backward masked faces in comparison to non-face objects have been recorded (Walentowska & Wronka, 2012). Moreover, subliminally shown images of faces or non-face objects were additionally presented in the upright or inverted orientation to follow normal and disrupted course of facial structural encoding and the processing of non-face objects. Our previous study (Walentowska & Wronka, 2012) did not investigate this issue. The second aim of the current study was to investigate the course of involuntary processing of facial emotions and the role of the structural analysis in this process, which was expected to be disrupted by the face inversion. To address these issues, participants were briefly (for 16 ms) shown images of upright or inverted faces (fearful, neutral) and non-face objects, immediately masked by an abstract image, and they were asked to categorize masking stimuli. Backward masking procedure was used to limit the access of the masked objects to conscious awareness. In addition, we assumed that this procedure would successfully solve the problematic issue of the facial masking stimulus together with forced-choice discrimination of the target stimulus.

We expected that the amplitude of the occipito-temporal, face-sensitive N170 component would be larger in response to faces when compared to non-face objects. This effect, similar to that observed previously using longer stimuli presentations (Batty & Taylor, 2003; Bentin et al., 1996; Eimer, 2000; Eimer & Kiss, 2010; Itier & Taylor, 2004a), can support the thesis that qualitative difference between face and non-face processing is independent of conscious awareness of stimuli, and can be observed even with subliminal exposition (Walentowska & Wronka, 2012). Regarding the emotional expression effects, we predicted that brain activity would be different when elicited by rapidly presented emotional and neutral faces. Specifically, we expected that the earliest possible effect can be observed over occipital sites starting from 100 ms after stimulus onset. This early modulation has been so far reported from studies using supraliminal presentations (Holmes, Kragh Nielsen, & Green, 2008; Holmes et al., 2009; Pourtois et al., 2005). We also expected larger amplitudes of the N170 elicited by emotional relative to neutral faces, as it has been previously found (Batty & Taylor, 2003; Blau et al., 2007; Miyoshi, Katayama, & Morotomi, 2004; Rigato, Farroni, & Johnson, 2010; Vlamings, Goffaux, & Kemner, 2009). Finally, we expected facial threat to elicit stronger negativity within the latency window of EPN component in comparison to neutral faces. Such effect has also been also shown supraliminal presentations (Sato et al., 2001; Schupp et al., 2004b; Wronka & Walentowska, 2011).

Notably, using the procedure with upside-down stimuli presentation, we hypothesized that face inversion would significantly influence facial structural encoding. In the same time, the upside-down presentation of non-facial stimuli would not influence their processing in an observed manner. Thus, we supposed that in case of facial stimuli there would be differences in the N170 ERP component. In the same time there would be no such differentiation in case of non-faces, as this effect has been systematically reported in studies with supraliminal stimuli presentation (Eimer, 2000; Rossion et al., 1999). The open question remains how face inversion would influence emotional expression effects, systematically recorded as the modulation of expression-sensitive EPN component (Sato et al., 2001; Schupp et al., 2004b; Wronka & Walentowska, 2011).

3.3. Methods

3.3.1. Participants

Forty one subjects (5 men and 36 women, mean age: 20.53, SD=2.98) were selected from a large pool of the first-year students to participate in the current experiment. All subjects declared to be right-handed, and had good health with normal or corrected vision. Prior to the beginning of the experiment subjects signed an approved consent form. Afterwards, their participation was awarded with course credits.

3.3.2. Stimuli

Color photographs of faces of 10 different individuals (5 men and 5 women) taken from a standard set of NimStim Face Stimulus Set (Tottenham et al., 2009; http://www.macbrain.org/resources.htm) were used as face stimuli. Facial expressions were fearful or neutral, resulting in a total of 20 different face stimuli. Color photographs of 10 houses and 10 trucks derived from the internet were used as non-face objects. Masking stimuli were purposely-prepared by the authors using Corel PaintShopPro software, resulting in the abstract symmetrical and asymmetrical images. Each masked object was presented at the fixation covering 17.5 cm x 11.5 cm, while the mask itself was presented at the fixation covering 17.5 cm x 23 cm.

3.3.3. Procedure

Subjects were comfortably seated in a dimmed, air-conditioned, and electrically isolated chamber. A computer screen was placed at a distance of approximately 70 cm. Subjects were instructed to maintain central eye fixation together with reducing eye blinks and excessive body movements during the procedure.

Each trial began with presentation of the fixation cross for 500 ms. It was followed by the exposition of object + mask stimuli for the next 500 ms. Images of various objects (faces, houses and trucks) were subliminally presented for 16 ms, and immediately backward masked by abstract images displayed for 484 ms. Masking stimuli was either symmetrical or asymmetrical abstract image. As the experimental task, subjects were asked to judge mask symmetry, and respond with their dominant-hand button press whenever the mask asymmetry was detected. Subjects were also instructed to restrain from motor response when symmetrical masking object was presented.

The whole task consisted of 400 trials. Because of an eventual fatigue the experimental procedure was split into four blocks, with 100 trials in each of them, and counterbalanced with respect to type of the object and the mask. Each category of stimuli (faces and non-face objects) was presented in 200 trials. Among faces, fearful and neutral expressions were presented in 100 trials per category. In half of the trials faces were presented in the upright orientation, while in the remaining half inverted faces were shown. Similarly, pictures of houses and trucks were presented in 100 trials per category. In half of the trials pictures of non-face objects were shown in the upright orientation, while in the remaining half inverted pictures were presented. Thus, each particular picture was presented 10 times in upright, and 10 times in the inverted position. Ninety percent of trials (45 trials per each category) consisted of object + symmetrical mask presentation, while in remaining 10% of trials (5 trials per each category) asymmetrical mask was used.

3.3.4. ERP Procedures and Analyses

The EEG was recorded using BioSemi ActiveTwo system with Ag–AgCl electrodes from 32 monopolar locations (AF3, AF4, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO7, PO3, PO4, PO8, O1, Oz, O2), according to the 10–20 system. Two additional electrodes, the common mode sense (CMS) active electrode and the driven right leg (DRL) passive electrode, were used as reference and ground electrodes, respectively; cf. www.biosemi.com/faq/cms&drl.htm. All cephalic electrodes were placed on the scalp using the Electro-Cap. Two additional electrodes were placed at both mastoids and were also referred to the CMS active electrode. The horizontal and vertical EOGs were monitored by 4 electrodes, placed above and below the right eye and in the external canthi of both eyes. The EEG was acquired at a sampling rate of 256 Hz. The EEG data was off-line filtered with bandpass 0.016-45 Hz (24 dB) and sampled for a 600-ms trial (150 ms prior to the stimulus onset and 450 ms after the stimulus onset) using BrainVision software. Finally, data were corrected for eye-movement artifacts (Gratton, Coles, & Donchin, 1983) and re-referenced to linked mastoids. Only the EEG obtained from trials containing symmetrical masking stimuli, so not followed by the motor response, was averaged.

The first set of analyses was based on the mean amplitude values computed within the N170 time window for two categories of objects (faces vs. non-face objects). Our aim was to investigate if brain responses reflected in the amplitude of face–specific N170 component to subliminally presented faces differ substantially from ERPs recorded to rapidly presented non-face objects. Moreover, we also aimed to examine the stimulus inversion effect, which has been reported to influence the N170 in case of face presentation. The N170 component was defined as the mean amplitude within 140-200 ms after stimulus onset. The analyses of the face effects on the N170 component were restricted to lateral parieto-occipital electrodes (PO7, PO3, PO4, PO8), which is in agreement with numerous previous findings (Bentin & Deouell, 2000; Itier & Taylor, 2004a; Jacques & Rossion, 2004; Sagiv & Bentin, 2001; Yovel et al., 2003). The amplitude of the N170 component was analyzed using repeated-measures analyses of variance (ANOVA) examining the effects of within-subjects factors of stimulus TYPE (face vs. non-face), stimulus ORIENTATION (upright vs. inverted), and LOCATION (left hemisphere vs. right hemisphere).

The second set of analyses was performed to investigate differences in brain activity during unconscious emotional expression processing. These analyses were conducted for two successive poststimulus time windows: 140–200 ms (N170 component), and 215–310 ms (EPN component), covering the time interval where systematic emotional expression effects have been observed in previous studies (Batty & Taylor, 2003; Blau et al., 2007; Holmes, Kragh Nielsen, & Green, 2008; Holmes et al., 2009; Miyoshi, Katayama, & Morotomi, 2004; Pegna, Landis, & Khateb, 2008; Pourtois et al., 2005; Rigato, Farroni, & Johnson, 2010; Sato et al., 2001; Schupp et al., 2004b; Vlamings, Goffaux, & Kemner, 2009; Walentowska & Wronka, 2012; Wronka & Walentowska, 2011). Analyses of the effects for the interval between 140-200 ms after the stimulus onset were restricted to lateral parieto-occipital electrodes (PO7, PO3, PO4, PO8) using repeated-measures analyses of variance (ANOVA) to test the effects of within-subjects factors of facial EXPRESSION (fearful vs. neutral), stimulus ORIENTATION (upright vs. inverted), and LOCATION (left hemisphere vs. right hemisphere). Mean amplitudes between 215-310 ms after the stimulus onset were analyzed for values recorded at occipital (O1, Oz, O2) and parieto-occipital (PO7, PO8) electrodes using repeated-measures analyses of variance (ANOVA) to test the effects of within-subjects factors of facial EXPRESSION (fearful vs. neutral) and stimulus ORIENTATION (upright vs. inverted).

All analyses of variance employed Greenhouse-Geisser corrections to the degrees of freedom when appropriate, and only the corrected probability values are reported. The Bonferroni method was used for *post-hoc* comparisons, with a significance level of 0.05.

3.4. Results

ERP responses obtained for trials containing facial stimuli differed significantly from the non-face ERPs within a time window of the face-sensitive N170 component. Specifically, increased negativity was obtained for face stimuli in comparison to non-face objects. Moreover, responses elicited by upright faces were significantly different from these obtained for trials containing inverted faces. Mean amplitudes of the N170 recorded in response to inverted faces were reduced in comparison to upright face stimuli. No differentiation of the N170 was observed as the effect of non-face objects inversion.

Early stage of face processing, revealed by the parieto-occipital N170 component, was generally not affected by the emotional expression. At later stages, exposition of emotional faces elicited enhanced parieto-occipital negativity (EPN component) when compared to neutral trials. This effect was additionally modulated by the stimulus orientation. In particular, the EPN component was apparent in case of trials containing upright faces, while it was virtually absent for the inverted face stimuli.

All these findings are presented in Figures 3.1-3.4., and are confirmed by the statistical analyses which can be found in the next four subsections.

3.4.1.Faces vs. non-face objects

Mean amplitudes for the interval between 140-200 ms post-stimulus recorded at parieto-occipital sites (PO7, PO3, PO4, PO8) were initially assessed with a three-factor (stimulus type x location x orientation) ANOVA. Results obtained from the analysis suggest that the amplitude measured in response to faces was larger in comparison to non-face objects (F[1,40]=14.07, p=.001). This difference is illustrated in Figure 3.1., which shows ERP responses to faces and non-face objects at parieto-occipital electrodes. Analysis of the main effect of location (F[1,40]=0.30, p=.865) brought no significant findings. At the same time, significant effect of the stimulus type x location interaction was obtained (F[1,40]=4.62, p=.038], which suggests that differences between the left and the right hemisphere measured for facial and non-facial stimuli were dissimilar. Particularly, higher amplitudes of the N170 elicited by faces were recorded over the right hemisphere, while the opposite pattern of results was obtained for non-face objects. However, when the location effect was analyzed separately for ERPs elicited by faces and by non-face objects, no significant effects were found (F[1,40]=0.47, p=.495 and F[1,40]=0.11, p=.745, for faces and non-face objects, respectively). Therefore, it can be definitely concluded that ERP responses to both faces and non-face stimuli were comparable for the left and the right hemisphere in our study.

Main effect of the stimulus orientation did not reach the level of significance (F[1,40]=3.25, p=.079). At the same time significant effect of the stimulus type x orientation interaction was found (F[1,40]=4.32, p=.044). These results suggest that the way in which stimuli were presented differently influenced ERP responses to faces and to non-face objects. Particularly, significant effect of the stimulus orientation was found for ERPs elicited by pictures of faces (F[1,40]=6.77, p=.013), but not for brain responses elicited by non-face objects (F[1,40]=0.04, p=.846). This effect is topographically presented in Figure 3.2. Significant result was also obtained for the stimulus location x orientation interaction (F[1,40]=5.59, p=.023). This effect suggests that stimuli inversion can remarkably influence responses recorded in the right hemisphere. However, this conclusion was not supported neither by the result from the three-way (stimulus type x location x orientation) interaction (F[1,40]=0.27, p=.606), nor by the results from the location x orientation interactions tested separately for two types of objects (F[1,40]=2.60, p=.114 and F[1,40]=1.55, p=.220, for faces and non-face stimuli, respectively).

Taken together, these results suggest that brain responses to faces, reflected in the amplitude of face-sensitive N170, differ significantly from those elicited by other objects. Specifically, we found larger amplitudes of the N170 elicited by faces when compared to non-facial stimuli. This effect was observed even when visual stimulation did not reach the conscious awareness, and it is indistinguishable from face effects previously reported in studies using supraliminal stimuli presentation. We also observed the influence of face inversion on the amplitude of the N170, and simultaneously, a lack of similar effect for objects other than faces. Correspondingly, similar dissociation was previously reported in studies with longer stimulus exposition.

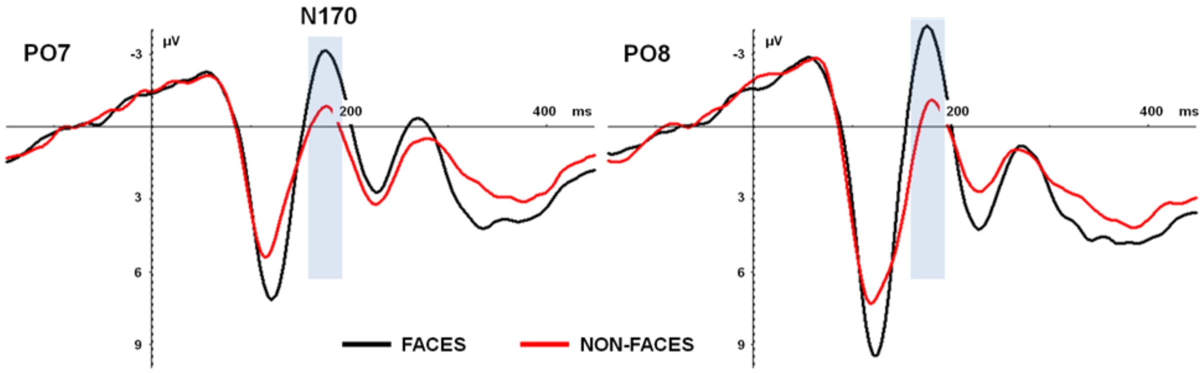

Figure 3.1. Event-related potentials evoked by subliminal presentation of faces and non-face objects masked by abstract picture. Time window of the N170 component (140-200 ms after stimulus onset) is highlighted.

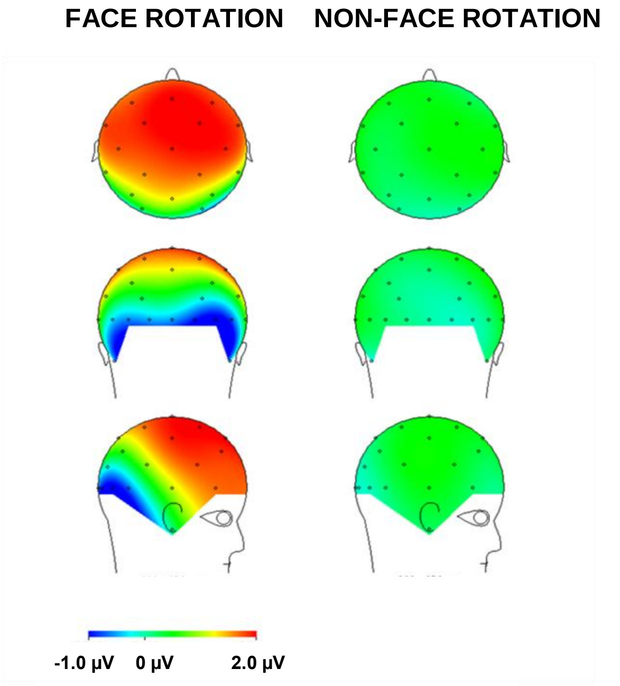

Figure 3.2. Spline maps showing the distribution of voltage differences (upright minus rotated) as the effect of rotation of faces and non-faces within the N170 component (140-200 ms post-stimulus).

3.4.2. Emotional expression effects

3.4.2.1. N170 component

Mean amplitudes recorded at parieto-occipital sites (PO7, PO3, PO4, PO8) for the interval between 140-200 ms after the stimulus onset were initially assessed with a three-factor (expression x location x orientation) ANOVA. We found that brain responses to fearful and neutral faces were highly similar, which was confirmed by the non-significant main effect of emotional expression (F[1,40]=0.07 p=.792). None of the two-factor interactions: expression x location (F[1,40]=0.09, p=.760) nor expression x orientation (F[1,40]=2.34, p=.134) were found to be significant. These results demonstrate that the effect of emotional expression was absent at this stage of face processing, with similar pattern of results obtained for upright and inverted faces. Moreover, no significant main effect of location was obtained (F[1,40]=0.49, p=.490), suggesting comparable amplitudes of the N170 recorded over the left and the right hemisphere. The effect of location x orientation interaction was found non-significant either (F[1,40]=2.38, p=.130), which suggests that the way in which the face was presented did not influence the pattern of the inter-hemispheric differences of the N170 amplitude. As it was described in the previous subsection, the main effect of the stimulus orientation was found to be significant (F[1,40]=7.15, p=.011), and similar effect of inversion was observed for each tested expression, as well as for both hemispheres. This conclusion was supported by non-significant expression x location x orientation interaction (F[1,40]=2.10, p=.155).

To summarize, emotional expression did not influence ERP responses measured within the face-sensitive N170 latency window. Simultaneously, brain activity recorded for upright faces differed significantly from the pattern of ERP responses obtained for inverted faces.

3.4.2.2. EPN component

Mean amplitude values computed for the interval between 215-310 ms after the stimulus onset were assessed with a two-factor (expression x orientation) ANOVA, performed for the recordings from occipital (O1, Oz, O2) and parieto-occipital electrodes (PO7, PO8) pooled together. Obtained results suggest that fearful faces elicited enhanced negativity in comparison to neutral stimuli, but only when faces were presented in the upright position. This suggestion was confirmed by observation that despite the fact that no significant main effect of emotional expression was obtained (F[1,40]=1.36, p=.250), the interaction between expression x orientation brought significant result (F[1,40]=7.52, p=.009). Moreover, when the effect of expression was tested separately for different stimulus orientations, significant result was obtained for upright trials (F[1,40]=6.82, p=.013), but not for inverted trials (F[1,40]=0.76, p=.389). What is also important, the main effect of stimulus orientation was found non-significant (F[1,40]=0.02, p=.875).

These findings suggest that emotional expression is able to modulate visual cortices activity even when the affective information is not perceived consciously. However, this modulation can only follow undisrupted structural analysis of face features. When facial structural encoding was disturbed by the face inversion, as a consequence the emotional expression effect reflected in EPN component was virtually absent. These effects are presented in Figures 3.3 and 3.4.

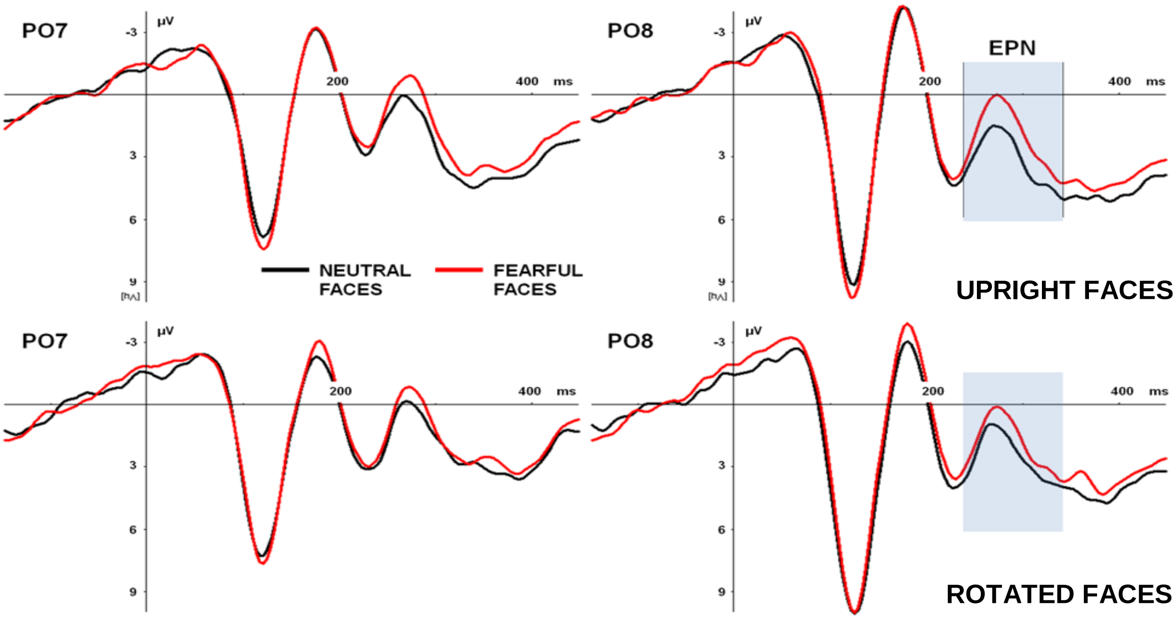

Figure 3.3. Event-related potentials evoked by subliminally presented and backward masked emotional and neutral faces in upright and rotated position. Time window of the EPN component (215-310 ms post-stimulus) is highlighted.

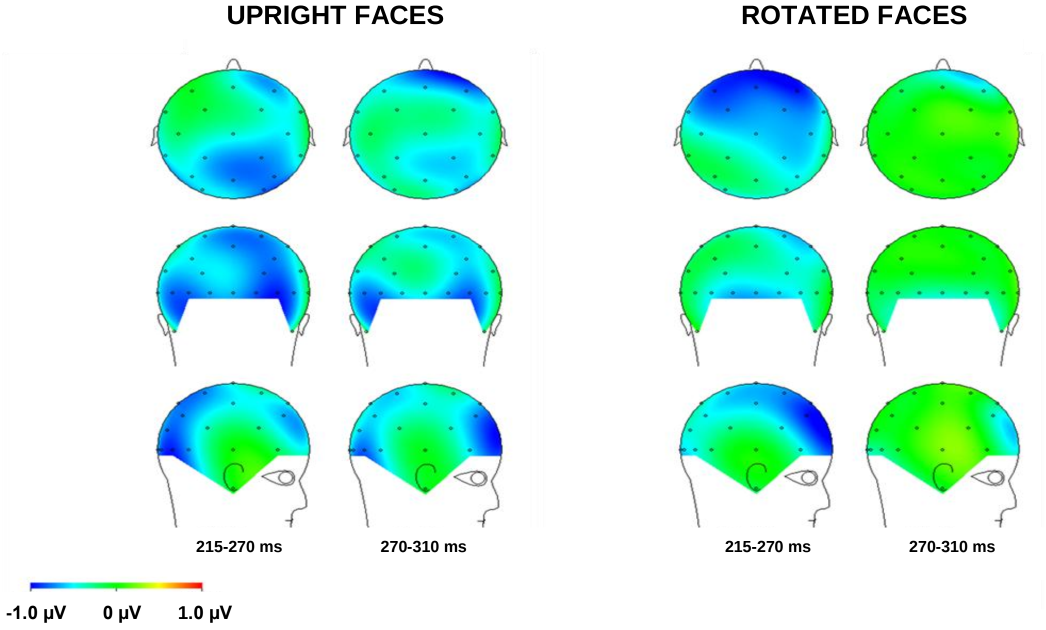

Figure 3.4. Spline maps showing the distribution of voltage difference between responses to emotional and neutral faces presented in upright and rotated position as reflected by the EPN component (215-310 ms post-stimulus).

3.5. Discussion

The current study was conducted to reveal specific forms of brain activity evoked by diverse objects presented in a condition of covert attention. Consistently with previous results, ERPs elicited by faces significantly differ from those evoked by non-face stimuli (N170 effect). Furthermore, the effects of face inversion (modulation of the N170 component), and facial emotion saliency (EPN effect) both support the hypotheses of the specificity of involuntary face and facial emotion processing. The most pronounced aim achieved in this study is related to the fact that face effect, as well as face inversion and emotional expression effects can be observed in case of subliminal and backward masked stimuli presentation. What is also interesting, all these effects are impossible to differentiate from the same effects observed with longer stimuli presentation. These findings support the thesis that face processing is fast, which reflects high biological and social significance of faces as specific visual stimuli. Furthermore, even in case of unintentional and unconscious processing, face and non-face objects evoke diverse patterns of brain activity during their upright or inverted presentations. Results from our experiment suggest that emotional and neutral faces can also be differentiated unintentionally and unconsciously.

As it has been reflected in the early ERP component, the N170, human brain reacted differently to faces when compared to other categories of objects (such as houses and trucks in the reported experiment). Over parieto-occipital cortex, the amplitudes of face-sensitive N170 (140-200 ms after stimulus onset) were significantly larger than those evoked by non-face stimuli, as it is shown in Figure 3.1. It is established in the literature that the N170 reflects early stages of the relational face processing, the structural encoding (Eimer, 2000; Itier & Taylor, 2004a). A specific configuration of facial non-redundant parts makes them belonging to a unique category of stimuli. This enables subsequent recognition of their identity or facial expression, which is essential for successful social communication. Significantly different brain responses to faces and non-faces at early stages of their processing were also recorded regardless of the fact that they were presented subliminally and probably were not perceived consciously. Very similar pattern of results (modulation of the N170 component) has been obtained in numerous studies using supraliminal stimuli presentations (Batty & Taylor, 2003; Bentin et al., 1996; Eimer, 2000; Eimer & Kiss, 2010; Itier & Taylor, 2004a) suggesting that subliminal face processing can influence brain activity over posterior brain areas indistinguishably from supraliminal processes.

Using the procedure with subliminal and masked presentations we also managed to reveal that the disruption of facial structural encoding, as the effect of face upside-down presentation, resulted in significant changes in the N170 morphology. Simultaneously, there was no such effect when non-face objects were inverted (see Figure 3.2.). The same findings have been reported as the effect of either face inversion (Eimer, 2000; Itier & Taylor, 2002, 2004b; Taylor, 2002), or contrast polarity reversal (Itier & Taylor, 2002, 2004b). According to the face-specific processing hypothesis, which argues for differential neural coding for faces and other objects, face inversion reflects the loss of configural information (Jemel et al., 1999). In the same time no loss of specific configural information has been described in object inversion. As a result of face upside-down presentation, neural systems responsible for object perception are additionally activated, which is reflected in stronger negativity of the N170 component during face inversion in comparison to non-face inversion. In our study, face inversion resulted in the differences in the N170 amplitude, with larger negativity recorded to upright when compared to inverted faces. This result is not, however, in opposition to previously reported ones, since Rossion with co-authors (1999) have suggested that stronger negativity of the N170 component can be registered as the effect of face inversion only if subjects perform in a task with explicit discrimination of faces. In our study, the task experimental procedure with subliminally presented and backward masked faces definitely unabled overt stimuli perception and recognition.

Not only static facial features form from the upright faces a special group of stimuli. In the present study emotionally-charged faces appeared to have a privilege in early processing, but only when their processing was not interrupted by stimulus inversion. As expected, the differences in the EPN component (between 215-310 ms after stimulus onset) were observed between fearful and neutral facial expressions, but only in case of their mono-oriented presentations. When the orientation was manipulated, differences could have not been observed (see Figures 3.3. and 3.4.). In numerous studies, negativity registered at posterior sites, mostly over parietal and occipital locations, is more pronounced for emotional, especially threatening images (Sato et al., 2001), or threat-related faces (Schupp et al., 2004b; Walentowska & Wronka, 2012; Wronka & Walentowska, 2011) when compared to neutral ones. There is general agreement that the EPN component reflects specific activation of brain regions engaged in visual information processing when stimuli of high evolutionary significance are presented. Our finding indicates that such modulation can be triggered even by subliminally presented facial stimuli, therefore the EPN differentiation can be related to their involuntary analysis. Similar effect has been reported by Jiang with colleagues (2009). Furthermore, our results not only validate these reports, but additionally show that this involuntary differentiation of facial expression can be determined by the accurate structural analysis of facial parts configuration. When faces were presented upside-down, facial structural encoding was disrupted. In effect, involuntary discrimination of facial affect was also disrupted, which resulted in lack of the EPN effect. However, these findings undoubtedly need further experimental investigation.

In contrast to these findings, we did not obtain the emotional expression effect in case of earlier processing phases, reflected in the N170 component, which is generally not in line with previous reports showing systematic emotional effects within this time window. However, in contrast to our experiment, these effects have been observed using different experimental procedures. Specifically, facial stimuli have been presented supraliminally, thus their conscious processing was possible. The modulation of the N170 component by facial emotions has been previously reported by several authors (Batty & Taylor, 2003; Blau et al., 2007; Miyoshi, Katayama, & Morotomi, 2004;

Pegna, Landis, & Khateb, 2008; Rigato, Farroni, & Johnson, 2010; Vlamings, Goffaux, & Kemner, 2009; Wronka & Walentowska, 2011), although some have failed to obtain such results in studies where procedures with subliminal processing have been used (Eimer, Kiss, & Holmes, 2008; Kiss & Eimer, 2008; Walentowska & Wronka, 2012). In one of our previous studies (Wronka & Walentowska, 2011), we have found that brain activity reflected by the N170 can be influenced by facial emotions only when their processing is voluntary. Thus, rapid detection of facial emotions is possible only as a result of the top-down attentional modulation. This may be one of the reasons why we have not obtained emotion-related differentiation of the N170 component in the current study, where involuntary facial emotion processing was implemented by the experimental procedure. This conclusion can be supported by results reported by Pegna with co-authors (2008), obtained in the backward masking procedure. They have observed the emotional expression effect within the latency of the N170 component for subliminally presented fearful and non-fearful faces. However, in this particular study attention was explicitly engaged in the detection of subliminally presented fearful faces. Therefore, although facial stimuli were processed without reaching conscious awareness, it can be concluded that their processing has undoubtedly been voluntary.

Automatic threat detection, especially from faces (mostly fearful ones), is an essential evolutionary ability to avoid danger and facilitate survival. Due to that, it is efficient even if threat-related facial stimuli are not perceived consciously. In the experimental conditions, subconscious processing can be provided with efficient masking procedures (Esteves & Öhman, 1993). As reported by numerous researchers, subliminal presentations of fearful faces evoke specific patterns of the amygdala activation (Whalen et al., 1998), or enhanced amplitudes of the early ERP components (Eimer, Kiss, & Holmes, 2008; Kiss & Eimer, 2008; Pegna, Landis, & Khateb, 2008). However, in these electrophysiological studies, subliminal presentations have been followed by the explicit discrimination tasks. In contrast to this, we have replaced the face or scrambled face mask with an abstract stimulus, and did not ask subjects to discriminate facial or non-facial stimuli, but to categorize masking objects. We thus consider that this alternative procedure offers entirely unintentional processing of subliminally presented information together with a guarantee that subjects have actively participated in the experiment.

However, when solving the troublesome issue of masking object together with the experimental task, our procedure can face at least one important limitation. Specifically, it was not designed to establish the conscious detection level in a precise fashion. To achieve this, a forced-choice task with objective threshold measurement should be used to gain insight into the real level of stimulus discrimination performance. In an objective manner, only chance-level thresholds can correspond to unconscious processing of the stimuli. From another point of view, a trial-after-trial discrimination procedure may evoke in participants a specific state of vigilance and anticipation of facial stimuli. Our procedure, although not providing an objective evaluation of the stimuli awareness, was free from this effect. However, as we were deeply interested in the visibility of the stimuli, after the experiment each participant was asked if he/she had seen something apart from the abstract mask. None confirmed that had seen faces, houses and trucks displayed prior to the mask. In future experiments this kind of examination will be employed in a more extended manner.

Another direction for the future research is the inclusion of clinical populations or subjects characterized by the specific tendencies in threat-related stimuli processing. In one of our previous studies, using very similar procedure we have shown that involuntary processing of faces and non-faces differs with respect to the self-reported level of subclinical anxiety (Walentowska & Wronka, 2012). Nevertheless, the assessment of other anxiety-related characteristics may be potentially helpful, as there is growing body of evidence from both electrophysiological and neuroimaging studies that responses to threat-related facial expressions are strongly influenced by the individual variation in common personality traits (Fox & Zougkou, 2011).

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Chapter 4.

THE INFLUENCE OF TRAIT ANXIETY ON THE INVOLUNTARY PROCESSING OF FACIAL EMOTIONS

This chapter is based on the modified version of Walentowska, W., and Wronka, E. (2012). Trait anxiety and involuntary processing of facial emotions. *International Journal of Psychophysiology, 85,* 27-36.

4.1. Abstract

There is suggestion that trait anxiety influences the processing of threat-related information. To test this hypothesis we recorded ERPs in response to subliminally presented and backward masked fearful and neutral faces, and non-face objects, in the preselected low- and high-anxious individuals. The amplitude of N170 was found to be larger when elicited by faces in comparison to non-faces, however it was not found to be emotion-sensitive or modulated by anxiety level. Differences between low- and high-anxious individuals appeared in a time window of the P1 component. At later stages, within the EPN component, stronger negativity specific for fearful faces was recorded exclusively in the low-anxious participants. Our findings indicate that anxiety level modulates early stages of information processing, as reflected in the P1 component. This leads to anxiety-related differences in involuntary emotional expression detection at later stages (EPN component).

4.2. Introduction

Emotional functioning determines important evolutionary adaptations involved in the control of behavior in complex social environments. Among other sources of social information, faces are salient stimuli conveying essential nonverbal signals. For that reason they are assumed to be the best direct indicator of current affective dispositions and attitudes, both positive and negative. Specifically, due to their biological and social significance, information about emotional states derived from faces should be processed very rapidly to be available for the immediate regulation of behavior.

Research on the brain structures relevant to perception and analysis of emotionally significant information has been conducted with the application of several complementary methods, such as electrophysiological recordings, functional brain imaging or neuropsychological investigation of focal brain damage. Recent findings suggest a separate brain module critically involved in face processing, located in the fusiform gyrus and in the superior temporal gyrus (Allison et al., 2000; Haxby et al., 2000). Moreover, brain regions generally engaged in the processing of faces are strongly activated during the processing of facial emotions. The initial perceptual analysis takes place in the inferior occipital cortex (Rossion et al., 2003) and in the lateral fusiform gyrus (Kanwisher et al., 1997) for invariant aspects of faces which determine face identity (Haxby et al., 2000). The superior temporal sulcus is involved in the processing of changeable aspects of faces, such as facial expression, eye and mouth movements (Allison et al., 2000). It has been moreover suggested that the amygdala and the orbitofrontal cortex mediate a rapid, preattentive evaluation of the emotional and motivational significance of facial expression (Sprengelmeyer et al., 1998), while the anterior cingulate, the prefrontal cortex and somatosensory areas are linked with forming conscious representations of facial emotional expressions (Adolphs, 2003).

Recent studies have indicated that a stimulus can be categorized as a face much earlier than other objects (Liu et al., 2002). Larger amplitudes of the N170 component of the ERP have been regularly obtained to faces when compared to non-face objects. The onset of the face effect has been observed remarkably early, between 140-200 ms poststimulus from occipito-temporal locations (Batty and Taylor, 2003; Bentin et al., 1996; Eimer, 2000; Eimer and Kiss, 2010; Itier and Taylor, 2004). Similarly, M170, the magnetic counterpart of the N170 scalp potential, is also face-sensitive, as revealed by Halgren et al. (2000).

There are also a number of studies in which the amplitude of N170 recorded in response to emotional faces has been found to be more pronounced than for neutral faces (Batty and Taylor, 2003; Blau et al., 2007; Miyoshi et al., 2004; Rigato et al., 2010; Vlamings et al., 2009). However, in our previous study (Wronka and Walentowska, 2011), the N170 modulation has been obtained exclusively in a task demanding emotional expression categorization, which suggests voluntary facial emotion processing at this stage of analysis. At later stages, authors have reported increased activity of the visual system elicited by facial emotions in comparison to neutral faces. This effect has been termed the Early Posterior Negativity (EPN; Sato et al., 2001; Schupp et al., 2004b; Wronka and Walentowska, 2011). In this case, the enhanced negativity elicited by emotional expressions was obtained about 200 ms after the stimulus onset. Recently, it has been suggested that the EPN reflects the activation of temporo-parieto-occipital areas engaged in the visual information processing, when stimuli of high evolutionary significance are presented (Schupp et al., 2003a, 2004a).

Numerous emotion-specific effects have been obtained in experiments with relatively long, supraliminal face presentations. However, affectively salient facial stimuli can capture attention and evoke specific electrophysiological responses even without reaching the level of conscious awareness. It has been suggested that subliminal processing of expressive facial cues may be mediated *via* a ‘short’ retino-thalamic-amygdalar neural pathway (see Pessoa, 2005 for discussion). Experimental evidence that facial threat is privileged in the processing comes mostly from studies where backward masking procedure has been used. With this technique, Whalen et al. (1998) have found stronger activity of the amygdala to fearful faces relative to happy ones. From the other hand, results obtained by Pessoa et al. (2006) suggest that the amygdala activity in response to fearful faces is probably related to the objectively assessed visibility of masked stimuli. However, fMRI technique with its rather low millisecond resolution does not provide information about the temporal characteristics of information processing. This can be obtained using electrophysiological recordings. In recent ERP studies authors report fear-specific patterns of brain activity in response to subliminal processing of backward masked facial stimuli (Eimer et al., 2008; Kiss and Eimer, 2008). Both experiments, conducted by the same group of researchers, have revealed no effects recorded in the time window of the N170 component. In contrast, Pegna et al. (2008) have found that subliminally presented fearful faces elicited larger N170 amplitudes than non-fearful (happy and neutral) faces. What should be noticed, this early effect has been obtained in a task demanding active detection of fearful faces, which can be related to voluntary attention involvement. Nevertheless, although all these experiments successfully explore the topic of subliminal processing of facial emotions, at least one imperfection can be found in the experimental procedures, which is the type of the mask. Eimer et al. (2008) and Pegna et al. (2008) used images of neutral faces as the masking stimuli. Kiss and Eimer (2008) used scrambled neutral faces, although the images probably still resulted in oval-shaped and face-similar masking objects. In this context it should be emphasised that the probability that brain responses to subliminally presented faces can interfere with responses to masking facial stimuli is relatively high and may serve to disrupt the analyses.

The general consensus comes from both ERP and neuroimaging studies that emotionally salient faces have a special status in capturing visual attention, even involuntarily, however still little is known about the emotionally rooted temperamental traits which influence information processing from the perspective of the subjects. Specifically, it has been suggested that the cognitive system of anxious individuals, characterized by the state or trait of apprehension, may be distinctively sensitive and may bias the processing of threat-related stimuli. Whalen (1998) suggests that fearful stimuli in comparison to angry ones evoke stronger brain responses due to their ambiguity. In the light of anxiety-related hypervigilance, perception of stimuli requiring more information to be interpreted may result in stronger activation of the anxious individuals. Generally, to study this issue more thoroughly, both clinical populations (displaying diverse anxiety disorders) and subclinical subjects (reporting high levels of trait anxiety in the State-Trait Anxiety Inventory; Spielberger et al., 1983) have been employed. It has been assumed that in high-anxious individuals threat-related information can rapidly capture attention (Bar-Haim et al., 2007; Mathews and Mackintosh, 1998; Mathews and MacLeod, 2002) even without conscious processing of the stimuli (Mogg and Bradley, 1998). Numerous neuroimaging studies confirm these results showing increased amygdala activity in highly trait anxious individuals during unconscious processing of fearful stimuli (Bishop, 2007; Etkin et al., 2004) when compared with low-anxious individuals. Consistent with these results, Ewbank et al. (2009) have obtained a significant positive correlation between the level of anxiety and the left amygdala activity in response to fearful expressions in condition when they were task-irrelevant and, due to attentional modulation, their processing was involuntary. Furthermore, early attentional orienting to threatening stimuli in high-anxious individuals has been shown in numerous electrophysiological studies suggesting privileged threat evaluation at initial stages (Fox et al., 2008; Li et al., 2005). One of the recent ERP studies in anxious individuals has aimed to examine the automaticity in facial emotion processing in tasks with different cognitive load (Holmes et al., 2009). Among others, the authors have revealed the modulation of P1 and EPN components specific for emotional faces. Notably, the EPN differentiation was more apparent within low-anxious group, while the P1 modulation was not influenced by the level of anxiety. Therefore, anxiety-related effects can be observed starting about 100 ms after the stimulus onset, which is consistent with the hypothesis that high level of anxiety can be linked with the hypervigilant processing of emotional information.

Our procedure was aimed to investigate the differences between brain responses to subliminally presented faces and non-face objects, as they have been extensively studied with supraliminally displayed stimuli, where the systematic face effect within the latency of N170 component has been observed. However, the open question is whether similar pattern of results can be recorded with very brief stimuli presentations. Moreover, the second aim of the current study was to investigate the course of involuntary face processing and facial emotion processing with respect to the level of self-reported trait anxiety. To address this issue, participants were briefly (for 16 ms) shown images of faces (fearful, neutral) and non-face objects, immediately masked by an abstract image, and they were asked to categorize masking stimuli. Backward masking procedure was used to limit the access of the masked objects to conscious awareness. In addition, we assumed that this procedure would successfully solve the problematic issue of the facial masking stimulus together with forced-choice discrimination of the target stimulus.

We hypothesised that if there is a qualitative difference between face and non-face processing, the amplitude of the occipito-temporal, face-specific N170 component would be larger in response to faces when compared to non-face objects, as it was previously revealed by researchers using longer stimuli presentations (Batty and Taylor, 2003; Bentin et al., 1996; Eimer, 2000; Eimer and Kiss, 2010; Itier and Taylor, 2004). To investigate the emotional expression effects, we anticipated that brain activity would be different in response to emotional and neutral faces. We predicted that faces with emotional expressions would modulate ERP waveforms over occipital sites starting from 100 ms after the stimulus onset, as this early modulation has been so far investigated with supraliminal face presentations (Holmes et al., 2008, 2009; Pourtois et al., 2005). Larger amplitudes of the N170 elicited by fearful relative to neutral faces can also be expected, relying on previous results (Batty and Taylor, 2003; Blau et al., 2007; Miyoshi et al., 2004; Rigato et al., 2010; Vlamings et al., 2009). At later stages, we expected facial threat to elicit stronger negativity of the emotion-specific EPN component in comparison to facial neutrality, which also has been shown using supraliminal presentations (Sato et al., 2001; Schupp et al., 2004b; Wronka and Walentowska, 2011). Notably, we also supposed that the emotional expression effects would be influenced by the level of subjects' trait anxiety. Results from the previous studies let us expect the differences in the course of facial emotion processing between low- and high-anxious subjects starting from 100 ms post-stimulus, overlapping with the P1 and EPN components.

4.3. Methods

4.3.1. Participants

Thirty six volunteers were selected from a large pool of first-year psychology students who had previously completed the trait scale from the State-Trait Anxiety Inventory (Spielberger et al., 1983) in Polish adaptation (Wrześniewski et al., 2002). Relying on the STAI scores, two groups were formed with 18 participants in each of them. Low-anxious (LA) individuals were defined as those scoring 35 and below, while high-anxious (HA) were those scoring 38 and more. For the LA group mean trait anxiety was 31.1 (SD=2.82), while mean trait anxiety for the HA individuals was 47.2 (SD=3.17). Difference in the level of trait anxiety was statistically significant ($F_{(1,35)}=100.8$, $p<.0001$), as revealed by one-factor ANOVA. The mean age for the LA group was 22 years (SD=2.62; 2 men and 16 women), while for the HA group the mean age was 20 years (SD=1.03; 1 man and 17 women). All participants declared to be right-handed and had normal or corrected vision. Additionally, participants were screened to ensure that they were free of any neurological or psychiatric disorders, and they were not regularly taking medications affecting the activity of the central nervous system. Prior to the beginning of the experiment subjects signed an approved consent form. Afterwards, their participation was awarded with course credits.

4.3.2. Stimuli

Color photographs of faces of 10 different individuals (5 men and 5 women) taken from the NimStim Face Stimulus Set (Tottenham et al., 2009; http://www.macbrain.org/resources.htm) were used as face stimuli. Facial expressions were fearful or neutral, resulting in a total of 20 different face stimuli. Color photographs of 10 houses and 10 trucks derived from the internet were used as non-face stimuli. Color masking stimuli were prepared by the authors using Corel PaintShopPro software, resulting in abstract symmetrical and asymmetrical images. Each masked object was presented at the fixation covering 17.5 cm x 11.5 cm, while the mask itself was presented at the fixation covering 17.5 cm x 23 cm.

4.3.3. Procedure

Subjects were comfortably seated in a dimmed, air-conditioned, and electrically isolated chamber. A computer screen was placed at a distance of approximately 70 cm. Subjects were instructed to maintain central eye fixation together with reducing eye blinks and excessive body movements during the procedure.

Each trial began with presentation of the fixation cross for 500 ms. It was followed by the exposition of object + mask stimuli for the next 500 ms. Images of various objects (faces, houses and trucks) were subliminally presented for 16 ms and immediately backward masked by abstract images displayed for 484 ms. Masking stimuli were symmetrical or asymmetrical abstract images. As the experimental task, subjects were asked to judge mask symmetry and respond with their dominant-hand button press whenever mask asymmetry was detected, and to restrain from motor response when a symmetrical masking object was presented.

The whole task consisted of 200 trials. Because of fatigue the experimental procedure was divided into two blocks, with 100 trials in each and counterbalanced with respect to type of the object and the mask. Each category of stimuli (faces and non-face objects) was presented in 100 trials. Among faces, fearful and neutral expressions were presented in 50 trials per category. Similarly, pictures of houses and trucks were presented in 50 trials per category. Ninety percent of trials (45 trials per each category) consisted of object + symmetrical mask presentation and in remaining 10% of trials (5 trials per each category) asymmetrical mask was used.

4.4.4. ERP Procedures and Analyses

The EEG was recorded using a BioSemi ActiveTwo system with Ag–AgCl electrodes from 32 monopolar locations (AF3, AF4, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO7, PO3, PO4, PO8, O1, Oz, O2), according to the 10–20 system. Two additional electrodes, the common mode sense (CMS) active electrode and the driven right leg (DRL) passive electrode, were used as reference and ground electrodes, respectively; cf. www.biosemi.com/faq/cms&drl.htm. All cephalic electrodes were placed on the scalp using an Electro-Cap. Two additional electrodes were placed at the mastoids and were also referred to the CMS active electrode. The horizontal and vertical EOGs were monitored by 4 electrodes, placed above and below the right eye and in the external canthi of both eyes. The EEG was acquired at a sampling rate of 256 Hz. The EEG data were off-line filtered with bandpass 0.016-45 Hz (24 dB) and sampled for a 600-ms trial (150 ms prior to the stimulus onset and 450 ms after the stimulus onset) using BrainVision software. Finally, data were corrected for eye-movement artifacts (Gratton et al., 1983) and re-referenced to linked mastoids. Only the EEG obtained from trials containing symmetrical masking stimuli, so not followed by the motor response, was averaged.

The first set of analyses was based on the mean amplitude values computed within the N170 time window for two categories of objects (faces vs. non-face objects). The N170 component was defined as the mean amplitude within 150-195 ms after the stimulus onset. The analyses of the face effects on the N170 component were restricted to parieto-occipital electrodes (PO7, PO8), in agreement with numerous previous findings (Bentin and Deouell, 2000; Itier and Taylor, 2004; Jacques and Rossion, 2004; Sagiv and Bentin, 2001; Yovel et al., 2003). The amplitude of the N170 component was analyzed using repeated-measures analysis of variance (ANOVA) examining the effects of within-subjects factors of STIMULUS TYPE (face vs. non-face) and LOCATION (left hemisphere vs. right hemisphere). The second set of analyses was performed to investigate differences in the brain activity during unconscious emotional expression processing. Moreover, we were interested in anxiety-related differences in the processing of facial emotional expression. These analyses were conducted for three successive poststimulus time windows: 100–120 ms (P1 component), 150–195 ms (N170 component), and 210–320 ms (EPN component), covering the time interval where systematic emotional expression effects have been observed in previous experiments (Batty and Taylor, 2003; Blau et al., 2007; Holmes et al., 2008, 2009; Miyoshi et al., 2004; Pegna et al., 2008; Pourtois et al., 2005; Rigato et al., 2010; Sato et al., 2001; Schupp et al., 2004b; Vlamings et al., 2009; Wronka and Walentowska, 2011). Mean amplitudes between 100-120 ms poststimulus were analyzed for occipital (O1, Oz, O2) and parieto-occipital locations (PO7, PO3, PO4, PO8). Analysis of the effects for the interval between 150-195 ms after the stimulus onset was performed at parieto-occipital electrodes (PO7, PO3, PO4, PO8). PO7 and PO8 electrodes were chosen due to the fact that at these locations N170 amplitude has been found to be maximal (Bentin and Deouell, 2000; Jacques and Rossion, 2004). PO3 and PO4 electrodes were chosen as they are located closely to posterior part of the superior temporal gyrus, the possible neural source of the N170 component (Itier and Taylor, 2004). Mean amplitudes between 210-320 ms poststimulus were analyzed for values recorded at occipital (O1, Oz, O2) and parieto-occipital electrodes (PO7, PO8). Repeated-measures analysis of variance (ANOVA) testing the effects of within-subjects factor of facial EXPRESSION (fearful vs. neutral), LOCATION (left hemisphere vs. right hemisphere for parieto-occipital sites), and between-subjects factor of GROUP (LA vs. HA) was used in case of the N170 component. While the P1 and EPN components were investigated, factor LOCATION was excluded and all electrodes were pooled together. All analyses of variance employed Greenhouse-Geisser corrections to the degrees of freedom when appropriate, and only the corrected probability values are reported. The Bonferroni method was used for *post-hoc* comparisons, with a significance level of 0.05.

Finally, we examined the relationship between the amplitudes of ERP components and the level of trait anxiety using the Pearson correlation coefficient.

4.4. Results

4.4.1. Faces vs. non-face objects

Mean amplitudes for the interval between 150-195 ms poststimulus recorded at parieto-occipital sites (PO7, PO8) were initially assessed with a two-factor (stimulus type x location) ANOVA. Results obtained from the analysis suggest that the amplitude measured in response to faces was larger in comparison to non-face objects ($F_{(1,35)}=27.17$, $p<.0001$), which is illustrated in Figure 4.1. Analysis of the main effect of location ($F_{(1,35)}=0.01$, $p=.970$), as well as the interaction between stimulus type x location ($F_{(1,20)}=3.46$, $p=.071$) brought no significant findings, which suggests that the amplitude of

N170 component recorded in response to both facial and non-facial stimuli was comparable for the left and the right hemisphere.

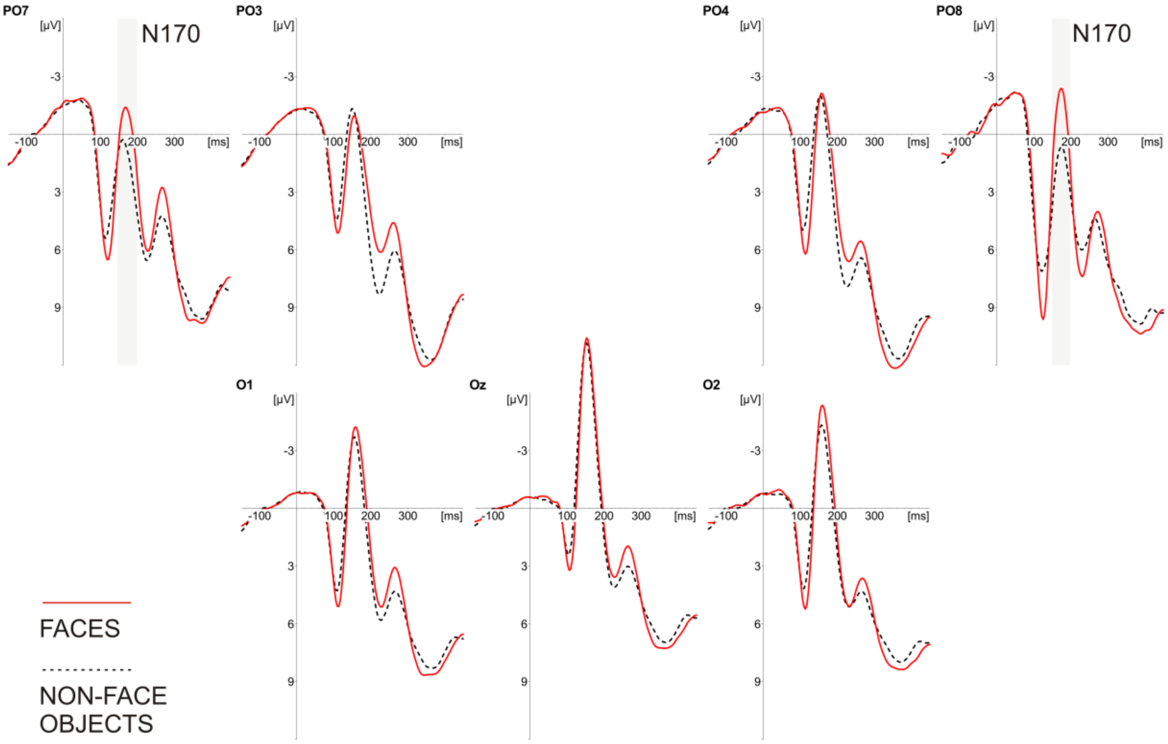

Figure 4.1. Grand average ERPs recorded at parieto-occipital (PO7, PO3, PO4, PO8) and occipital electrodes (O1, Oz, O2) in response to faces (solid lines) and non-face objects (dashed lines). Time window of the N170 component (150-195 ms poststimulus) is highlighted for lateral parieto-occipital electrodes (P07, P08).

4.4.2. Emotional expression effects and the level of anxiety

4.4.2.1. The P1 component (100-120 ms poststimulus)

Mean amplitude recorded for the interval between 100-120 ms after the stimulus onset was initially assessed with two-factor (expression x group) ANOVA, performed for values computed for parieto-occipital and occipital locations pooled together.

We found that brain responses to fearful and neutral faces were similar when tested at these electrodes. Main effect of emotional expression was found to be non-significant ($F_{(1,34)}<0.01$, p=.999). Similar pattern was obtained for low- and high-anxious individuals, which was confirmed by non-significant interaction between expression and group ($F_{(1,34)}=0.35$, p=.555). These findings suggest that emotional expression was not able to modulate early brain responses, at least when faces were presented very briefly. At the same time, we found higher positive values for the low-anxious group when contrasted with subjects with high level of anxiety. It was also confirmed by significant effect of group ($F_{(1,34)}=4.30$, p=.046).

This finding suggests that the higher was the level of trait anxiety, the lower was the amplitude of the P1 component measured at parieto-occipital and occipital sites. To test this hypothesis, we correlated STAI scores with the amplitude of the P1 component recorded in response to fearful and neutral facial stimuli. We obtained a negative correlation between the mean P1 amplitude averaged across seven tested electrodes and the level of trait anxiety (r = -.259, p=.064 and r = -.259, p=.063, all 1-tailed, for fearful and neutral stimuli, respectively). Similarly, negative coefficients were also obtained when correlation analysis was performed separately for each electrode. Here, significant correlations between STAI scores and the amplitude of P1 elicited by neutral faces were recorded for the left hemisphere electrodes, PO3 and PO7 (r = -.338, p=.022 and r = -.363, p=.015, 1-tailed, respectively), while correlations obtained for the other sites were weaker and non-significant (r = -.251, p=.070; r = -.161, p=.175; r = -.164, p=.169; r = -.198, p=.123, and r = -.175, p=.153, all 1-tailed, for O1, Oz, O2, PO4 and PO8, respectively). Significant correlations were also obtained for the left hemisphere sites when a relationship between STAI scores and the amplitude of P1 component elicited by fearful faces was tested (r = -.293, p=.042 and r = -.319, p=.029, 1-tailed, for PO7 and PO3, respectively). Weaker and non-significant correlations were obtained for the other electrodes (r = -.219, p=.100; r = -.126, p=.232; r = -.200, p=.122; r = -.224, p=.095, and r = -.242, p=.078, all 1-tailed, for O1, Oz, O2, PO4, and PO8, respectively). These results suggest a specific relationship between the level of trait anxiety and the magnitude of early brain response reflected in the P1 amplitude. Specifically, high level of trait anxiety can be linked with reduced amplitude of the P1 recorded over left visual areas in response to neutral faces and diminished amplitude of P1 obtained at right hemisphere locations in response to fearful faces.

To investigate the group effect more thoroughly, we additionally tested the hypothesis that the level of trait anxiety is able to modulate not only early stages of face processing, but also the analysis of non-face objects. For that reason mean amplitudes between 100-120 ms poststimulus were analyzed for occipital (O1, Oz, O2) and parieto-occipital locations (PO7, PO3, PO4, PO8) using repeated-measures analysis of variance (ANOVA) testing the effects of within-subjects factor of STIMULUS TYPE (face vs. non-face), and between-subjects factor of GROUP (LA vs. HA). The main effect of group remained almost significant ($F_{(1,34)}$=3.97, p=.054). What should be noticed, analysis of the interaction between stimulus type and group brought no significant result ($F_{(1,34)}$=0.64, p=.430), which suggests that anxiety-related modulation of visual information processing could have been observed at early stage for facial, as well as non-facial stimuli.

Taken together, these results suggest that brain responses to emotional and neutral faces were comparable for the interval between 100-120 ms post-stimulus, which corresponds with the P1 component. Emotional expression effect was absent in all tested locations, and it was not observed in any of the investigated groups. Simultaneously, brain activity within this same time window recorded for the low-anxious subjects differed significantly from the pattern of ERP responses obtained for the subjects with high level of trait anxiety. Specifically, mean amplitude of the P1 component computed for the LA group was higher in comparison to the HA group. Moreover, analogous group effect was also obtained for the comparison of faces and non-facial objects. This anxiety (group) effect is illustrated in Figure 4.4.

4.4.2.2. The N170 component (150-195 ms poststimulus)

Mean amplitude values computed for the interval between 150-195 ms after the stimulus onset were initially assessed with a three-factor (expression x location x group) ANOVA. This analysis was restricted to parieto-occipital locations (PO7, PO3, PO4, PO8).

We did not observe the differences between ERP responses to fearful and neutral faces, which was confirmed by non-significant main effect of emotional expression ($F_{(1,34)}$=0.41, p=.527). No significant finding was also obtained for the interaction between expression and group ($F_{(1,34)}$=2.22, p=.145), which suggests that the brain activity elicited at parieto-occipital locations by the exposition of emotional and neutral faces was similar in both groups differentiated by the level of trait anxiety. Analysis of the main effect of location ($F_{(1,34)}$=2.58, p=.118), as well as the interaction between expression and location ($F_{(1,34)}$=0.21, p=.649) brought no significant findings, which suggest that the amplitude of N170 recorded in response to both stimuli was comparable for the left and the right hemisphere. However, significant result was obtained for the interaction between location and group ($F_{(1,34)}$=4.99, p=.032). This effect suggests that higher N170 amplitude in the right hemisphere when compared to the left one could have been be obtained for low-anxious group, while the opposite difference could have been recorded for high-anxious group. This suggestion was confirmed by the results of two separate ANOVAs performed separately for the low- and high-anxious subjects. The main effect of location was found to be significant for the LA group ($F_{(1,17)}$=7.00, p=.017) suggesting that the amplitude of N170 measured over the right hemisphere was higher than its left hemisphere counterpart. Similar analysis for the HA group revealed no significant results ($F_{(1,17)}$=0.21, p=.654). Results from a three-factor ANOVA (expression x location x group) brought no significant findings either ($F_{(1,34)}$=0.37, p=.545). What also should be noticed, we did not observe any anxiety-related between-group differences for the mean ERP amplitudes computed at parieto-occipital locations in the latency window of N170 component ($F_{(1,34)}$=0.23, p=.635). This result suggests that group effect specifically observed for the interval between 100-120 ms after the stimulus onset was diminished at later stage of face processing.

Obtained results show that the N170 amplitude (150-195 ms poststimulus) was not sensitive to facial emotions, as the expression effect was found to be non-significant. Moreover, the N170 amplitude was comparable in groups with low and high level of trait anxiety.

4.4.2.3. The EPN component (210-320 ms poststimulus)

Mean amplitudes values computed for the interval between 210-320 ms after the stimulus onset were assessed with a two-factor (expression x group) ANOVA performed for occipital (O1, Oz, O2) and parieto-occipital electrodes (PO7, PO8) pooled together.

Obtained results suggest that fearful faces elicited enhanced negativity in comparison to neutral stimuli. This suggestion was confirmed by significant main effect of emotional expression ($F_{(1,34)}$=5.42, p=.026). Analysis of the interaction between expression and group also brought significant result ($F_{(1,34)}$=4.10, p=.051) suggesting that the emotional expression effect was different in both groups. However, at the same time non-significant main effect of group was found ($F_{(1,34)}$=0.06, p=.813), which suggests that brain activity recorded for the latency window between 210-320 ms after the stimulus onset did not differ substantially. For that reason we performed two additional analyses of the expression effect separately for the low- and high-anxious subjects. These analyses revealed significant emotional expression effect for the low-anxious group ($F_{(1,17)}$=8.52, p=.010), while similar analysis performed for the high-anxious group brought no significant results ($F_{(1,17)}$=0.05, p=.823).

These results suggest that the higher was the level of trait anxiety, the smaller was the difference between brain responses to fearful and neutral faces reflected in the EPN component. To test this hypothesis we directly correlated STAI scores with the magnitude of the EPN component, and obtained a negative correlation between the level of trait anxiety and the average values computed for five tested electrodes (r = -.242, p=.078, 1-tailed). It should be, however, noticed that the EPN component reflects the relative difference between brain responses to fearful and neutral faces. Therefore, negative values can be obtained when enhanced negativity elicited by fearful faces is recorded, and more positive values when this difference is diminished. Results from correlation analysis suggest that low STAI scores could have been related to bigger differences between brain responses to fearful and neutral stimuli, while in the group of high-anxious subjects, the EPN component was relatively reduced. Similarly, positive coefficients were also obtained when the analysis was performed separately for each electrode. Significant correlation was observed for midline occipital electrode, Oz (r =.298, p=.039, 1-tailed). The correlations obtained for the other sites were weaker and non-significant (r =.238, p=.081; r =.180, p=.146; r =.170, p=.161; r =.227, p=.091, all 1-tailed, for PO7, O1, O2, and PO8, respectively). These effects are illustrated in Figures 2 and 3, which show ERP responses, as well as in topographical maps presented in Figure 4.4.

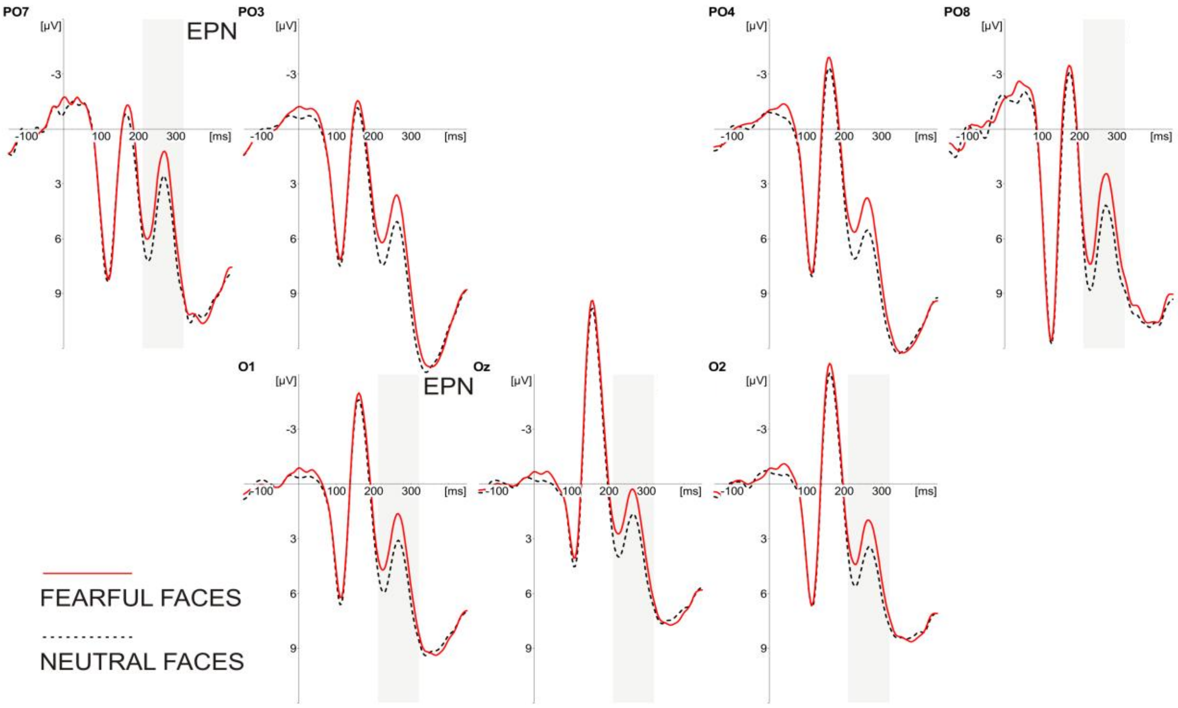

Figure 4.2. Grand average ERPs recorded at parieto-occipital (PO7, PO3, PO4, PO8) and occipital electrodes (O1, Oz, O2) in response to fearful (solid lines) and neutral faces (dashed lines) in the low-anxious group (LA). The time window of the EPN component (210-320 ms poststimulus) is highlighted.

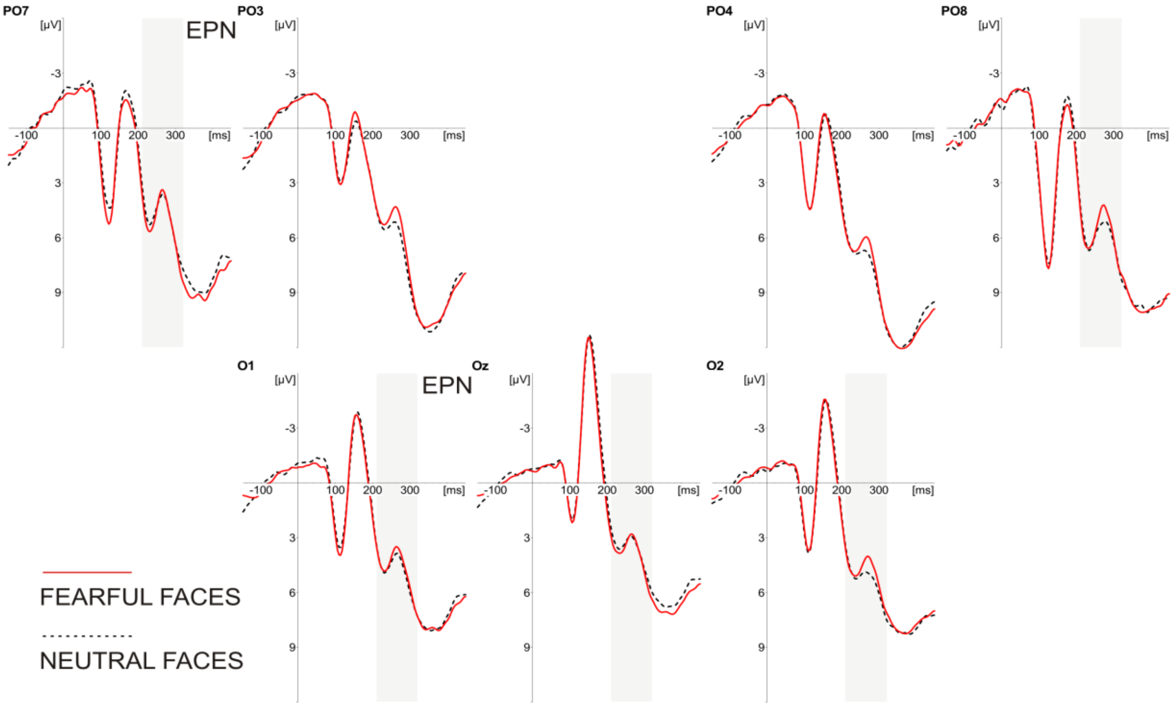

Figure 4.3. Grand average ERPs recorded at parieto-occipital (PO7, PO3, PO4, PO8) and occipital electrodes (O1, Oz, O2) in response to fearful (solid lines) and neutral faces (dashed lines) in the high-anxious group (HA). The time window of the EPN component (210-320 ms poststimulus) is highlighted.

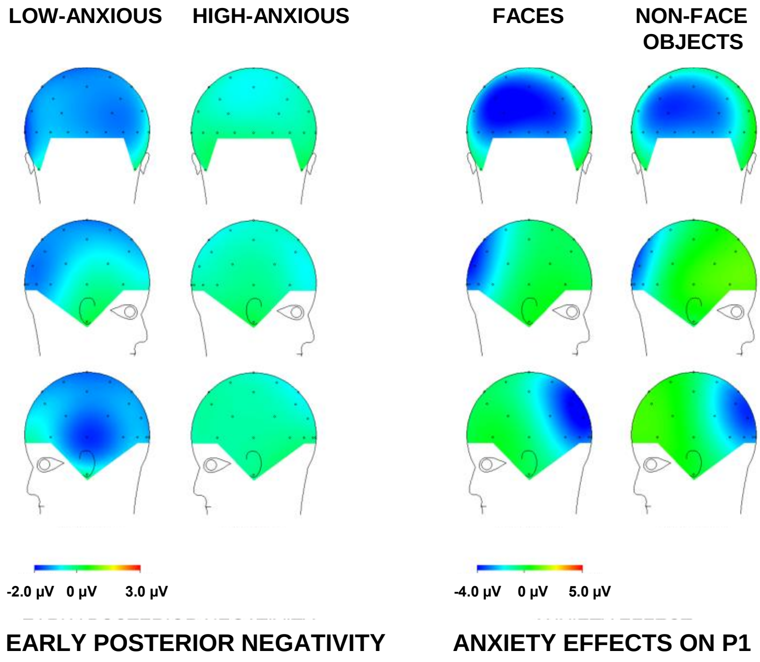

Figure 4.4. Topographical maps representing two main effects observed in this study. Left panel shows voltage differences in brain activity elicited by fearful and neutral faces in the time interval of the Early Posterior Negativity (EPN, 210-320 ms poststimulus) for low-anxious and high-anxious subjects. Right panel shows topography of the anxiety effects observed in the time interval of the P1 component (100-120 ms poststimulus) for facial and non-facial stimuli.

To test whether anxiety-related reduction of the emotional expression effect reflected in the diminished EPN component can be related to anxiety (group) effect observed at early stages of face processing in the P1 amplitude, we performed correlation analysis. We expected that higher P1 amplitude would be related to the more pronounced EPN component (enhanced negativity in response to fearful faces) resulting in negative correlation coefficients. We found that the mean P1 amplitude, averaged across all tested electrodes, recorded in response to neutral faces correlated significantly with the EPN component, also averaged across all tested electrodes (r = -.320, p=.028, 1-tailed). Weaker and non-significant correlation was obtained for the P1 elicited in response to fearful faces (r = -.113, p=.256, 1-tailed). Additionally, we performed similar analysis separately for each of the five electrodes included in the EPN calculation. Consistently, significant correlations between amplitude of the P1 elicited by neutral faces and the EPN magnitude were recorded for the left hemisphere electrodes, PO7 and O1 (r = -.422, p=.005 and r = -.344, p=.020, 1-tailed, respectively), while correlations obtained for the other sites were weaker and non-significant (r = -.172, p=.157; r = -.116, p=.251, and r = -.238, p=.081, all 1-tailed, for Oz, O2, and PO8, respectively). Remarkably, no such relationship was observed when the amplitudes of the P1 elicited by fearful faces were correlated with the EPN values (r = -.171, p=.160; r = -.094, p=.293; r =.029, p=.434; r =.105, p=.271, and r = -.030, p=.432, all 1-tailed, for PO7, O1, Oz, O2, and PO8, respectively).

4.5. Discussion

The current study was conducted to reveal specific forms of brain activity evoked by subliminally presented and backward masked faces and non-face objects. Consistently with previous results from studies where brain responses were recorded to supraliminally presented stimuli, ERPs elicited by faces significantly differ from those evoked by non-face stimuli at parieto-occipital locations (modulation of the N170, 150-195 ms poststimulus). Early stages of face processing revealed in the P1 and N170 components were generally not affected by emotional expression in either group differentiated by the level of anxiety. At the same time, however, difference in brain responses to all used stimuli was observed between low- and high-anxious individuals between 100-120 ms poststimulus, overlapping with the P1 component. Larger positivity was obtained for subjects with low scores on trait anxiety scale when compared to high-anxious group. Finally, exposition of emotional faces elicited enhanced posterior negativity when compared to neutral trials at later stages of processing between 210-320 ms after the stimulus onset, which corresponds to the EPN component. This effect was additionally modulated by the level of trait anxiety. In particular, the EPN component was apparent in the low-anxious group, while it was virtually absent for the high-anxious subjects.

The novel input of the study can be considered in several areas of interest. Firstly, in the condition of subliminal presentations, we have managed to obtain the differential early brain responses to faces and non-faces, which is consistent with findings from studies with longer stimuli presentations (Batty and Taylor, 2003; Bentin et al., 1996; Eimer, 2000; Eimer and Kiss, 2010; Itier and Taylor, 2004). This finding suggests that the specific activity of the system involved in the face perception can be registered irrespective of the stimulus awareness level, as well as the duration of stimulus presentation. It also supports the thesis that face processing is fast and efficient, which reflects high biological and social significance of this type of visual stimuli. Secondly, in contrast to some previous studies (Eimer et al., 2008; Kiss and Eimer, 2008; Pegna et al., 2008), we have replaced the face or scrambled face mask with an abstract stimulus and did not ask our participants to discriminate facial or non-facial stimuli, but to categorize masking objects. We consider that this alternative procedure offers entirely unintentional processing of subliminally presented information together with a guarantee that subjects have actively participated in the experiment. Thirdly, results from our experiment suggest that the differentiation of emotional faces can be observed in case of their unintentional and unconscious processing, which was reflected in emotion-specific brain responses starting from 200 ms poststimulus (Early Posterior Negativity, EPN). This finding is consistent with results reported by Jiang et al. (2009). Fourthly, we have obtained anxiety-related modulation of visual information processing at early stages, starting from 100 ms poststimulus (P1 component). Furthermore, the difference between low- and high-anxious individuals has been recorded also at later stage of processing. However, this specific effect was restricted to emotional expression differentiation revealed by the EPN component.

As revealed by the early ERP component, the N170, human brain reacts differently to faces when compared to other categories of objects (such as houses and trucks). Over parieto-occipital locations, the amplitudes of face-sensitive N170 were significantly larger than those evoked by non-faces, as it is shown in Figure 4.1. The N170 reflects early stages of the relational face processing, termed structural encoding (Eimer, 2000; Itier and Taylor, 2004). A specific configuration of facial non-redundant parts, like eyebrows, eyes and mouth, makes faces belong to a unique category of stimuli and enables subsequent recognition of their identity or facial expression, which is essential for successful social communication. Moreover, we have recorded significantly different brain responses to faces and non-faces at early stages of their processing regardless of the fact that they were presented subliminally and probably were not perceived consciously. Analogous pattern of results with a modulation of the N170 component has been obtained in numerous studies using supraliminal image presentations (Batty and Taylor, 2003; Bentin et al., 1996; Eimer, 2000; Eimer and Kiss, 2010; Itier and Taylor, 2004) suggesting that subliminal face processing can influence brain activity within the extrastriate cortex indistinguishably from supraliminal processes.

Differences between brain responses elicited by fearful and neural faces appeared at later stages of stimulus processing. This effect was observed 210-320 ms after the stimulus onset at occipital and parieto-occipital locations, overlapping with the Early Posterior Negativity (EPN component). It is consistent with numerous findings where the negativity recorded at posterior sites around 200 ms poststimulus has been more pronounced for emotional, especially threatening, images (Schupp et al., 2003a, 2003b, 2004a), or threat-related faces (Sato et al., 2001; Schupp et al., 2004b, Wronka and Walentowska, 2011) relative to neutral ones suggesting their preferential emotional processing. There is general agreement that the EPN component reflects specific activation of brain areas engaged in visual information processing when stimuli of high evolutionary significance are presented. Our finding indicates that such modulation can be triggered by subliminally presented facial stimuli. In our experiment stimuli were processed unconsciously, therefore the EPN differentiation can be related to their involuntary analysis. Similar effect has been reported by Jiang et al. (2009) where the interocular suppression paradigm has been used.

In contrast to this, we did not obtain the emotional expression effect in case of earlier processing phases, reflected in the P1 and N170 components. It is generally not in line with previous reports showing systematic emotional-neutral differentiation in brain responses. Differential activity elicited by fearful when compared to neutral faces within the time window of P1 component has been reported by numerous researchers (Holmes et al., 2008, 2009; Pourtois et al., 2005). This early ERP effect has been linked with the enhanced sensory encoding in visual brain areas as a result of a feedback projection from the amygdala, where rapid evaluation of significant stimuli takes place (see, e.g., Vuilleumier and Pourtois, 2007). However, in contrast to our experiment, these effects have been observed using different experimental procedures. Specifically, facial stimuli have been presented supraliminally, thus their conscious processing was possible. The modulation of the N170 component by facial emotions has also been previously reported by several authors (Batty and Taylor, 2003; Blau et al., 2007; Miyoshi et al., 2004; Pegna et al., 2008; Rigato et al., 2010; Vlamings et al., 2009; Wronka and Walentowska, 2011), although some have failed to obtain such results in studies where procedures with subliminal processing have been used (Eimer et al., 2008; Kiss and Eimer 2008). In our previous study (Wronka and Walentowska, 2011), we have found that brain activity reflected by the N170 can be influenced by facial emotions only when their processing is voluntary. Thus, rapid detection of facial emotions is possible only as a result of the top-down attentional modulation. This may be one of the reasons why we have not obtained emotion-related differentiation of the N170 component in the current study, where involuntary facial emotion processing was implemented by the experimental procedure. This conclusion can be supported by results reported by Pegna et al. (2008), obtained in the backward masking procedure. They have observed the emotional expression effect within the latency of the N170 component for subliminally presented fearful and non-fearful faces. However, in this particular study attention was explicitly engaged in the detection of subliminally presented fearful faces. Therefore, although facial stimuli were processed without reaching conscious awareness, it can be concluded that their processing has undoubtedly been voluntary.

Results obtained in our study support the thesis that trait anxiety can modulate processing of facial expression. We have found the differences between low- and high-anxious subjects in the activity of visual brain areas within the latency of Early Posterior Negativity (EPN, 210-320 ms poststimulus). Specifically, the EPN component was evident in case of participants with low level of anxiety and it was virtually absent for high-anxious group (see Figures 4.2-4.4). This effect can reflect distinct pattern of brain activity when it is engaged in the processing of visual stimuli characterized by high evolutionary significance. Comparable results have been obtained by Holmes et al. (2008, 2009). What is important in this context, in contrast to the effect reported by these authors, our experimental procedure has eliminated voluntary processing of facial stimuli and their accessibility to subject’s consciousness. At the same time, emotional expression did not influence ERP responses measured at earlier stages of processing, and similar pattern has been observed in our both investigated subgroups. This finding suggests that early phases of facial emotion processing are not modulated by the level of trait anxiety. However, we have also found anxiety-related differences in brain activity elicited by visual stimuli for the interval between 100-120 ms poststimulus. Specifically, larger amplitude of early P1 component has been recorded for the low-anxious participants when compared to high-anxious group. Moreover, analogous effects have been observed for facial and non-facial stimuli (see Figure 4.4). This finding suggests that early stages of visual information processing can be remarkably altered in case of high-anxious group. We assume that early anxiety effect overlapping with P1 component can be functionally linked with later differences in magnitude of the EPN component, which has been confirmed using correlation analyses. There are at least two alternative explanations of this phenomenon. Firstly, alteration of visual information processing at early stages (P1 component) can result in deficits in facial emotion discrimination at later stages (EPN component), which suggests that high-anxious individuals should demonstrate problems with emotional expression recognition. However, there is no consistent support from experimental studies for this assumption. Secondly, early P1 effect can reflect hypervigilant tendency to process neutral stimuli as emotional ones in high-anxious subjects, which results in lack of the EPN effect. As the EPN is defined as the difference in brain responses to emotional and neutral stimuli, then this hypervigilance can lead to comparable visual areas activation elicited by all stimuli irrespective of their content. Therefore, the EPN component can not be observed in high-anxious subjects. This explanation has been supported by the significant correlation between the amplitude of P1 elicited by neutral faces and the magnitude of the EPN component, reported in the current study. However, these speculations definitely need further research.

Among other incentives, at least a few arise from the limitations of the current study. The experimental task was designed to explore the subliminal processing of stimuli, which was provided with brief presentations followed by backward masking. However, it was not aimed to precisely establish conscious detection level. Objectively, only chance-level thresholds can correspond to unconscious processing of the stimuli. However, explicit discrimination procedure may evoke in participants a specific state of expectation of facial stimuli. Our procedure was free from this effect. However, as we were interested in the visibility of the stimuli, in the end of experiment each participant was asked if he/she had seen something apart from the abstract mask. None confirmed to had seen faces, houses and trucks followed by the mask. Nevertheless, future experiments need to examine this issue in a more extended manner.

Secondly, this study was narrowly designed to compare emotionally salient (fearful faces) versus neutral stimuli (neutral faces and non-faces). Therefore, it has not been optimized to determine if other facial emotions, both positive and negative, are able to elicit comparable brain responses, which can be indisputably considered as one of the disadvantages of the current study. Thus, future research from this area of interest should incorporate a wider range of facial emotions used as the stimuli. Moreover, it has also been suggested that threat-related facial expressions, like fear or anger, may result in the differences in brain activity. Using fMRI technique, Ewbank et al. (2009) have shown that perceiving facial fear and facial anger leads to different patterns of the left amygdala activation. Although in our opinion using fearful stimuli to investigate anxiety-related differentiation is more reasonable (for arguments see Whalen, 1998), a direct comparison of both ‘faces’ of threat, fear and anger, is certainly worth more thorough experimental investigation, also with ERPs.

Results from this research show that involuntary processing of faces and non-faces differs with respect to the level of subclinical anxiety. Some important implications arise from these findings, as numerous psychiatric or neurological disorders, such as wide spectrum of anxiety disorders or depression, are characterized by the impaired processing of facial emotions in everyday life. Therefore, a deeper understanding of how self-reported, subclinical anxiety shapes human cognition may help in better diagnose and treatment of numerous affective disorders. The assessment of other anxiety-related characteristics may be potentially helpful, as there is growing body of evidence from both electrophysiological and neuroimaging studies that responses to threat-related facial expressions are strongly influenced by the individual variation in common personality traits. Particularly, biases towards threatening information derived from faces in anxious individuals have been reported by numerous authors (Fox, 2011, for review). Hence, one another limitation of the current study was the lack of control of other characteristics, such as social phobia/social anxiety or depression levels.

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Chapter 5.

THE INFLUENCE OF TRAIT ANXIETY ON EARLY AND LATE STAGES OF EMOTIONAL EXPRESSION PROCESSING

This chapter is based on the modified version of Walentowska, W., and Wronka, E. (submitted). Anxiety modulates early and late stages of facial emotion processing.

5.1. Abstract

Emotional expression can influence brain activity even when the subject is not explicitly involved in the recognition. Trait anxiety is supposed to influence the processing of threat-related information, and therefore can alter brain responses to facial emotions (fearful faces). To test this hypothesis, we recorded ERPs in response to faces (fearful & neutral) and non-faces in preselected low- and high-anxious individuals (STAI scores). We found increased amplitude of the N170 elicited by faces in comparison to non-face objects. Additionally, emotional expression effects starting from 140 ms poststimulus have also been observed. Larger amplitudes of the N170 component were obtained in response to fearful faces when compared to neutral ones. Moreover, we observed enhanced negativity (EPN) elicited by emotional expression at occipital sites between 220-300 ms poststimulus. These effects were partially modulated by the level of anxiety. Specifically, the EPN effect was only evident for low-anxious subjects, and was diminished for high-anxious group. At earlier stages, the P1 component was more positive in case of high-anxious group, and this effect was observed irrespective of the stimulus type (for faces and non-face objects). These results suggest that in high-anxious group early hypervigilance (P1 effect) can lead to withdrawal from the processing of threat-related information at later stages (lack of EPN effect).

5.2. Introduction

Research on the brain structures relevant to perception and analysis of emotionally significant information has been conducted with the application of several complementary methods, such as electrophysiological recordings, functional brain imaging or neuropsychological investigation of focal brain damage. This effort has been for many years invested into the examination of the specifity of affective information processing, as emotional functioning determines important evolutionary adaptations involved in the control of behavior in complex social environments. Among other sources of social information, faces are salient stimuli conveying essential nonverbal signals. For that reason they are assumed to be the best direct indicator of current affective dispositions and attitudes. Specifically, due to their biological and social significance, information about emotional states derived from faces should be processed very rapidly to be available for the immediate regulation of behavior. Therefore, it has been very often postulated that facial affect processing is automatic (Palermo and Rhodes, 2007).

Some recent findings suggest a separate brain module critically involved in face processing, within the fusiform gyrus and in the superior temporal gyrus (Allison et al., 2000; Haxby et al., 2000). The initial perceptual analysis takes place in the inferior occipital cortex (Rossion et al., 2003) and in the lateral fusiform gyrus (Kanwisher et al., 1997) for invariant aspects of faces which determine face identity (Haxby et al., 2000). The superior temporal sulcus is involved in the processing of changeable aspects of faces, such as facial expression, eye and mouth movements (Allison et al., 2000). Moreover, it has been suggested that the amygdala and the orbitofrontal cortex mediate a rapid, preattentive evaluation of the emotional and motivational significance of facial expression (Sprengelmeyer et al., 1998), while the anterior cingulate, the prefrontal cortex and somatosensory areas are linked with forming conscious representations of facial emotional expressions (Adolphs, 2003).

Electrophysiological studies using Event-Related Potentials (ERPs) technique have indicated that stimulation can be categorized as a face much earlier than other objects (Liu et al., 2002). Other studies also suggest that emotional information from faces can be registered and discriminated very rapidly. Larger amplitudes of the N170 ERP component have been regularly obtained to faces when compared to non-face objects. The onset of the face effect has been observed remarkably early, between 140-200 ms poststimulus from occipito-temporal locations (Bentin et al., 1996; Walentowska and Wronka, 2012; Walentowska and Wronka, submitted). Similarly, M170, the magnetic counterpart of the N170 scalp potential, is also face-sensitive, as revealed by Halgren et al. (2000). In numerous studies the amplitude of N170 recorded in response to emotional faces has been found to be more pronounced than for neutral faces (Batty and Taylor, 2003; Blau et al., 2007; Miyoshi et al., 2004; Rigato et al., 2010; Vlamings et al., 2009; Wronka and Walentowska, 2011). However, in one of our previous studies (Wronka and Walentowska, 2011), the N170 modulation has been obtained exclusively in a task demanding emotional expression categorization, which suggests voluntary facial emotion processing at this stage of analysis. In our other studies (Walentowska and Wronka, 2012; Walentowska and Wronka, submitted), where the unconscious and involuntary emotional expression processing was implemented by the experimental procedure, the N170 morphology was not influenced by facial affect.

At later stages, researchers have reported increased activity of the visual system elicited by facial emotions in comparison to neutral faces. This effect has been termed the Early Posterior Negativity (EPN; Sato et al., 2001; Schupp et al., 2004b; Walentowska and Wronka, 2012; Walentowska and Wronka, submitted; Wronka and Walentowska, 2011). In this case, the enhanced negativity elicited by emotional expressions was obtained about 200 ms after stimulus onset. EPN effect has been suggested to reflect the activation of temporo-parieto-occipital brain areas engaged in visual information processing, exclusively when stimuli of high evolutionary value are presented (Schupp et al., 2003, 2004a). As revealed by our previous studies, facial affect processing is involuntary at this stage of analysis. The EPN effect has been observed irrespective of the experimental procedure (Wronka and Walentowska, 2011), even during unconscious emotional expression processing (Walentowska and Wronka, 2012; Walentowska and Wronka, submitted).

Given these findings, it can be assumed that facial emotional expressions, which are considered to be complex visual stimuli, are detected rapidly. Moreover, evoked brain responses to emotional expressions are noticeably different than ERPs elicited by neutral faces. However, it can be found in the literature that emotional expressions effects differ substantially between studies, which can be related to diverse experimental procedures. The emotional expression effects on the N170 have not been observed during entirely involuntary processing, where subliminal presentations and backward masking procedures had been used (Walentowska and Wronka, 2012; Walentowska and Wronka, submitted). In contrast to this, the effects have been registered when researchers explicitly instructed their subjects to attend presented faces and to discriminate emotional expressions (Leppänen, et al., 2007; Wronka and Walentowska, 2011). Secondly, they were also observed when participants were asked to attend facial stimuli and to identify face gender (Sato et al., 2001), or to discriminate faces from non-faces (Batty and Taylor, 2003). Interestingly, emotional expression effects have also been obtained in studies where no specific response was required from the participants (Miyoshi et al., 2004; Schupp et al., 2004b). Therefore, it can be suggested that attention was differently engaged in perception of emotional expression in all these studies. The emotional expression effects were observed in case of both voluntary and involuntary processing, which sheds a new light on the issue of automatic facial emotion processing. In our previous studies, late EPN component has been found to be non-sensitive to attentional influence (Walentowska and Wronka, 2012; Walentowska and Wronka, submitted; Wronka and Walentowska, 2011). In the same time, early N170 component has been related to voluntary facial affect processing (Wronka and Walentowska, 2011). As a confirmation of these findings, we did not observe the N170 modulation during unconscious processing of facial emotions (Walentowska and Wronka, 2012; Walentowska and Wronka, submitted). However, the open question remains whether the N170 modulation depends on the explicit attention engagement, or on the duration of stimulus presentation. To address these issues, the first aim of the current study is the investigation of facial emotion processing during involuntary (but supraliminal) information processing.

Some recent ERP and neuroimaging studies have revealed that emotionally salient faces have a special status in capturing visual attention, what very often happens involuntarily. Until today, however, little is known about emotionally rooted temperamental traits which also can influence information processing. Specifically, it has been suggested that the cognitive system of anxious people, who are characterized by the state or trait of apprehension, may be distinctively sensitive and may bias the processing of threat-related stimuli. To study this issue more thoroughly, both clinical populations (displaying diverse anxiety disorders) and subclinical subjects (reporting high levels of trait anxiety in the State-Trait Anxiety Inventory; Spielberger et al., 1983) have been employed. It has been assumed that in high-anxious individuals threat-related information can rapidly capture attention (Bar-Haim et al., 2007; Mathews and Mackintosh, 1998; Mathews and MacLeod, 2002). Numerous neuroimaging studies confirm these results showing increased amygdala activity in highly trait anxious individuals during unconscious processing of fearful stimuli (Bishop, 2007; Etkin et al., 2004) when compared with low-anxious individuals. Consistent with these results, Ewbank et al. (2009) have obtained a significant positive correlation between the level of anxiety and the left amygdala activity in response to fearful expressions. Furthermore, early attentional orienting to threatening stimuli in high-anxious individuals has been shown in numerous electrophysiological studies, suggesting privileged threat evaluation at initial stages (Fox et al., 2008; Li et al., 2005). One of the recent ERP studies in anxious individuals has aimed to examine the automaticity in facial emotion processing in tasks with different cognitive load (Holmes et al., 2009). Authors have reported the modulation of the P1 and EPN components specific for emotional faces. Notably, the EPN differentiation was more apparent within low-anxious group, while the P1 modulation was not influenced by the level of anxiety. In our previous study (Walentowska and Wronka, 2012), we have observed similar effect within the EPN component. Specifically, the differences in the brain activity elicited by fearful and neutral faces were registered in low-anxious individuals, while in the high-anxious group this effect was absent. In contrast to Holmes and colleagues (2009), we have also observed the anxiety-dependent modulation of the P1 component. Specifically, larger amplitudes of early P1 component have been recorded for low-anxious participants when compared to high-anxious ones. Moreover, analogous effects have been observed for facial (fearful and neutral) and non-facial stimuli. Taken together, these findings suggest that early anxiety effects within the P1 component can be functionally linked with later differences in the EPN component. In high-anxious subjects, early P1 effect probably reflects a hypervigilant tendency to process neutral stimuli as emotional ones. Comparable early activation of the visual cortex in high-anxious subjects results in the lack of further EPN effect, which is emotion-sensitive. Therefore, it can be assumed that this anxiety-related hypervigilant tendency reflects some aspects of automatic emotional expression processing, as it was defined by Palermo and Rhodes (2007). Importantly, effects described in our previous studies have been registered using procedure with subliminal and backward masked stimuli presentations. Therefore, stimuli processing was unconscious and entirely involuntary in these studies. The second aim of the current study is further investigation of the above described effects. This time, however, although information processing is involuntary, stimuli presentation is supraliminal.

To address these issues, participants were supraliminally shown images of faces (fearful and neutral) and non-face objects for 1s. During some trials, red asterix was presented on the background of the photograph. As the experimental task, participants were asked to respond to red asterix. We assumed that this procedure would give participants the opportunity for involuntary processing of faces and non-face stimuli, presented for relatively long time. Particularly, we hypothesised that brain activity would be different in response to emotional and neutral faces. We predicted that faces with emotional expressions would modulate ERP waveforms over occipital and parieto-occipital sites starting from around 150 ms after stimulus onset. Larger amplitudes of the N170 elicited by fearful relative to neutral faces can be expected, relying on previous results (Batty and Taylor, 2003; Blau et al., 2007; Miyoshi et al., 2004; Rigato et al., 2010; Vlamings et al., 2009; Wronka and Walentowska, 2011). At later stages, we expected facial threat to elicit stronger negativity of the emotion-specific EPN component in comparison to facial neutrality (Sato et al., 2001; Schupp et al., 2004b; Walentowska and Wronka, 2012; Walentowska and Wronka, submitted; Wronka and Walentowska, 2011). Moreover, we also supposed that early and late emotional expression effects would be influenced by the level of subjects' trait anxiety, overlapping with the P1 and EPN components (Holmes et al., 2009; Walentowska and Wronka, 2012).

5.3. Methods

5.3.1. Participants

Thirty five volunteers were selected from a large pool of students. In the first step they were asked to complete the trait scale from the State-Trait Anxiety Inventory (Spielberger et al., 1983) in Polish adaptation (Wrześniewski et al., 2002). Relying on the STAI scores, two groups were formed, with 17 and 18 participants in the low- and high-anxious group, respectively. Low-anxious (LA) individuals were defined as those scoring 34 and below (26-34), while high-anxious (HA) were those scoring 45 and more (45-60). For the LA group mean trait anxiety was 30.3 (SD=2.47), while mean trait anxiety for the HA individuals was 51.4 (SD=5.05). The mean age for the LA group was 23 years (SD=2.61; 4 men and 13 women), while for the HA group the mean age was 21 years (SD=1.22; 1 man and 17 women). All participants declared to be right-handed, and had normal or corrected vision. Additionally, they claimed to be free of any neurological or psychiatric disorders, and they were not regularly taking medications affecting the activity of the CNS. Prior to the beginning of the experiment subjects signed an approved consent form. Afterwards, their participation was awarded with course credits.

5.3.2. Stimuli and Procedure

Color photographs of fearful and neutral faces taken from the NimStim Face Stimulus Set (Tottenham et al., 2009; http://www.macbrain.org/resources.htm) were used as face stimuli. Color photographs of houses and trucks derived from the internet were used as non-face stimuli. Each photograph was presented at the fixation covering 17.5 cm x 11.5 cm.

Prior to the experiment subjects were comfortably seated in a dimmed, air-conditioned, and electrically isolated chamber. They were instructed to maintain central eye fixation together with reducing eye blinks and excessive body movements during the procedure. During the procedure each trial began with presentation of the fixation cross for 350 ms. It was immediately followed by the exposition of face (fearful or neutral) or non-face stimulus presented for 1000 ms (1 s). 400 ms, 550 ms, or 700 ms after stimulus onset a red asterix was appearing for 50 ms. It was presented in the central part of the photograph, in a position of previous fixation cross. The exposition of the asterix was always below the eyes and above the mouth, with different parts of the nose in the background. As the experimental task, subjects were asked to respond with their dominant-hand button press whenever a red asterix was presented on the background of face or non-face photograph, and to restrain from any motor responses whenever a blank photograph was presented. If no response was given, after 2000 ms (2s) the next trial was presented.

The whole task consisted of 360 trials. Because of the eventual fatigue, the experimental procedure was divided into three blocks, with 120 trials in each of them, and counterbalanced with respect to type of the stimulus. Each category of stimuli (fearful faces, neutral faces, and non-face objects) was presented in 120 trials. In half of them (in 60 trials per category), red asterix was presented on the background of the photograph. In 20 trials per category it was presented 400 ms after stimulus onset, in 20 trials – 550 ms after stimulus onset, and in 20 trials – 700 ms after stimulus onset.

5.3.3. Data Analysis

The EEG was recorded using a BioSemi ActiveTwo system with Ag–AgCl electrodes from 32 monopolar locations (AF3, AF4, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO7, PO3, PO4, PO8, O1, Oz, O2), according to the 10–20 system. Two additional electrodes, the common mode sense (CMS) active electrode and the driven right leg (DRL) passive electrode, were used as reference and ground electrodes, respectively; cf. www.biosemi.com/faq/cms&drl.htm. All cephalic electrodes were placed on the scalp using an Electro-Cap. EOGs (horizontal and vertical) were monitored by 4 electrodes placed above and below the right eye and in the external canthi of both eyes. The EEG was acquired at a sampling rate of 512 Hz. The EEG data were off-line filtered with bandpass 0.016-30 Hz, and sampled for a 800-ms trial (150 ms prior to the stimulus onset and 650 ms after the stimulus onset) using BrainVision software. Finally, data were corrected for eye-movement artifacts (Gratton et al., 1983), and off-line re-referenced to average montage.

The first set of analyses was performed to investigate differences in the brain activity during emotional expression processing in the whole group of participants. To achieve this, the N170 and EPN components were examined. The N170 component was defined as the mean amplitude within 145-195 ms after the stimulus onset. The analyses on the N170 component were restricted to parieto-occipital electrodes (PO7, PO3, PO4, PO8), which is in agreement with numerous previous findings (Bentin and Deouell, 2000; Itier and Taylor, 2004; Jacques and Rossion, 2004; Sagiv and Bentin, 2001; Yovel et al., 2003). The time window of 220-300 ms post-stimulus was investigated as reflecting the EPN component. The analyses on this component were restricted to occipital electrodes (O1, Oz, O2), which is in agreement with previous experimental reports (Sato et al., 2001; Schupp et al., 2003a, 2003b, 2004a, 2004b). Mean amplitudes of the N170 and EPN components were analyzed using repeated-measures analysis of variance (ANOVA) examining the effects of within-subjects factor of facial EXPRESSION (fearful vs. neutral) for all electrodes pooled together.

The second set of analyses was performed to investigate anxiety-related differences in the brain activity during face and non-face, as well as emotional expression processing. These analyses were conducted for three successive post-stimulus time windows: 90–120 ms (P1 component), 145–195 ms (N170 component), and 220–300 ms (EPN component). Taken together, they cover the time interval where systematic emotional expression effects have been described in previous reports (Batty and Taylor, 2003; Blau et al., 2007; Holmes et al., 2008, 2009; Miyoshi et al., 2004; Pegna et al., 2008; Pourtois et al., 2005; Rigato et al., 2010; Sato et al., 2001; Schupp et al., 2004b; Vlamings et al., 2009; Walentowska and Wronka, 2012; Wronka and Walentowska, 2011). Mean amplitudes between 90-120 ms poststimulus were analyzed for occipital (O1, Oz, O2), and parieto-occipital locations (PO7, PO3, PO4, PO8). Analysis of the effects observed for the N170 and EPN components are in details described in the previous subsection. In case of the P1 component, repeated-measures analysis of variance (ANOVA) testing the effects of within-subjects factor of the facial EXPRESSION (fearful vs. neutral), STIMULUS type (fearful face vs. neutral face vs. non-face), as well as between-subjects factor of GROUP (LA vs. HA) was employed. The analyses performed at the N170 and EPN components were restricted to the within-subject factor of facial EXPRESSION (fearful vs. neutral), and between-subjects factor of GROUP (LA vs. HA). Moreover, in case of each component analyses were performed for all electrodes pooled together.

All analyses of variance employed Greenhouse-Geisser corrections to the degrees of freedom when appropriate, and only the corrected probability values are reported. The Bonferroni method was used for *post-hoc* comparisons, with a significance level of 0.05.

5.4. Results

5.4.1. Emotional expression effects

Mean amplitudes for the time interval between 145-195 ms after stimulus onset recorded at parieto-occipital sites (PO7, PO3, PO4, PO8) were assessed with the ANOVA analysis examining the effect of facial emotional expression for all electrodes pooled together. Results obtained from the analysis suggest that the N170 amplitude measured in response to fearful faces was larger in comparison to neutral faces. The main effect of expression was highly significant (F[1,32]=34.03, p<.001).

Similarly, mean amplitudes for the time interval between 220-300 ms after stimulus onset recorded at occipital sites (O1, Oz, O2) were assessed with the ANOVA analysis examining the effect of facial emotional expression for all occipital electrodes pooled together. Results obtained from the analysis suggest that stronger negativity within the EPN component was recorded in response to fearful faces when compared to neutral ones. Once again, the main effect of facial expression was highly significant (F[1,32]=25.30, p<.001).

Taken together, these results suggest that facial affect can evoke specific pattern of brain activity over posterior areas even if emotional expression processing was involuntary. Both emotional expression effects are illustrated in Figures 5.1. and 5.2.

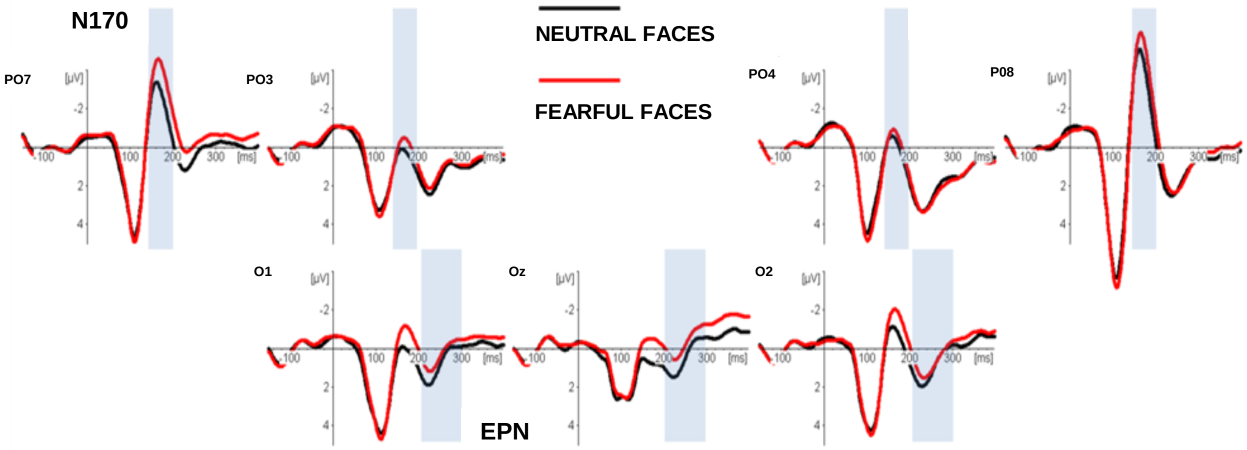

Figure 5.1. Grand average ERPs recorded at parieto-occipital (PO7, PO3, PO4, PO8) and occipital electrodes (O1, Oz, O2) in response to fearful faces (red lines) and neutral faces (black lines). Time windows of the N170 component (145-195 ms poststimulus) and EPN component (220-300 ms poststimulus) are highlighted.

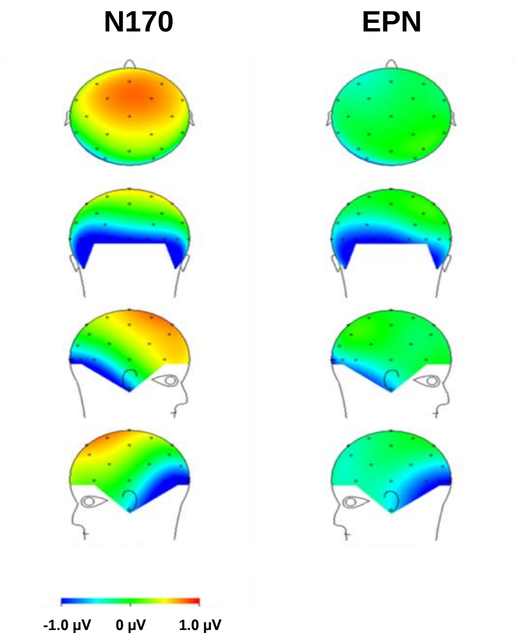

Figure 5.2. Topographical maps representing voltage differences between brain activity elicited by fearful and neutral faces within the N170 (145-195 ms poststimulus) and EPN (220-300 ms poststimulus) components.

5.4.2. Emotional expression effects and the level of anxiety

5.4.2.1. The P1 component (90-120 ms poststimulus)

Mean amplitudes recorded for the interval between 90-120 ms after stimulus onset were initially assessed with two two-factor ANOVAs. Expression x group analysis was performed separately for values computed for occipital (O1, Oz, O2), and parieto-occipital electrodes (PO7, PO3, PO4, PO8). Stimulus type x group analysis was performed for values computed for occipital, and parieto-occipital locations pooled together.

When investigated at occipital electrodes, similar pattern of the differences between fearful and neutral faces was obtained for low- and high-anxious individuals, which was confirmed by non-significant interaction between expression and group (F[1,32]=2.11, p>.01). These findings suggest that emotional expression was not able to modulate early brain responses. At the same time, we found higher positive values for the high-anxious group when contrasted with subjects with low level of anxiety. It was confirmed by significant effect of group (F[1,32]=9.71, p=.004). When tested at parieto-occipital electrodes, similar pattern of the differences between fearful and neutral faces was also obtained for low- and high-anxious individuals. This effect was confirmed by non-significant interaction between expression and group (F[1,32]=2.37, p>.01). These results suggest that facial emotional expression was not able to modulate early brain responses. At the same time, similarly higher positive values for the high-anxious group were found when contrasted with low-anxious group. It was confirmed by significant effect of group (F[1,32]=5.92, p=.014).

To investigate the group effect more thoroughly, we tested the hypothesis that the level of trait anxiety is able to modulate not only facial emotion processing, but also the processing of non-face stimuli. As a result, in further analyses the factor of emotional expression was substituted with the stimulus type, and the analyses were performed for all electrodes pooled together. Enhanced positivity within the latency window of the P1 component was found in high-anxious group when compared to low-anxious individuals across all types of stimuli. The main effect of group was statistically significant in case of fearful faces (F[1,32]=8.47, p=.007), neutral faces (F[1,32]=10.77, p=.002), as well as in case of non-face objects (F[1,32]=7.72, p=.009). What should be noticed, stimulus type x group interaction brought no significant result (F[1,32]=1.64, p=.430), which suggests that comparable differences between facial emotions and non-facial stimuli were observed for low- and high-anxious individuals.

Taken together, these results suggest that brain activity within the P1 time window recorded for low-anxious subjects differed significantly from the pattern of ERP responses obtained for the subjects with high level of trait anxiety. Specifically, mean amplitude of the P1 component computed for the HA group was higher in comparison to the LA group. Moreover, analogous group effect was also obtained for the comparison of fearful and neutral faces, and non-face objects. All these effects are illustrated in Figures 5.3 and 5.4.

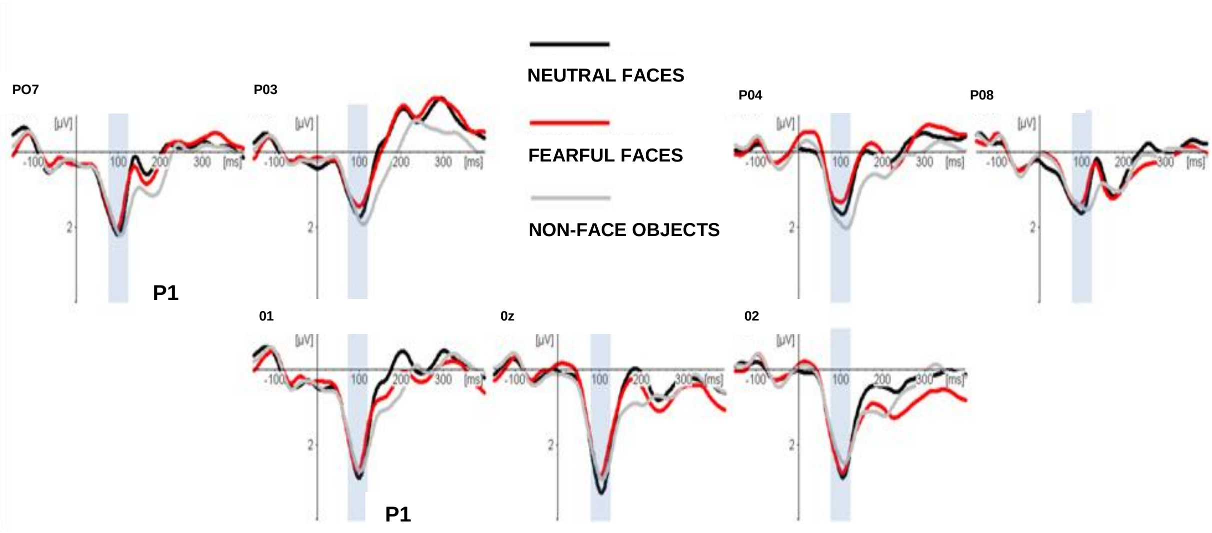

Figure 5.3. Difference waveforms (high-anxious minus low-anxious group) presented separately for neutral faces, fearful faces, and non-face objects. The time window of the P1 component (90-120 ms poststimulus) is highlighted.

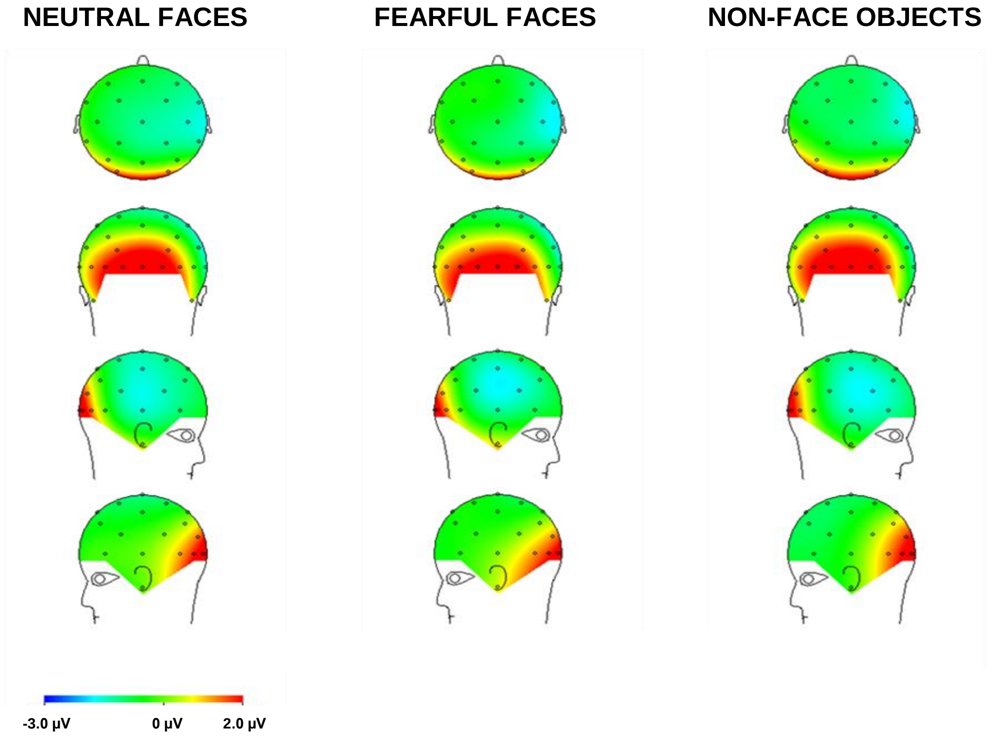

Figure 5.4. Topographical maps representing voltage differences between high-anxious and low-anxious groups during the processing of neutral faces, fearful faces, and non-face objects in the time window of the P1 component (90-120 ms poststimulus).

5.4.2.2. The N170 component (145-195 ms poststimulus)

Mean amplitude values computed for the interval between 145-195 ms after stimulus onset were initially assessed with a two-factor (expression x group) ANOVA. This analysis was restricted to parieto-occipital electrodes (PO7, PO3, PO4, PO8) pooled together.

Previously, the main effect of emotional expression on the N170 component was found to be statistically significant, with stronger negativity recorded in response to fearful faces when compared to neutral ones (see section 5.4.1.). In the same time, the interaction between expression and group factors was non-significant (F[1,32]=0.10, p>.01) suggesting that the brain activity elicited at parieto-occipital locations by the exposition of emotional and neutral faces was similar in both groups differentiated by the level of trait anxiety. We also did not observe any anxiety-related between-group differences for the mean ERP amplitudes computed in the latency window of the N170 component, which was confirmed by a non significant main effect of group (F[1,32]=0.08, p>.01).

These results show that the N170 amplitudes were not found to be modulated by the level of trait anxiety. Moreover, emotional expression effects previously found at the N170 were comparable in low- and high-anxious individuals. These comparable effects are shown in Figure 5.5.

5.4.2.3. The EPN component (220-300 ms poststimulus)

Mean amplitude values computed for the interval between 220-300 ms after stimulus onset were assessed with a two-factor (expression x group) ANOVA performed for occipital electrodes (O1, Oz, O2) pooled together.

The main effect of emotional expression on the EPN component was formerly found to be statistically significant, with more negative responses recorded to fearful faces than to neutral ones (see section 5.4.1.). Further analysis of the interaction between expression and group also brought significant result (F[1,32]=6.53, p=.019), suggesting that the emotional expression effect was different in each group. However, at the same time non-significant main effect of group was found (F[1,32]=0.65, p>.01), suggesting that brain activity recorded within the latency window between 220-300 ms after stimulus onset did not differ significantly. As a consequence of that, we performed two additional analyses of the emotional expression effects separately for low- and high-anxious individuals. They revealed significant emotional expression effect within the EPN component in LA group (F[1,16]=8.52, p=.011), while the same analysis performed for HA group brought no significant results (F[1,17]=0.05, p=.823).

Taken together, these results suggest that the lower was the level of trait anxiety, the more pronounced was the difference between brain responses to fearful and neutral faces reflected in the time interval of the EPN component. This differential effect is illustrated in Figure 5.5.

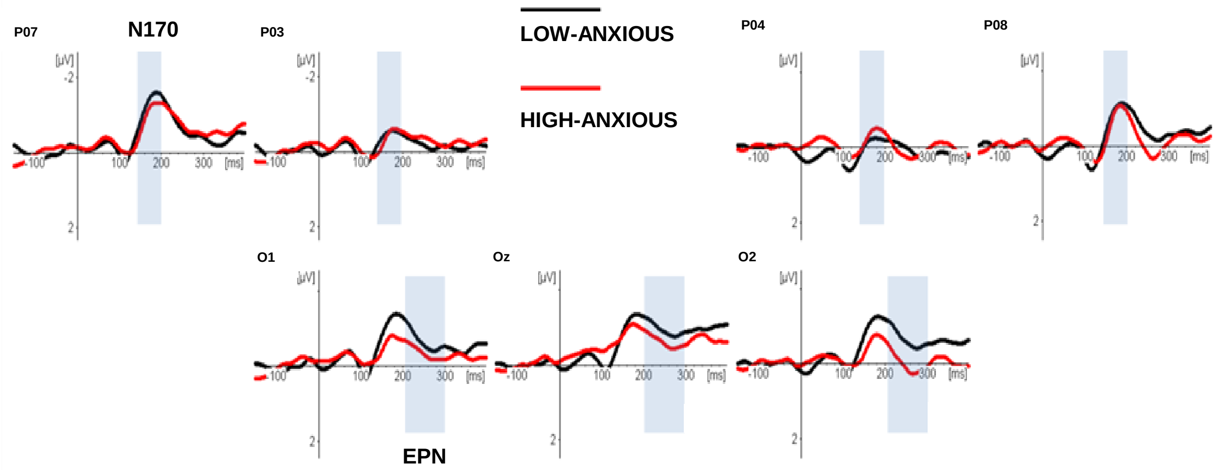

Figure 5.5. Difference waveforms (fearful minus neutral faces) presented separately for low- and high-anxious groups. The time windows of the N170 component (145-195 ms poststimulus) and EPN component (220-300 ms poststimulus) are highlighted.

5.5. Discussion

The current study was conducted to investigate specific forms of evoked brain activity in response to faces and non-face objects during their supraliminal presentations and involuntary processing. Consistently with numerous previous results, ERPs elicited by emotional faces differed from those evoked by neutral ones at parieto-occipital locations (modulation of the N170 component), as well as at later stages over occipital locations (modulation of the EPN component). Moreover, while the effect on the N170 was not influenced by the level of anxiety, the EPN effect was different in low- and high-anxious individuals. Anxiety also influenced very early stages of information processing, as the P1 effect had a different course in low- and high-anxious groups.

The novelty of the current study can be considered in at least two areas of interest. Firstly, using a procedure with supraliminal presentations and involuntary stimulus processing, we have managed to obtain emotional expression effects, which so far has been observed exclusively in voluntary facial emotion processing (Leppänen, et al., 2007; Wronka and Walentowska, 2011). While the modulation of the EPN component was widely anticipated (Sato et al., 2001; Schupp et al., 2004b; Walentowska and Wronka, 2012; Walentowska and Wronka, submitted; Wronka and Walentowska, 2011), the emotional expression effect on the N170 component should be further discussed. In our previous study with supraliminal image presentations (Wronka and Walentowska, 2011), the N170 modulation has been obtained exclusively in a task demanding explicit emotional expression categorization, thus the face processing was intentional. In the current study, supraliminal face presentations have also been used, however subjects were not explicitly involved in facial affect discrimination, thus the processing was involuntary. Nevertheless, one important factor, which should be additionally considered, is the duration of image presentation. In the current study it was established for 1000 ms, which is relatively long. Relying on that, it can be proposed that although no explicit facial affect discrimination was required from subjects, the duration of stimulus presentation could have been sufficient for effective information processing. Nevertheless, involuntary processing observed in the current study differs from the processes observed in our previous studies (Walentowska and Wronka, 2012; Walentowska and Wronka, submitted), where subliminal presentations of facial emotions were used. The difference between experimental procedures was perfectly reflected in diverse experimental findings. Secondly, we have managed to obtain and confirm previously observed (Walentowska and Wronka, 2012) anxiety-related modulation of early (P1 effect) and later (EPN effect) stages of visual information processing. This time, differences between low- and high-anxious individuals have been recorded also with supraliminal image presentations.

Differences between brain responses elicited by fearful and neural faces appeared both at early and later stages of facial stimulus processing (see Figures 5.1 and 5.2.). Stronger negativity for fearful faces when compared with neutral ones was observed between 145-195 ms poststimulus from parieto-occipital locations (the N170 modulation), which is consistent with numerous previous findings (Batty and Taylor, 2003; Blau et al., 2007; Miyoshi et al., 2004; Rigato et al., 2010; Vlamings et al., 2009; Wronka and Walentowska, 2011). Analogous effect was observed 220-300 ms poststimulus at occipital locations, overlapping with the Early Posterior Negativity (EPN component). This effect is consistent with numerous findings, where the negativity recorded at posterior sites around 200 ms poststimulus has been more pronounced for emotional, especially threatening, images (Schupp et al., 2003, 2004a), or threat-related faces (Sato et al., 2001; Schupp et al., 2004b, Wronka and Walentowska, 2011) relative to neutral ones, which suggests their preferential emotional processing. There is general agreement that the EPN component reflects specific activation of brain areas engaged in visual information processing when stimuli of high evolutionary significance are presented. Therefore, the EPN effect can be registered irrespective of the experimental procedure, also during entirely involuntary facial affect analysis (Jiang et al., 2009, Walentowska and Wronka, 2012; Walentowska and Wronka, submitted). In contrast, the emotional expression effects on the N170 component are more sensitive to experimental conditions.

Results obtained in our study support the thesis and confirm our previous findings (Walentowska and Wronka, 2012) that trait anxiety can modulate processing of facial expression. While no anxiety-related effect has been found within the latency window of the N170 component (145-195 ms poststimulus), we have found the differences between low- and high-anxious subjects in the activity of visual brain areas within the latency of Early Posterior Negativity (EPN, 220-300 ms poststimulus). Specifically, the EPN effect was evident in case of participants with low level of anxiety, and it was absent in high-anxious group (see Figure 5.5.). Analogous results have been obtained by Holmes with co-authors (2008, 2009). The EPN effect reflects specific pattern of brain activity when the visual system is engaged in the processing of stimuli characterized by high evolutionary significance. Thus, we can conclude that in high-anxious individuals the processing of these type of stimuli was somehow disrupted.

At earlier stages, we have also found anxiety-related differences in brain activity elicited by visual stimuli for the interval between 90-120 ms poststimulus. Specifically, more enhanced amplitudes of the P1 component have been recorded for high-anxious participants when compared to low-anxious group. Importantly, analogous effects have been observed irrespective of the stimuli content for fearful faces, neutral faces, and non-facial stimuli (see Figures 5.3. and 5.4.). These findings suggest that early anxiety effect overlapping with the P1 component can be functionally linked with later differences in the EPN component. What is in line with our previous suggestions (Walentowska and Wronka, 2012), in high-anxious subjects early P1 effect probably reflects a hypervigilant tendency to process all stimuli as a signal of threat. Similar early activation of the visual cortex in response to all stimuli leads to further withdrawal from the processing of threat-related stimuli. Thus, the effects on the emotion-sensitive EPN component can not be detected in high-anxious subjects.

The current findings may be explained in a light of the idea that early P1 effect can be linked with the enhanced sensory encoding in visual brain areas. This early analysis is a result of a feedback projections from the amygdala, where rapid evaluation of significant stimuli probably takes place (Vuilleumier and Pourtois, 2007). Stronger activity of the amygdala in high-anxious subjects in response to facial emotions has been well-documented (Whalen, 1998; Whalen et al., 1998). Moreover, there is a suggestion that affective-cognitive system of anxious people is distinctively sensitive to threatening stimulation (Bishop, 2007). Taken together, we may conclude that in high-anxious individuals biologically-rooted anxiety shapes the cognitive system to be particularly sensitive to all stimuli, which may be a signal of potential threat. From the clinical perspective, this hypervigilance unables proper analysis and discrimination of the surrounding information, together with disordered social and emotional functioning. From the experimental point of view, anxiety-related hypervigilant tendencies biasing human cognition are very often treated as one of the aspects of the automaticity in information processing.

Therefore, numerous important implications and directions for future research arise from the current findings. One of them is definitely the necessity for further investigation and comparison of other anxiety-related characteristics, such as social phobia, social anxiety, or depression susceptibility. Secondly, this study was narrowly designed to compare emotionally salient (fearful faces) versus neutral stimuli (neutral faces and non-faces). Therefore, it has not been optimized to determine if other facial emotions, both positive and negative, are able to elicit comparable brain responses. Thus, future research from this area of interest should incorporate a wider range of facial emotions used as the stimuli. Moreover and importantly, it has also been suggested that threat-related facial expressions, like fear or anger, may elicit diverse patterns of brain activity. Using fMRI method, Ewbank wit co-authors (2009) have shown that perceiving facial fear and facial anger leads to different patterns of the left amygdala activation. Although in our opinion using fearful stimuli to investigate anxiety-related differentiation is more reasonable (for arguments see Whalen, 1998), a direct comparison of both ‘faces’ of threat, fear and anger, is certainly worth more thorough experimental investigation, also using ERP method.

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Chapter 6.

GENERAL DISCUSSION: HOW AUTOMATIC IS EMOTIONAL EXPRESSION PROCESSING?

6.1. Introduction

Faces, which are considered to be one of the most important objects in human visual perception, frequently convey socially and emotionally significant information. Its relevance for the adaptive control of action and effective emotional functioning implicates important evolutionary adaptations in a complex social environment. Along with other sources of information, emotional faces are the most salient stimuli communicating essential nonverbal signals. Therefore, the hypothesis concerning a high priority and automaticity of facial emotion processing has been launched. This hypothesis was tested multidimensionally using complementary neuroscientific methods (fMRI, ERPs). According to this hypothesis, due to the biological and social significance of facial emotions, information about emotional states derived from faces should be processed very rapidly to serve for the immediate regulation of human behaviour. The most recent definition proposes that the automaticity of emotional expression processing should be defined in terms of rapid, obligatory, unconscious, and capacity-free processes (Palermo and Rhodes, 2007).

From the other point of view, it is commonly known that the entire understanding of the complexity of human behaviour requires the inclusion of the individual differences' factor. Specifically, some cognitively-oriented models of anxiety suggest the existence of a privileged and largely automatic facial emotion processing structure (Bishop, 2007). Therefore, there is some experimental evidence that considering the issues of clinical anxious tendencies or subclinical anxious traits to reveal the exact nature of facial emotion processing is undoubtedly relevant.

As a consequence, in this dissertation the automatic aspects of facial affect processing have been indentified both from the perspective of the nature of the processes, as well as from the perspective of the perceiver. Nevertheless, some evidence that the idea of the automaticity of facial affect processing can be limited has also been presented. The only aspect of the automaticity, which can not be refuted, is indisputably the speed of facial expression processing. Emotional expression effects have been systematically observed within the brain activity starting from 100 milliseconds post-stimulus. However, other aspects of the emotional expression automaticity, which are obligatory and unconscious processing, can not be confirmed with a huge dose of reliability. Importantly, Pessoa with co-authors (2002), as well as Eimer and Holmes (2002) have revealed that the manipulation of subject's attention can observably influence brain activity within the time windows where systematic emotional expression effects had previously been registered. This observation suggests that facial emotion processing is voluntary, which means that it is under the control of some cognitive processes. Moreover, some recent studies testing the effects elicited by subliminally presented and backward masked stimuli have faced the problem of not entirely unconscious processing (Eimer et al., 2008; Kiss and Eimer, 2008), thus the evidence that conscious awareness is not required to effectively process facial affect has not been convincingly presented.

Taken all these considerations into account, the argument that emotional expression processing is entirely automatic, can no longer be defended. As it has been suggested by Moors and De Houwer (2006), the clearly defined dichotomy between entirely automatic or controlled facial emotion processing is untenable. Therefore, in line with this general deliberation, a sequence of four experiments investigating facial emotion processing reflected in evoked brain activity has been conducted, and is reported in this dissertation (Chapters 2-5).

6.2. Main experimental findings

The general investigation of the time course of emotional expression processing, with an emphasis put on the rapidness of facial emotion processing, as well on the possible influence of attentional modulation was presented in Chapter 2. Results extend the knowledge about the automaticity of emotional expression processing twofold. Firstly, the hypothesis about a high speed of facial affect processing can be confirmed, as emotional expression effects have been registered relatively early, starting from 140 milliseconds post-stimulus. Secondly, the hypothesis about the entirely involuntary facial expression processing can not be supported, as it has been shown that attention effectively modulates facial emotion processing at early stages (as revealed by the N170; 140-185 milliseconds post-stimulus), while involuntary differentiation of facial expression can be observed later (as revealed by the AP and EPN; 160-340 milliseconds post-stimulus). This differentiation suggests that structural encoding relevant to gender recognition and simultaneous facial expression analysis are independent processes.

To track these aspects, participants were asked to perform two tasks. The first task was to discriminate emotional expressions, so in this task subjects were explicitly asked to focus their attention on emotional expression recognition. The task was designed to elicit voluntary and intentional facial stimuli processing. In this task enhanced negativity of the face-specific N170 was elicited by emotional as opposed to neutral faces. Moreover, the same pattern of results was obtained within the early posterior negativity (EPN component). In the second task subjects were asked to classify face gender. In this task they were asked to explicitly focus on gender, nevertheless it can be assumed that during the gender recognition facial emotion processing was also occurring, but this process was involuntary and was not under the influence of attention. Here, the N170 was unaffected by the emotional expression, however later emotional expression effects were expressed in the anterior positivity component (AP) and the subsequent occipital negativity component (EPN).

In the next steps, the main effort has been invested into the exploration of the necessity of conscious awareness during the processing of facial emotional expression, as there has been a growing evidence that facial emotions can trigger selective brain responses even when they are presented subliminally. Results presented in Chapter 3 extend the knowledge about the automaticity of face and facial emotional expression processing more extensively. Firstly, the findings highlight that faces, even in the absence of conscious awareness and attention, were processed differently than other stimuli. Due to the fact that it has been observed as the modulation of the N170 ('early' component), the effect of rapid face and facial affect processing has been replicated. Secondly, in the same conditions of entire unconsciousness, which has been achieved using a procedure with abstract masking stimuli together with a task involving participants into its discrimination, involuntary differentiation of facial affect was possible, as revealed by the EPN ('late' component). Interestingly, one more important aspect has been exposed, namely that involuntary differentiation of facial expression is strongly determined by the structural analysis of face features. This effect was disrupted by the face inversion. It may suggest that even when facial emotions are processed in fully involuntary conditions, some manifestation of the cognitive processes, involved in the facial structural encoding, can be observed.

To investigate this, ERPs in response to briefly presented and backward masked faces and non-facial objects were recorded. The N170 component was found to be larger when recorded in trials with faces in comparison to non-facial stimuli. Moreover, a significant difference in the N170 was observed as the effect of face inversion, while no such differentiation was obtained for non-facial objects. More importantly for this thesis, when ERPs to fearful and neutral faces were compared, the negative shift specific for fearful stimuli within the EPN component was recorded. However, this result was obtained only when faces were presented in their upright orientation, while it was not observed when faces were inverted.

There is a suggestion that trait anxiety can influence the processing of threat-related information, and this influence can be a manifestation of the anxiety-related oversensitivity and automaticity in facial threat processing. To broaden the investigation of the automaticity of emotional expression processing, the factor of individual differences has been added to the next experiments, described in Chapters 4 and 5.

In Chapter 4, a modified version of the experimental procedure presented in Chapter 3 was used. The modification excluded the factor of the inverted stimulus presentation. Therefore, brain activity was recorded in response to subliminally presented and backward masked fearful and neutral faces, and non-face objects, in the preselected low- and high-anxious individuals. The hypothesis of the rapid and unconscious face processing was replicated, as the amplitude of N170 was found to be larger when elicited by faces in comparison to non-faces. However it was not found to be emotion-sensitive, or modulated by the anxiety level. These results are in a line with previous ones, where the emotion-specific modulation of the N170 was observed only when attention was explicitly engaged in facial affect recognition (presented in Chapter 2), and was also not observed in a study with similar procedure (Chapter 3). More importantly, differences between low- and high-anxious individuals appeared in a time window of the P1 component. At later stages, within the EPN component, stronger negativity specific for fearful faces was recorded exclusively in the low-anxious participants. These findings indicate that anxiety level modulates early stages of information processing, as it was reflected in the P1 component. This leads to later, anxiety-related differences in involuntary emotional expression detection, reflected in the EPN component.

Lastly, in the study described in Chapter 5, the hypothesis investigating the influence of anxiety on the involuntary face processing was tested once more. This time, however, with a procedure using supraliminal facial emotion presentation, together with a task not explicitly involving participants in its recognition. Subjects' brain activity was recorded in response to faces (fearful and neutral), and non-faces in preselected low- and high-anxious individuals. Increased amplitude of the N170 elicited by faces in comparison to non-face objects has been found, which confirms results obtained in experiments described in Chapters 3 and 4. Interestingly, emotional expression effect starting 140 milliseconds post-stimulus has also been observed. Higher amplitudes of the N170 component were obtained in response to fearful faces when compared to neutral ones, which validates that facial emotions are processed rapidly. More importantly, enhanced negativity (EPN) elicited by emotional expression at occipital sites has also been recorded. Additionally, some of these effects were modulated by the level of anxiety. Specifically, the modulation of the EPN component was evident for low-anxious subjects, and diminished in high-anxious group. At earlier stages, more enhanced positivity was observed within the latency of the P1 component in case of high-anxious individuals. This early anxiety-related effect was evident irrespective of the stimulus type, in both face and non-face object presentations.

6.3. Conclusions

The main objective of this dissertation was to explore the issue of automatic facial emotion processing. According to existing literature, it should be regarded as rapid, involuntary, and unconscious (Palermo and Rhodes, 2007), nevertheless there is also experimental evidence that the processing of emotional expression can be under the influence of cognitive processes (e.g. attentional processes). Therefore, there was a real incentive to investigate this topic more thoroughly, and to inspect the extent of the automaticity, specifically in a time domain. To achieve this, the ERP technique served with the best temporal resolution. Moreover, it was combined with a measurement of the level of trait anxiety, which is often linked with the tendency to process facial threat automatically.

This approach enabled the entire insight into the specificity of when facial affect processing is automatic, and when it is not.

To conclude the main findings from four conducted experiments, results have shown that facial emotions can influence ERP responses at two stages of information processing. These different effects are related to diverse psychological processes. Firstly, attention voluntarily engaged in emotional expression processing can effectively influence brain activity at occipito-temporal sites (N170 component). Thus, attention can promote rapid detection and recognition of facial emotion. This top-down modulation has been observed starting from 140 milliseconds post-stimulus in the study described in Chapter 2. However, it was not observed in the studies presented in Chapters 3-5, where facial emotion processing was not explicitly directed by attention. Although expression-related modulation of the N170 component was observed in the study described in Chapter 5, it was not the effect of voluntary attention engagement. Secondly, when attention is captured by the facial affect, emotional face can modulate the activity of posterior brain areas involved in sensory analyses (EPN component). This effect has been reflected in increased negativity recorded after 200 milliseconds post-stimulus. It has been triggered involuntarily, as it could have been observed irrespective of the experimental procedure, and in all studies described in Chapters 2-5. Only in study described in Chapter 3, the effect has been additionally modulated by the disruption of face structural encoding, as the effect of face inversion.

At least one controversy arises as a consequence of the above described results. It is well established in the literature that the first stage of stimulus processing (early stage) is linked with involuntary processing, while the later stages are observed to be under the control of cognitive processes (e.g. Luck et al., 2000). This sequence does not reflect the general pattern of results described in Chapters 2-5, showing that early stages of facial emotion processing are proved to be voluntary, while later stages reflect unintentional processes. Here, the additional comment should be provided. Although it was not directly tested in the conducted experiments, it should be emphasized that each stimulus appearing in the visual field involuntarily captures attention, therefore it is processed unintentionally at very early stages of processing, before 100 milliseconds post-stimulus. In case of facial emotion processing, this effect probably also exists. At the next stages (in this dissertation termed ‘early’, starting from 100 milliseconds post-stimulus), emotional expression processing requires attention. This is due to the fact that face itself is a complex stimulus, and its structural encoding requires the availability of cognitive (attentional) processes. After the complete structural encoding, starting from 200 milliseconds post-stimulus the involuntary processing of the emotional content of the face takes place (regarded as ‘late’ stages). The general assumption comes from this findings, as the experimental results shown that not all phases of facial emotion processing are entirely automatic. While later stages are generally automatic, early stages are under the influence of cognitive (attentional) processes. This assumption will help to describe the entire characteristic of automatic facial emotion processing in the end of this chapter.

As it has been mentioned in the previous chapters, trait anxiety is often linked with a specific pattern of reactions during the processing of negative facial expressions. Firstly, results described in Chapters 4 and 5 support the general thesis that trait anxiety can modulate processing of facial expression at later stages, starting from 200 milliseconds post-stimulus. This effect can reflect distinct pattern of brain activity when it is engaged in the processing of visual stimuli characterized by high evolutionary significance. Secondly, early stages of visual information processing, starting from 100 milliseconds post-stimulus, can be remarkably altered in case of high-anxious group. This early anxiety effect, overlapping with the P1 component, can be functionally linked with later differences in magnitude of the EPN component. As it has been mentioned in Chapters 4 and 5, in high-anxious subjects early P1 effect can reflect a oversensitive tendency to process neutral stimuli as emotional ones, which results in lack of subsequent EPN effect. The EPN is defined as the difference in brain responses to emotional and neutral stimuli, thus early hypervigilance can lead to comparable activation of the visual areas elicited by all stimuli irrespective of their content. In the other words, at early stages high level of anxiety can be linked with withdrawal from the processing of threatening stimulation, therefore at later stages the EPN differentiation can not be observed in high-anxious subjects. Although these explanations have been supported by the results presented in Chapters 4 and 5, they definitely need further research. Nevertheless, they are in line with the supposition that anxiety understood as a clinical disorder, or as a subclinical temperamental trait can be associated with a specific hypervigilant tendency. This tendency biases early processing of not only facial affective information, but all stimuli irrespective of their content. Going further, it subsequently unables successful processing of emotional expression at later stages.

This anxiety-related assumption, together with findings that facial emotional expression is only partially processed involuntarily, undoubtedly extends the knowledge concerning the automaticity of the processing of facial visual information. So far, the model of rapid, involuntary, and unconscious processing (Palermo and Rhodes, 2007), as well as the anxiety-related bias in facial threat processing (Bishop, 2007) have been postulated as the evidences confirming the entire automatic facial expression processing. However, after conducting and describing the results from the studies described in Chapters 2-5, it can be postulated that previous approaches can not be fully defended, which implies their modifications, mostly in temporal aspects (in a domain of time). Firstly, although facial affect processing can be characterized by some aspects of automaticity (it was always proved to be rapid, and almost always to be unconscious), the issue of the influence of attention should be redefined. Secondly, subclinical anxiety can not only be accused of the specific biases towards the processing of threat-related information. High level of trait anxiety occurred to be linked with an early hypervigilant tendency to process all types of stimulation as highly-significant. This bias indisputably disrupts later processing of salient information, with facial emotions as the best examples.

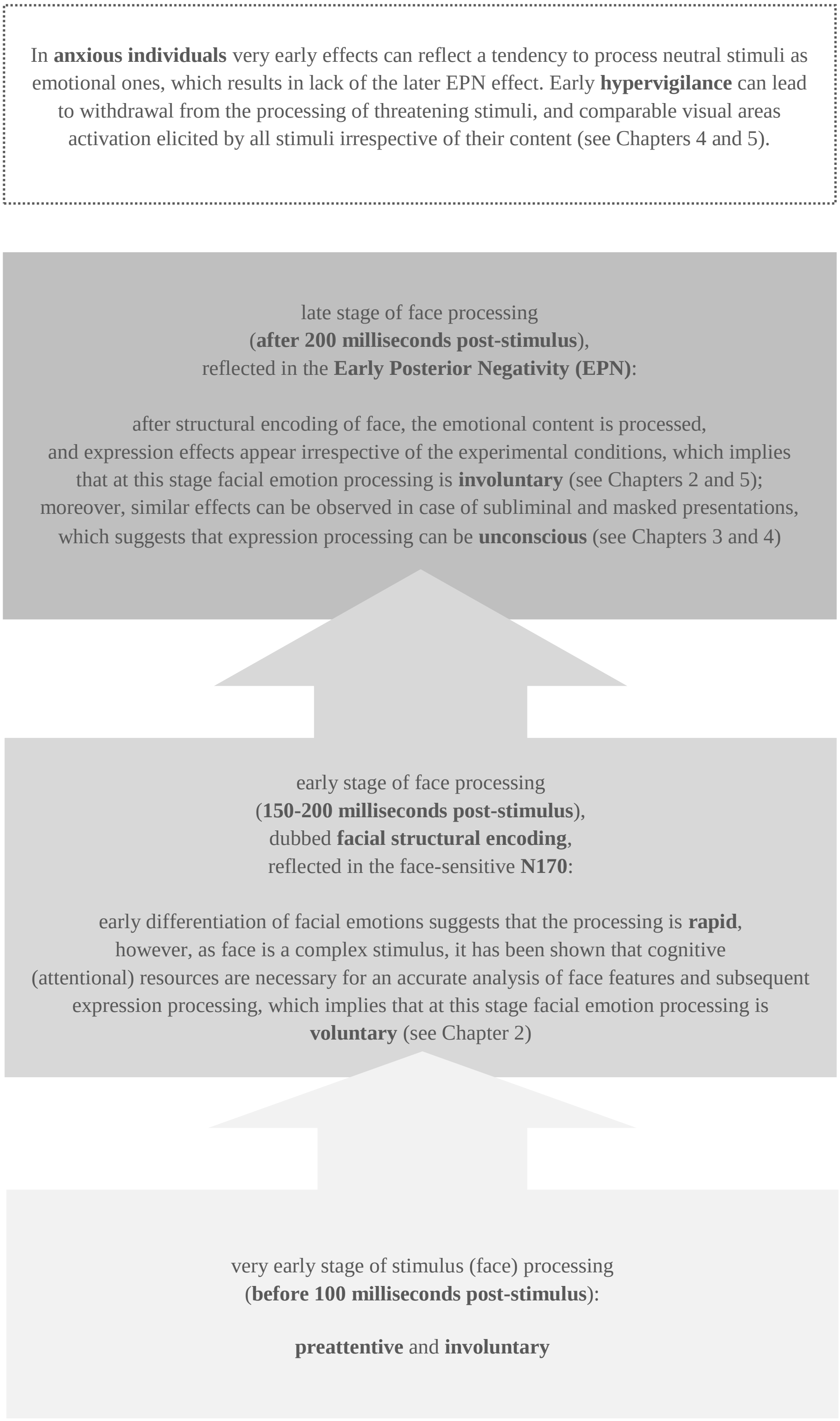
To summarize, the proposal of Moors and De Houwer (2006) that ‘all processes are automatic to some degree’ is in line with experimental findings described in this dissertation. Therefore, explanation of the automaticity of facial emotion processing should be redefined. The approach postulating entire automaticity should be substituted with the approach suggesting that facial affect processing is automatic, but only to some extent, and at some stages. Moreover, anxiety-related automaticity (hypervigilance) should no longer be linked only with threat-related information processing, as its characteristic is much broader.

6.4. Summary of the dissertation

There has been an ongoing debate on the automaticity of facial emotion processing. Automaticity has been mainly defined as rapid, involuntary, and unconscious processes. However, some factors like attention engagement, awareness of the stimuli, or temperamental traits can effectively modulate its nature. So far, this issue has been largely defined in terms of a dichotomy (automatic versus controlled processes), however the main problem should rather concentrate around the extent of the automaticity, together with conditions under which it can be observed. Using ERP method, which tracks fast changes in the evoked brain activity, the effort has been put into answering the following questions: Can all aspects of the automaticity of facial emotion processing be confirmed? Is the processing always automatic? If not, when (at which stage) it is? What external factors can influence emotional expression processing? Can internal dispositions of the perceiver modulate facial emotion processing? Is this influence always the same?

It has been proved that facial emotional expression processing reflects many aspects of the automaticity. Specifically, emotional expressions are processed rapidly, as distinct brain responses to emotional and neutral faces have been observed after 100 milliseconds post-stimulus (N170 component). However, at this early stage emotional expression detection has been effectively modulated by attention. Specific brain activity has been observed exclusively when attention was voluntarily directed to emotional expression recognition. Facial emotions can also be processed involuntarily. At later stages, after 200 milliseconds post-stimulus, specific brain responses to emotional faces have been observed irrespective of the experimental instruction (EPN component). Emotional expression effect within the same time window has been obtained even in the absence of conscious awareness showing that subliminal processing can influence brain activity indistinguishably from supraliminal processes. Furthermore, anxiety level can additionally modulate facial information processing. Specifically, high-anxious individuals have shown automatic (hypervigilant) tendency to react to all facial stimuli.

To summarize the main findings, facial emotion processing is rapid, however only at later stages it is involuntary and unconscious, so entirely automatic. Early stages are generally under the influence of cognitive (attentional) processes. Moreover, anxious individuals have shown a specific hypervigilance towards all facial information. These findings undoubtedly extend our knowledge about the nature of the automaticity of facial emotion processing. They also allow to redefine the main issue from a simple dichotomy into a more sophisticated sequence of automatic and controlled processes (for a general summary see Figure 6.1 below).



In **anxious individuals** very early effects can reflect a tendency to process neutral stimuli as emotional ones, which results in lack of the later EPN effect. Early **hypervigilance** can lead to withdrawal from the processing of threatening stimuli, and comparable visual areas activation elicited by all stimuli irrespective of their content (see Chapters 4 and 5).

late stage of face processing
(**after 200 milliseconds post-stimulus**),
reflected in the **Early Posterior Negativity (EPN)**:

after structural encoding of face, the emotional content is processed, and expression effects appear irrespective of the experimental conditions, which implies that at this stage facial emotion processing is **involuntary** (see Chapters 2 and 5); moreover, similar effects can be observed in case of subliminal and masked presentations, which suggests that expression processing can be **unconscious** (see Chapters 3 and 4)

early stage of face processing
(**150-200 milliseconds post-stimulus**),
dubbed **facial structural encoding**,
reflected in the face-sensitive **N170**:

early differentiation of facial emotions suggests that the processing is **rapid**, however, as face is a complex stimulus, it has been shown that cognitive (attentional) resources are necessary for an accurate analysis of face features and subsequent expression processing, which implies that at this stage facial emotion processing is **voluntary** (see Chapter 2)

very early stage of stimulus (face) processing
(**before 100 milliseconds post-stimulus**):

preattentive and **involuntary**

Figure 6.1. **Redefinition of the construct of the automaticity of facial emotion processing.** Expression processing is rapid, at early stage it is voluntary, while at later stage it is involuntary and unconscious. Emotional expression effects can additionally be modulated by anxiety-related, hypervigilant processing biases.

6.5. Implications

From a scientific point of view, it can be cautiously stated that with this new model the existing knowledge has been extended, and an important step towards clarifying the nature of automaticity of facial emotion processing has been made. Results from the present experiments allow to formulate the theses that: (1) early and late phases of automatic emotional expression processing differ significantly, and (2) automatic facial emotion processing differs with respect to the level of emotionally-rooted individual differences. As the affective neuroscience continuously lacks in well-established assumptions, these theses can be further used in the elaboration and introduction of more detailed theories of human emotional functioning in subclinical populations. Therefore, conclusions from these experiments should be considered as a preliminary framework for future research, although they unquestionably require further investigation. It is also obvious that every new model of automatic processing of facial affect needs to combine several aspects of automatic processes together with the inclusion of affective individual characteristics.

From a practical point of view, this kind of comprehensive approach is helpful to apply theoretical knowledge in clinical practice. Threat-related biases and oversensitive processing have been experimentally investigated in a variety of clinical anxiety disorders, such as generalized anxiety disorder (GAD), post-traumatic stress disorder (PTSD), panic disorders, and specific phobias. At least some of them, like social phobia, together with depression and autism, are additionally characterized by the impaired processing of facial emotions in everyday life (Green and Phillips, 2004; Phillips et al., 2003). The social implications of these findings become even more clear when one has in mind that anxiety-related disorders are highly prevalent in the society. Moreover, turning this into a condition requiring medical attention, they can be quite a crippling experience not only for the affected individual, but also for the social environment. With the research facts postulating that sub-clinical anxiety (high level of trait anxiety) is a vulnerability factor for developing anxiety-related disorders (Mathews and Mackintosh, 1998; Mogg and Bradley, 1998; Williams et al., 1997), clinical psychologists may soon be better prepared for a rapid diagnose and treatment of anxiety-related repercussions in everyday life.

To summarize, one of the possible directions for future research should undoubtedly be linked with the fact that a large portion of the previous and current research has been conducted with adult participants. However, the nature of processing of facial features varies with development. Moreover, both the amygdala and the prefrontal cortical regions develop dramatically between childhood and adulthood, especially during adolescence (Nelson et al., 2002), which may contribute to an increasing self-control over emotional behavior (Killgore et al., 2001). Therefore, particularly missing are longitudinal studies tracing the development and the associations over time between cognitive biases in emotional expression processing and the vulnerability for anxiety disorders. Accordingly, future efforts should predominantly be invested into a deeper and more detailed understanding of childhood pathways leading to anxiety, which can mostly be achieved with longitudinal research.

6.6. References

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Samenvatting

Al geruime tijd wordt er gediscussieerd of de verwerking en herkenning van gezichtsuitdrukkingen een automatisch, onwillekeurig, dan wel een gecontroleerd, willekeurig, proces is. Een automatisch proces is daarbij gedefinieerd als een snel verlopend, onwillekeurig en onbewust proces, terwijl een gecontroleerd proces minder snel kan zijn en meer willekeurig en bewust van aard is. Er zijn evenwel factoren, zoals de aandacht voor de stimulus, de bewustwording van de stimulus, of persoonlijkheidstrekken, die de automatische dan wel gecontroleerde verwerking van emotionele gelaatsuitdrukkingen kunnen moduleren. Tot dusver is dit onderwerp benaderd in termen van een dichotomie, dat wil zeggen het is een geheel automatisch dan wel een geheel gecontroleerd proces. De vraagstelling zou echter horen te zijn in hoeverre de verwerking van gezichtsuitdrukkingen een automatisch, en in hoeverre het een gecontroleerd proces is. Ook is er de vraag welke omstandigheden of condities een rol zouden kunnen spelen bij een verandering van een automatische naar een gecontroleerde verwerking van gezichten. Met gebruikmaking van de ERP methode, waarmee snelle veranderingen in de activiteit van het brein vastgesteld kunnen worden, is een poging gedaan om antwoorden op de volgende vragen te krijgen. Kunnen alle aspecten van de automatische verwerking van gezichtsuitdrukkingen vastgesteld en bevestigd worden? Verloopt die verwerking geheel automatisch? En zo niet, welke fase verloopt wel automatisch en welke verloopt gecontroleerd? Welke externe factoren kunnen het verloop van de verwerking van de emotionele stimuli moduleren? Kunnen interne disposities van de ontvanger de gezichtsuitdrukkingen van de zendend persoon beïnvloeden? En verloopt deze beïnvloeding altijd op dezelfde wijze?

Het is aangetoond dat de verwerking van gelaatsuitdrukkingen meerdere aspecten van automatisme laat zien. In het bijzonder worden emotionele uitdrukkingen op een snelle wijze verwerkt. Goed waarneembare en specifieke breinreacties op neutrale en emotionele gezichten zijn al vanaf 100 milliseconden na de stimulus zichtbaar. Het blijkt echter wel dat in dit vroege stadium een effectieve modulatie met name door aandachtsprocessen mogelijk is. Een specifieke hersenactiviteit ten gevolge van gecontroleerde attentie, welke direct gericht is op de herkenning van emotionele uitdrukkingen, kan in een ERP geobserveerd worden. Maar faciale emoties kunnen ook op een automatische, onwillekeurige wijze verwerkt worden, maar dat gebeurt in een later stadium, zo’n 200 milliseconden na de stimulus. Dan kunnen specifieke breinveranderingen, zoals een reactie op emotionele gezichten, herkend worden, die onafhankelijk zijn van experimentele instructies. In dit tijdsinterval kan de breinrespons op een emotionele stimulus zelfs afgeleid worden in de afwezigheid van een bewuste waarneming. Dit toont aan dat er sprake is van een subliminale verwerking, die niet onderscheidbaar is van een supraliminale verwerking. Verder kan de aanwezigheid van angst de verwerking van gezichtsinformatie sterk beïnvloeden. Meer specifiek is het zo dat angstige mensen een automatische (en zelfs hypervigilante) tendens vertonen om op alle gezichtsstimuli te reageren.

De belangrijkste bevindingen van de gepresenteerde experimenten kunnen als volgt samengevat worden. De verwerking van gezichtsuitdrukkingen is een snel proces, maar is slechts in de latere stadia van verwerking onwillekeurig en onbewust, en daarmee geheel automatisch. Vroegere stadia staan onder de invloed van cognitieve, aandachts- en attentie-gerelateerde processen. Voorts vertonen angstige individuen een sterke vigilantie in hun reactie op alle faciale informatie. Deze gegevens breiden de kennis inzake de aard van de automatische dan wel gecontroleerde verwerking van gezichtsuitdrukkingen uit. Ook leiden deze bevindingen tot een herdefiniëring van de dichotome, zwart-witte opvatting (van een volledig automatische verwerking versus een volledig gecontroleerde verwerking van gezichten), naar een meer continue, glijdende opvatting van het proces, waarin zowel automatisme als controle een rol spelen. Dat houdt in dat deze bevindingen een evidente wetenschappelijke implicatie hebben. Als in gedachte gehouden wordt dat deze bevindingen ook het onderwerp van subklinische angst raken, dan hebben deze resultaten eveneens klinische implicaties. Op grond van deze informatie kunnen dan kernaspecten van angstgerelateerde stoornissen beter en grondiger onderzocht worden.

Podsumowanie

Pomiędzy neuronaukowcami od dłuższego czasu trwa spór o prawdziwy charakter procesów percepcji oraz analizy ekspresji emocjonalnych. Większość z nich skłania się ku stwierdzeniu, iż procesy te przebiegają automatycznie, czyli bardzo szybko, mimowolnie oraz nieświadomie. Niemniej jednak sporo badaczy tego zagadnienia wskazuje, iż takie czynniki jak modulacja uwagowa czy też specyficzne uwarunkowania osobowościowo-temperamentalne mogą znacząco wpływać na przebieg automatycznego przetwarzania ekspresji emocjonalnych. Dotychczas charakter procesów poznawczych definiowano zazwyczaj w kategoriach prostej dychotomii (czyli procesy automatyczne versus procesy kontrolowane), niemniej jednak więcej uwagi powinno się poświęcić zagadnieniu kiedy, do jakiego stopnia oraz w jakich warunkach percepcja i analiza ekspresji emocjonalnych ma charakter automatyczny. Wykorzystując metodę mózgowych potencjałów wywołanych (ERPs), która pozwala na precyzyjne śledzenie zmian w aktywności mózgu przebiegających w określonej jednostce czasu, w niniejszej rozprawie próbowano odpowiedzieć na następujące pytania: Czy można zaobserwować wszystkie aspekty automatycznych procesów percepcji i analizy ekspresji emocjonalnych? Czy procesy te są zawsze automatyczne? Jeśli nie, to kiedy (na jakim etapie) są? Jakie czynniki zewnętrzne mogą wpływać na przebieg procesów percepcji i analizy ekspresji emocjonalnych? Czy cechy osobowościowo-temperamentalne również mogą wpływać na przebieg procesów percepcji i analizy ekspresji emocjonalnych? Czy wpływ ten jest zawsze jednakowy?

W oparciu o wyniki czterech przeprowadzonych eksperymentów dowiedziono, iż procesy percepcji i analizy ekspresji emocjonalnych są pod wieloma względami automatyczne. Procesy te przebiegają szybko, na co wskazują specyficzne formy aktywności mózgu zarejestrowane już na bardzo wczesnych etapach, po około 100 milisekundach po prezentacji bodźca. Jednocześnie wykazano, iż na tym etapie procesy percepcji i analizy ekspresji emocjonalnych mogą być modulowane uwagowo. Efekty ekspresji emocjonalnej (czyli aktywność mózgu wywołanej prezentacją ekspresyjnych zdjęć twarzy w porównaniu do aktywności mózgu wywołanej prezentacją zdjęć twarzy neutralnych) zostały zaobserwowane jedynie wtedy, gdy uwaga osób badanych była skierowana na kategoryzowanie twarzy afektywnych. Na etapach późniejszych, po około 200 milisekundach po ekspozycji bodźca, efekty ekspresji emocjonalnej były obserwowane niezależnie od zaangażowania uwagi osób badanych. Ponadto, na tym samym etapie efekty ekspresji emocjonalnej zostały zaobserwowane również wtedy, kiedy osoby badane, dzięki podprogowej prezentacji bodźców, nie były świadome ich percepcji i analizy. Dodatkowo wykazano, że zróżnicowany indywidualnie poziom lęku jako stałej cechy może wpływać na przebieg związanej z percepcją i analizą twarzy afektywnych aktywności mózgu. W szczególności, osoby charakteryzujące się wysokim poziomem lęku wykazywały tendencję do bardzo szybkiego (nadwrażliwego) reagowania na wszystkie rodzaje bodźców jak na źródło potencjalnego zagrożenia.

Podsumowując najważniejsze wyniki warto podkreślić, iż percepcja i analiza ekspresji emocjonalnych przebiega szybko, jednakże tylko na późniejszych etapach przebiega w sposób całkowicie mimowolny oraz niezależny od zaangażowania świadomości. A zatem, jedynie na późniejszych etapach procesy percepcji i analizy ekspresji emocjonalnych są całkowicie automatyczne. Wczesne etapy pozostają natomiast pod wyraźnym wpływem procesów poznawczych (uwagowych). Dodatkowo, osoby charakteryzujące się wysokim poziomem lęku wykazują specyficzną skłonność do nadwrażliwego (automatycznego) reagowania na wszystkie rodzaje bodźców. Uzyskane wyniki niewątpliwie wzbogacają wiedzę na temat charakterystyki automatycznego przebiegu procesów percepcji i analizy ekspresji emocjonalnych. Dzięki temu mają one szereg implikacji teoretycznych i praktycznych. Mając w pamięci fakt, iż wyniki po części opisują funkcjonowanie osób charakteryzujących się podwyższonym poziomem lęku, co prawdopodobnie predysponuje je do zapadania na zaburzenia lękowe w przyszłości, można wykorzystać je do pogłębionego opisu funkcjonowania oraz potencjalnych metod terapii osób cierpiących na zaburzenia afektywne.

Acknowledgements

It was a nice and sunny day in April 2002, when I have, for the first time, visited Kraków and entered the building of the Institute of Psychology of the Jagiellonian University. And it was even more sunny, when I have, for the first time, come to Nijmegen as a participant of the Radboud Summer Universtity 2006. That is how the beginning looked like… Many years have lapsed since then, and during this time I have faced plenty of people, both friends and enemies. Now I have a unique opportunity to express my gratitude to some of you (or to express my triumph over some others) and say: I DID IT!

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Wiola

Podziękowania

Był słoneczny, kwietniowy dzień 2002 roku, kiedy po raz pierwszy pojawiłam się Krakowie i zobaczyłam budynek Instytutu Psychologii UJ. Było jeszcze bardziej słonecznie, kiedy wraz z grupą krakowskich studentów przyjechałam po raz pierwszy do Nijmegen, aby uczestniczyć w Radboud Summer University 2006. Taki był początek… Od tamtych dni upłynęło sporo czasu, a ja na swojej drodze spotkałam wiele osób, zarówno przyjaciół, jak i wrogów. Teraz nadarza się niepowtarzalna okazja, aby wszystkim powiedzieć: DZIĘKUJĘ, dzięki Wam (lub na przekór Wam) UDAŁO SIĘ!

Na swojej naukowej drodze spotkałam przynajmniej trzy osoby, które niewątpliwie przyczyniły się do tego, że dziś jestem dokładnie tym, kim jestem i to właśnie im – profesorowi Janowi Kaiserowi, profesorowi Antonowi M.L. Coenenowi oraz doktorowi Eligiuszowi Wronce – chciałabym najbardziej podziękować. Profesor dr hab. Jan Kaiser – mój polski opiekun i promotor – od zawsze służył radą i dzielił się ze mną wyważonymi sugestiami. Niejednokrotnie wykazywał się też dużą cierpliwością w oczekiwaniu na kolejne etapy mojej pracy. Nawet jeśli czasami nasze opinie się różniły, zawsze starałam się brać pod uwagę jego zdanie. Nad holenderskimi etapami mojej pracy czuwał profesor Anton M.L. Coenen. To właśnie dzięki niemu miesiące spędzone w Nijmegen wspominam nie tylko jako okres wytężonej pracy, ale także jako czas spędzony w przemiłym otoczeniu i wśród zawsze chętnych do pomocy osób. Nigdy nie ukrywałam, że w każde wakacje czym prędzej wyjeżdżałam do Nijmegen, gdzie mogłam pracować w ciszy i spokoju, których bardzo często brakowało mi w Krakowie. W tym miejscu warto również wspomnieć, iż moje pobyty w Nijmegen były możliwe dzięki trwającej już blisko 40 lat współpracy pomiędzy kierownikami dwóch zaprzyjaźnionych jednostek: profesorów Kaisera i Coenena. Miałam też niewątpliwą przyjemność spotkać w swoim życiu osobę, która jeszcze w studenckich czasach wzbudziła we mnie pasję do uprawiania nauki, a przez ostatnie lata umiejętnie kształtowała postawę idealnego eksperymentatora i nauczyciela akademickiego. Eli, za wszystko to po prostu d-z-i-ę-k-u-j-ę!

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Wiola

Curriculum Vitae

Wioleta (Wiola) Walentowska was born on April 4th, 1983 in Świdnica (Poland). After graduating from the secondary school in 2002, she began the psychology studies at the Institute of Psychology of the Jagiellonian University in Kraków (Poland). In 2007 she successfully completed them with a thesis entitled *'Emotional intelligence, emotional expression categorization, and specific forms of the evoked brain activity'* supervised by Jan Kaiser. In 2006 she participated in the Radboud Summer University in Nijmegen, which was a trigger to establish contacts with Anton M.L. Coenen from the Radboud University Nijmegen (the Netherlands). As a continuation, in 2007 she began Ph.D. studies in Kraków, and in 2008 she became a fellow Ph.D. student in Nijmegen, under the supervision of Jan Kaiser and Anton M.L. Coenen, respectively. During the past five years she effectively co-worked with Eligiusz Wronka, Ph.D., conducting scientific projects on the neural correlates of facial emotional expression processing. Recently her scientific interests are focused on the automaticity of facial emotion processing, also from the perspective of individual differences (trait anxiety).

As a member of the Society for Psychophysiological Research (SPR), she has been regularly attending its annual meetings, as well as other international conferences and workshops. In the past few years she gained a priceless experience as one of the main organizers of the NEURONUS Neuroscience Forum, a meeting of young neurobiologists and cognitive neuroscientists, annually held in Kraków. Moreover, during the last four years she was teaching first-year students the biological background of psychology.

Doctoral thesis entitled *'Facing emotional faces. The nature of automaticity of facial emotion processing studied with ERPs'* summarizes her so-far scientific work experimentally conducted at the Psychophysiology Laboratory of the Jagiellonian University in Kraków. This work was supported by two grants from the Polish Ministry of Science and Higher Education (N N106 1958 33, N N106 0983 38, coordinator: Eligiusz Wronka) and by the Young Scientists' Grant from the Jagiellonian University.

List of publications

1) publications in peer-reviewed journals:

Wronka, E., and **Walentowska, W.** (submitted). Attentional modulation at early stages of emotional expression processing studied with Event-Related Potentials and Low Resolution Electromagnetic Tomography (LORETA).

Walentowska, W., and Wronka, E. (submitted). Anxiety modulates early and late stages of facial emotion processing.

Walentowska, W., and Wronka, E. (submitted). ERP correlates of subliminal processing of facial emotions.

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2) conference abstracts:

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Abstracts published in *Psychophysiology* come from the Society for Psychophysiological Research (SPR) Annual Meetings organized in New Orleans, USA (2012), Boston, USA (2011), Portland, USA (2010), and Berlin, Germany (2009).

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