

**FEAR IN YOUR EYES?
THE IMPORTANCE OF THE EYES FOR RAPID DISCRIMINATION
OF FEARFUL FACIAL EXPRESSIONS**

University of Tampere
Department of Psychology
Master's Thesis
Krista Koskinen
May 2008

UNIVERSITY OF TAMPERE

Department of Psychology

KOSKINEN, KRISTA: Fear in your eyes? The importance of the eyes for rapid discrimination of fearful facial expressions.

Master's Thesis, 29 pages.

Psychology

May 2008

The human face and its profound relevance for social cognition has been a topic of interest in psychology for a long time. Many different aspects of face processing have been investigated and one of these areas of interest is how we perceive and process the facial expressions of other people to recognize their emotions. Another issue that has caused a considerable amount of debate in the past decade is the question of how the eyes are processed and how important a facial feature they are. Hypotheses have been formed about a separate eye processor that coexists in the human brain with a distinct face processor. The present study sought to find out if there is a connection between the above mentioned two issues, and to find answers to the question of whether the eyes are important for the rapid discrimination of fearful and neutral facial expressions as measured with event-related potentials. The participants of this study were healthy volunteer adults (22 participants, mean age 27 years). The participants viewed fearful and neutral faces in three different conditions regarding the eye region of the stimulus. The conditions were intact full faces, full faces with the eyes covered with sunglasses, and isolated eyes. The participants viewed the stimuli from a computer screen while their EEG activity was recorded. ERP waveforms were then averaged from the data, and peak amplitude and latency of the early P100 and N170 components of the ERP were analysed. Based on prior research, a clear difference was expected to be found between the responses to the fearful and neutral stimuli, and also that the isolated eyes would evoke a distinct response from the full faces. The visibility of the eye region was expected to have an effect on the responses to the facial expressions. The results lent support for the eyes being a special facial feature but conclusive evidence was not found for a critical role of the eyes in the discrimination of fearful and neutral expressions. Specifically, the results of the present study partly replicated results of prior studies in showing enhanced N170 amplitude and delayed N170 latency for isolated eyes as compared to full face stimuli (irrespective of facial expression). The results also showed that fearful stimuli delayed the N170 latency across all three conditions, suggesting that fearful expressions may delay responses due to the involvement of the subcortical route in emotional information processing, or that they may hold the attention of the observer more effectively and thus take longer to process than the neutral faces. The fact that the latency difference was observed when the eye region alone was presented supports the hypothesis that the eye region is important for the discrimination of fearful and neutral facial expressions. The P100 component reflected only the difference between the isolated eyes and the full face stimuli. Contrary to the expectations, no effects of emotional expression were found on the P100 component or the N170 amplitude. There are several possible explanations as to why the results of the present study were inconclusive. One of these includes the possibility that openness of the eyes (i.e., whether the expression fearful or not) could be read from all the stimuli because the eyebrows were in plain sight in all three conditions. Further investigation is needed to find more solid evidence for the importance of the eyes.

KEY WORDS: emotion, fear, facial expressions, eye detector, ERP.

1. INTRODUCTION	1
1.1 Social cognition and the significance of faces	1
1.2 The processing of faces in the brain	3
1.3 ERPs as a method for measuring face processing	6
1.4 The aims of the present study	9
2. METHODS AND MATERIALS	10
2.1 Participants	10
2.2 Stimuli and procedure	11
2.3 EEG recording and ERP procedures	12
2.4 Data analysis	12
3. RESULTS	13
3.1 P100	15
3.1.1 P100 amplitude	15
3.1.2 P100 latency	15
3.2 N170	15
3.2.1 N170 amplitude	15
3.2.2 N170 latency	16
4. DISCUSSION	16
REFERENCES	23

1. INTRODUCTION

1.1 Social cognition and the significance of faces

Social cognition has been a field of growing interest in the past few decades. It is an area of psychology that studies how we acquire an understanding of the social world, of what other people are like and how we explain the reasons behind their behaviour. These functions occupy such a great part of our everyday life that the interest this field has evoked is very understandable. Research has been conducted on a multitude of viewpoints and on different modalities of perception but visual perception and its social aspects has probably drawn the most attention, since humans rely so profoundly on vision in their everyday activities. Emery (2000) says in his review of social attention that the increased reliance of primates on visual signals may have been driven by the increased sophistication of social interactions. Visual signals contain vast potential complexity, and it is possible for these signals to carry multiple meanings. Emery also states that an important first step in social interaction is recognizing a conspecific. The easiest way to accomplish this is through vision.

One area of social cognition that has generated plenty of research is the human face and its use in social communication. The face has been described as a biologically salient cue (Johnson, 2005), and faces evidently play a crucial part in everyday communication. Haxby, Hoffman and Gobbini (2000) state that face perception is probably the most developed visual perceptual skill in humans and that most face viewing occurs in the context of social interactions. We recognize other people based more on their facial appearance than any other characteristic (Gazzaniga, Ivry & Mangun, 2002), and even newborn babies at the age of just a few hours begin to favour their mother's face over others showing that they recognize her in some rudimentary way (Bushnell, 2001). We use gaze cues from other people's eyes to direct our attention in the social context (Hietanen, 1999; Hietanen, 2002; Perrett, Hietanen, Oram & Benson, 1992). Emery (2000) states that the eyes are important as they especially can provide information on the other person's emotional and mental states; they are a major part of a facial expression. We use facial expressions to communicate with each other and convey our own feelings and moods to the people around us. We can interpret another person's mental states, feelings and intentions by looking at that person's face and the expressions on it (Leppänen & Hietanen, 2004). Haxby and colleagues (2000) suggest a division of face processing into invariant (facial identity) and changeable (e.g., facial expression, gaze direction) aspects, out of which the changeable aspects are more important to social communication and interaction. They have also suggested that different aspects of faces are processed by mostly

separate but sometimes overlapping systems. For example, recognition of identity and facial expression seem to proceed relatively independently in the human neural systems.

Gazzaniga and colleagues (2002) state that in all cultures of the world, facial expressions provide the most salient cues regarding the affective states of people. The question of classifying facial expressions has caused a lot of debate because of the vast cultural diversity connected to it. However, a general consensus has been reached that there are some universal and basic emotional facial expressions. Most sources list six basic facial expressions: happiness, sadness, fear, disgust, anger and surprise that are recognized all over the world (e.g., Batty & Taylor, 2003). The value of emotions and emotional expressions is emphasized by how useful it is for a primate to have the ability to rapidly decode the emotional state of conspecifics (Halgren, Raij, Marinkovic, Jousimäki & Hari, 2000).

The present study concentrated on one emotional facial expression, namely fear. One of the main reasons why the facial expression of fear warrants the attention is that it has special evolutionary significance. Threat-related cues and their attention-capturing potential have been of interest in psychology for a long time. Uncertainty exists whether emotional facial expressions automatically capture the attention of the observer or if these processes are dependent on conscious attention orienting. Evidence has been found to support automatic processing on one hand (e.g., Bentin, Allison, Puce, Perez and McCarthy, 1996; Eger, Jedyak, Iwaki & Skrandies, 2003; Hietanen & Leppänen, 2003; Leppänen & Hietanen, 2004) and attention dependency on the other hand (e.g., Holmes, Vuilleumier & Eimer, 2003). Automatic responses have been reported especially to fear stimuli (e.g., Winston, Vuilleumier & Dolan, 2003). It has been suggested on numerous occasions that the expression of fear on another individual's face is one of those cues that captures attention faster and may also hold it longer (i.e., make it harder for the observer to disengage attention) than expressions of other emotions (Pourtois, Grandjean, Sander & Vuilleumier, 2004). It is a powerful signal because it alerts us to potential danger in the environment. Vuilleumier, Armony, Driver and Dolan (2003) suggest that a subcortical (retinal-collicular-pulvinar) route conveys information to a danger-detection system in the brain (the amygdala) that processes these cues. It has also been suggested that one important function of emotions is to enhance the processing of signals on many levels, and it makes sense that this capturing of attention would be an automatic process because of its great survival value (Armony & Dolan, 2002; Leppänen & Hietanen, 2004). Williams, Palmer, Liddell, Song and Gordon (2006) take it even further and suggest that fear-related stimuli take precedence and suppress the seeking of positive stimulation until vigilance for potential danger is complete and safety assured. However, this potential may at least partly be dependent on the observer's own mental state, in that the

emotional nature of directional cues and emotionality of the observer can interact in modifying the basic operations of visual attention (Mathews, Fox, Yiend & Calder, 2003). This is to say that anxious individuals pay more attention to threat cues than non-anxious ones (Hietanen & Leppänen, 2003; Leppänen & Hietanen, 2004), and nondysphoric subjects even show bias away from threat cues (Bradley et al., 1997).

1.2 The processing of faces in the brain

Visual perception in the brain is a complex phenomenon and involves numerous separate but cooperating brain areas. The cells in our retina have evolved to sense our environment with great precision, and our brain has large areas and well-defined functions for processing the information we receive from our environment through our eyes. There are two main cortical visual processing pathways in the human brain: the ventral stream (or the “what” pathway) and the dorsal stream (the “where” or “how” pathway). According to Bentin and colleagues (1996) there seems to be considerable functional specialization in the ventral pathway and for example, faces are processed in this stream. There are three kinds of ganglion cells in the human visual system; parvocellular, magnocellular and koniocellular. The functions of the first two types are better known than the third. The parvocellular neurons provide the visual brain areas with detailed analysis of stationary objects, and the magnocellular neurons with movement and broad outlines of shape (Kalat, 2007). The processing of faces relies on both inputs to varying degrees.

Face sensitive areas and cells have been found in the human and non-human primate brain (e.g., Perrett et al., 1992). These brain areas dedicated to or participating in face processing have mostly been found in the occipital and temporal cortices in the extrastriate visual cortex, with a few exceptions. These brain areas include the fusiform gyrus (FG) and especially a part of it called the “fusiform face area” (FFA) located in the mid-fusiform gyrus (e.g., Allison, Puce & McCarthy, 2002; Gauthier, Tarr, Moylan, Skudlarski, Gore & Anderson, 2000; George, Dolan, Fink, Baylis, Russell & Driver, 1999; Grill-Spector, Knouf & Kanwisher, 2004), the inferior occipital gyrus (IOG) and in it, the occipital face area (OFA) (Gauthier et al., 2000; Rossion, Caldara, Seghier, Schuller, Lazeyras & Mayer, 2003; Schiltz & Rossion, 2006), the middle occipital gyrus (Steeves et al., 2005), the inferior temporal gyrus (ITG) (Haxby et al., 2000), and the superior temporal sulcus (STS) (Marinkovic, Trebon, Chauvel & Halgren, 2000; Puce, Smith & Allison, 2000). Some researchers have divided the functions of these areas so that the FG areas are more responsible for the invariant aspects of face processing and the STS areas have more to do with the processing of the changeable aspects (Haxby et al., 2000). Arguments have been made that the FFA (especially in

the right hemisphere) is essential for face processing (e.g., McCarthy, Puce, Gore & Allison, 1997) but Steeves and colleagues (2005) present an interesting case of a patient with an intact right FFA but bilateral OFA damage who has severe difficulties in face processing. Based on this evidence they state that what is necessary for normal, higher level face processing is a complex intact neural network.

Other areas mentioned in connection with face processing include the orbito-frontal cortex (OFC) (Whalen et al., 2004; Winston et al., 2003), the prefrontal cortex (PFC) (Herrmann, Ehli, Muehlberger & Fallgatter, 2005; Marinkovic et al., 2000), and the amygdala (Armony & Dolan, 2002; Vuilleumier, Richardson, Armony, Driver & Dolan, 2004; Whalen et al., 2004; Winston et al., 2003). These areas seem to be connected to emotion processing. Batty and Taylor (2003) state that evidence from recent studies has implicated differing brain regions for different emotions. Some research has focused on the subcortical route of face processing (de Gelder & Stekelenburg, 2004; Johnson, 2005). This route involves brain areas such as the superior colliculus, the pulvinar and the amygdala. Suggestions have been made that this route only works during development in childhood and ceases to function in adulthood but recent evidence has shown that it does contribute to cortical processes by modulating them in adulthood as well (de Gelder & Stekelenburg, 2004; Johnson, 2005).

The above mentioned brain areas have been investigated with several different methods. These methods include for example, intracranial (Allison et al., 2002; Marinkovic et al., 2000) and surface (Eimer, 1998a; Latinus & Taylor, 2005; Sagiv & Bentin, 2001) electroencephalogram (EEG) and event-related potentials (ERPs), functional magnetic resonance imaging (fMRI) (Gauthier et al., 2000; George et al., 1999), positron emission tomography (PET) (Rossion et al., 2000a), magnetoencephalography (MEG) (Halgren et al., 2000), single neuron recordings in nonhuman primates (Baylis, Rolls & Leonard, 1987; Perrett et al., 1992), and lesion studies with animals and humans who have sustained or were born with brain damage (Vuilleumier et al., 2004).

Evidence has also accumulated supporting the hypothesis of right hemisphere dominance in face, eye and/or emotion processing (e.g., Bentley, Vuilleumier, Thiel, Driver & Dolan, 2003; Eger et al., 2003; Schiltz & Rossion, 2006; Taylor, Edmonds, McCarthy & Allison, 2001a; but see Puce et al., 2000). McCarthy and colleagues (1997) found the right hemisphere advantage for faces particularly strong in complex visual environments. Suggestions have been made that the right hemisphere processes information in a synthetic, holistic and configurational manner (which would be more in line with the theories of face processing), while the left hemisphere uses analytical, part-based and serial processing (e.g., Rossion et al., 2000a; but see Halgren et al., 2000). Some have found this advantage only under special circumstances. For example, Kanwisher, McDermott and

Chun (1997) in their series of experiments found the right hemisphere advantage for face processing only in right-handed individuals, so there may be some effect of handedness to this hypothesis. Noesselt, Driver, Heinze and Dolan (2005) found the advantage only for fearful but not for neutral faces. Borod, Bloom, Brickman, Nakhutina and Curko (2002) provide a summary of the right hemisphere dominance in regard to emotion processing. They state that emotion processing involves strategies and functions for which the neuroanatomical design and neurophysiological organization of the right hemisphere is better suited. Thus, the right hemisphere may have an important role in the complex, multimodal, and integrative nature of emotion processing. They also review the valence hypothesis and the motoric direction hypothesis. The former says that the right hemisphere specializes in negative emotions and the left in positive emotions. The latter is overlapping to a certain extent in saying that the right hemisphere processes emotions related to avoidance orientation and the left one to approach orientation. They also mention that negative emotions are linked with survival, and the appropriate behaviours in these situations involve synthetic processing. Bentley and colleagues (2003), who conducted experiments on attention and emotion processing with cholinergic enhancement, state that the right hemisphere may already be sensitive to faces but the left may become more so with the enhancement.

Perception of faces seems to be qualitatively different from object recognition (Eimer 2000a). Eger and colleagues (2003) state that face perception places exceptional processing demands on the human brain since faces are a very homogenous class of objects but facial features can change their appearance considerably for example, with different facial expressions. It has been said that face recognition requires within-category discrimination of visually similar objects (McCarthy et al., 1997) whereas object recognition usually requires between-category discriminations (Gazzaniga et al., 2002). Neurophysiological dissociations between face and object recognition suggest two systems for object recognition. The following hypothesis has been proposed on the two systems: a part-based and a holistic processing system (Farah, Wilson, Drain & Tanaka, 1998; see also Gazzaniga et al., 2002). These systems are used to varying degrees depending on the task. Face recognition is at the holistic end of the continuum; with relatively little part composition involved in face perception and recognition, and word recognition is at the part-based end, being almost completely reliant on analytical processing. Object recognition falls somewhere in between the two extremes, using both systems to differing degrees. Allison and colleagues (2002) in their study of category-sensitive excitatory and inhibitory processes suggest that the above mentioned two processes may be reciprocally inhibitory. They measured brain activity intracranially and found maximal inhibition for face-specific cells when words were presented and vice versa. This evidence coincides with the continuum approach of visual processing presented above. Goffaux and Rossion

(2006) propose that holistic representation is extracted somewhat before the representation of face parts is fully resolved. There has also been debate about whether holistic processing takes place in the perceptual stage (Schiltz & Rossion, 2006) or in a later decisional stage (Wenger & Ingvalson, 2003) but evidence seems to be accumulating in support of the perceptual stage hypothesis. Gazzaniga and colleagues (2002) point out that faces are special in the sense that the representation derived from analysis by parts is not sufficient for recognition.

The face inversion effect has been used as evidence for the holistic processing of faces. Several studies have produced evidence that faces are harder to recognize when turned upside down (e.g., Latinus & Taylor, 2005) but that this effect disappears when the participants are instructed to encode faces in parts (Farah et al., 1998). The inversion effect is said to be caused by loss of configurational information (i.e., information about the spatial relations between facial features) (e.g., Rossion et al., 2000b; Yovel & Kanwisher, 2004). Sagiv and Bentin (2001) integrate the approaches of whole- and part-based processing by proposing a multiple-component neural system with anatomically separate but cooperating areas that provide both whole- and part-based information for face processing.

1.3 ERPs as a method for measuring face processing

Event-related potentials (ERPs) are an excellent method for examining the time course of face processing. ERPs reflect phasic modulations of brain activity that is time-locked to the onset of external or internal events (e.g., Eimer, 1998b). ERPs can be obtained by averaging the EEG activity measured in response to such events over several event repetitions. The resulting ERP waveforms consist of positive and negative deflections that are labelled according to their polarity and latency, and that reflect different perceptual and cognitive processes. ERPs provide a non-invasive method of monitoring brain activity during cognitive processing. Because of their non-invasive nature, ERPs are also suitable for measuring the brain activity of infants and children. They can be obtained without overt response requirements. ERPs can be used for example, to measure the effects of attention, and as markers for the selective impairment of different processing stages of face identification (Eimer, 1998a, 2000c). Williams and colleagues (2006) used ERPs for investigating the temporal sequence of emotion processing. They described the early ERP sequence of emotion processing as follows: “within the first 120 ms post-stimulus, coarse perceptual discrimination of visual signals of emotion may be achieved via direct feedforward pathways. Finer-grained perceptual analysis occurring around 170 ms post-stimulus may be subserved by slower cortical pathways operating in parallel, which may be reciprocally modulated by salient

signals of emotion.” The spatial resolution of ERPs is not very accurate because they are recorded on the scalp surface while their generators lie in the pyramidal cells in the cerebral cortex and hippocampus. Mathematical models for the localization of ERP generators have been developed but other methods of imaging are preferable for localizing face specific activity in the brain. ERP studies of face processing have typically focused on the early ERP components, P100 and N170. These two components are most pronounced in posterior scalp regions and they are referred to as exogenous components as they are stimulus-driven (Eimer, 1998b).

The P100 is the first positive deflection in the ERP waveform. It reflects the early stages of visual processing and is evoked by virtually all types of visual stimuli. The P100 has, however, also been linked with face processing, in particular to rapid global processing of face stimuli and early processing of emotional facial expressions (Batty & Taylor, 2003). Its latency window varies slightly from study to study but it is usually found in the window of 80-180 ms post-stimulus (Williams et al., 2006), most often at about 100 ms post-stimulus. Other aspects of face processing that the P100 has been linked to besides emotional expressions are the mechanisms of spatial selectivity and attention (Eimer, 1998b; Pourtois, Thut, de Peralta, Michel & Vuilleumier, 2005). The P100 component is most likely generated in the ventro-lateral extrastriate cortex (Eimer, 1998b), in the fusiform gyri (Herrmann et al., 2005), and appears to be relatively bilateral (Pourtois et al., 2005). This lends support to the interpretation that the P100 may reflect early face processing (but see Eimer, 1998b). Williams and colleagues (2006) suggest that this component may reflect processes related to the initial processing of threat-related information and processes that serve an early alerting function.

Johnson (2005) defines the N170 as an ERP component whose latency and amplitude are modulated by the viewing of faces. It is the first ERP commonly associated with face perception (Taylor et al., 2001a); although findings exist that the N170 can be recorded for other categories besides faces (Rossion et al., 2000b). Rossion and colleagues (2000b) note, however, that the N170 is larger for faces than other categories. It is the first negative deflection in the ERP waveform and the latency window for measuring it is 120-220 ms after stimulus onset (Williams et al., 2006) over lateral occipital and temporal recording sites. It most often appears around 170 ms post-stimulus. The focal region for N170 recordings is the right inferior temporal scalp (Puce et al., 2000). The N170 generators have been located in several areas including the FG and IOG (Itier, Latinus & Taylor, 2005) and the STS (Rousselet, Macé & Fabre-Thorpe, 2003; Itier & Taylor, 2004). While the N170 is obtained by surface recordings, Allison and colleagues (2002) recorded an N200 component intracranially. This component seems to reflect similar processes as the N170 but it

likely does not share the same generators with the N170 because of the latency difference (Eimer, 2000b).

A lot of research on the N170 component has been conducted but the question of what it reflects is still under debate. Several hypotheses and suggestions have been made on this subject. The N170 has been linked with the structural encoding of faces (Eimer, 2000d). It is a stage of face processing where representations of global face configurations are produced in order to provide a basis for further face recognition processes (Holmes et al., 2003). These processes are said to be devoted to the configurational analysis of whole faces (Eimer, 2000d). It has also been said that the configurational analysis of faces will be delayed when structural information is inadequate because of face inversion or the absence of face components (Eimer, 1998a); although Rousselet and colleagues (2003) suspect that the spatial organization needed to generate the N170 is relatively coarse. It has been suggested that the timing of structural encoding processes can be affected by stimulus properties and attentional factors (Eimer, 2000b), and Holmes and colleagues (2003) found enhanced N170 amplitudes to faces that were attended. Conversely, the N170 component has also been recorded for unattended faces (Carmel & Bentin, 2002), even when they are presented peripherally (de Gelder & Stekelenburg, 2004). The N170 component seems to be unaffected by face identity, stimulus repetition, and learning (Eimer, 2000b, 2000c; Latinus & Taylor, 2005). This argues in favour of the N170 reflecting early pre-categorical structural encoding of faces rather than face identity recognition processes that appear to follow later. The N170 component is connected to face identification through one important point though; impaired structural encoding will also impair face recognition and identification (Eimer, 2000c).

Another view of what the N170 component reflects is the “eye processor” hypothesis. Bentin and colleagues (1996) suggest that this processor is an extension of the structural encoding system. They state that there is an area in the occipito-temporal sulcus that acts as a separate eye processor. The N170 reflects the activity of this processor. Isolated eyes usually give rise to larger N170 amplitudes (Carmel & Bentin, 2002), and the argument that Bentin and colleagues (1996) made was that this is evidence for the eye processor because the other face features in their appropriate spatial orientation diminish the N170 evoked by the eyes, whereas feature dislocation or isolation enhance it. Taylor, Itier, Allison and Edmonds (2001b) also found longer latencies for isolated eyes as opposed to full faces. In their study of the development of face perception across age groups, they found that different maturational processes seem to exist for the N170 for eyes, upright faces and inverted faces based on their different developmental patterns and ages of emergence. This also brought them to propose different neuroanatomical sources for the N170 related to eyes and to full faces. Itier and colleagues (2005) have proposed an interesting hypothesis on the inhibition of

neurons responsive to faces and eyes. They suggest that with upright faces, the face-selective neurons respond and inhibit the operation of the eye-selective neurons. In the case of face inversion and/or contrast reversal, the face-selective neurons are inhibited by the disruption of facial configuration and the eye-selective neurons are allowed to function. Thus, the larger N170 to inverted faces is driven mostly by the eye-region of the face. Itier and colleagues (2005) conclude that the N170 is selective to human faces and eyes. The specificity of the N170 to human faces as opposed to animal faces is not clear, however. Evidence has been found for human specificity (Bentin et al., 1996) and against it (Carmel & Bentin, 2002; Rousselet et al., 2003). Bentin and colleagues (1996) tie their evidence to the eye processor hypothesis by suggesting that human faces are special because humans are the only species whose eyes show a lot of white sclera contrasting with a darker iris. Eimer (2000d) presents a strong argument against the eye processor hypothesis with his experiments where he obtained similar N170s to faces even when the internal features were completely obscured or when the eyes were removed from the face stimulus (1998a). He states that the reason why the N170 can be obtained to isolated eyes may depend on a single salient feature being able to evoke structural encoding processes (Eimer, 1998a).

The N170 has also been linked to the processing of emotional facial expressions. Batty and Taylor (2003) conducted an experiment that yielded N170 latency and amplitude differences between the six basic emotional facial expressions at 140 ms post-stimulus. Their results showed that the N170 evoked by negative emotional expressions (fear, disgust and sadness) had longer latency than the N170 evoked by neutral or positive expressions. The N170 evoked by a fearful expression had larger amplitude than any of the other expressions. They concluded that the second stage of early processing, reflected by the N170 component, may be influenced by rapid feedback connections from the subcortical route to the cortical areas, yielding slightly slower but more detailed cortical processing that allows differentiation of basic emotions. Holmes and colleagues (2003) found no effects of emotional expression on the N170. They proposed that facial expression processing takes place earlier and independently of global facial configuration processing. Eger and colleagues (2003) provide an interesting insight to explaining the lack of emotional facial expression effects when they criticize traditional ERP studies for not using dense enough electrode arrays and thus not obtaining early emotional processing evidence.

1.4 The aims of the present study

The present study involved two important aspects of face processing: facial expressions and the importance of an individual facial feature for face processing. The purpose of this study was to

examine differences in early ERPs to fearful as opposed to neutral faces, and the importance of the eye region for face processing and the ERP differentiation of fearful and neutral faces. The aim was to find out if the eyes truly are as important to the recognition of the facial expression of fear as one could assume. The eyes in a fearful facial expression appear much wider than in a neutral expression and show much more white sclera. Prior research has shown that the size of the sclera is an important factor in producing amygdala activation that in turn modulates cortical responses especially with fearful facial expressions (Whalen et al., 2004). The face stimuli used in this study were still photographs of male and female faces presented to the participants on a computer screen. Computer-drawn pictures of cars were used as target stimuli to ensure the participants' attention to the stimulus display but the ERPs to these target stimuli were not analyzed. The participants were presented with three kinds of different conditions regarding the eye region of the stimuli. In one condition, intact fearful and neutral faces were shown. In the second condition, the participants viewed fearful and neutral face stimuli where the eye region was covered with sunglasses. In the third condition, they viewed fearful and neutral faces where only the eye region was visible while the rest of the face had been removed from the photograph. Somewhat similar stimuli have been used before (e.g., Eimer, 1998a; Taylor et al., 2001a) but the present study incorporated both covered and isolated eyes in the design. Based on prior research (e.g., Batty & Taylor, 2003; Bentin et al., 1996; Taylor et al., 2001b; Williams et al., 2006), the fearful expression was expected to produce larger (N170 and possibly P100) responses than the neutral expression. Given the assumed importance of the eyes to a facial expression, attenuated and delayed responses were expected to be found in situations where the eyes were not visible. The difference between the fearful and neutral expressions was expected to be less pronounced when the participants could not see the eyes in the stimulus face. The isolated eyes were expected to produce generally larger and delayed (N170) responses in comparison to the full face stimuli. In addition, all responses were expected to be larger over the right hemisphere than the left.

2. METHODS AND MATERIALS

2.1 Participants

22 volunteers (7 males) participated in this study. Their age range was 18-50 years (mean 27 years). All participants reported normal or corrected to normal vision and had no diagnosed neurological impairments. The participants were unaware of the purpose of the study.

2.2 Stimuli and procedure

The participants were comfortably seated in a dimly lit, sound proof room. The visual stimuli were presented on a computer screen (Nokia 930C 17", 75Hz refresh rate) within a viewing distance of 77 cm. The stimuli presented were photographs of faces and computer drawn images of cars. Three different types (conditions) of face photographs with 4 different identities (2 male, 2 female) were used in the experiment. One condition showed an intact full face, the second condition showed the same full face images but the eyes were covered with sunglasses and the third condition showed only the eye region of the images. All the images showed either a fearful or a neutral facial expression. Figure 1 shows an example of the images. The stimuli were presented at the centre of the screen on a black background. The full face stimuli subtended a visual angle of $8.9^\circ \times 12.4^\circ$, and the isolated eyes stimuli $6.7^\circ \times 3.0^\circ$.



Fig. 1 An example of the stimuli

The experiment consisted of three blocks each containing 128 face photograph trials (64 fearful and 64 neutral expressions) and 12 trials with an image of a car. In each trial the stimulus remained on the screen for 500 ms with a 1000 ms inter-trial interval. The three conditions were presented in separate blocks. The presentation of the blocks was counterbalanced between participants. The face photograph trials required no response from the subject. The images of cars were used as target stimuli to maintain attention during testing. In these trials the participants were instructed to press a button on the response pad (Neuroscan Stig systems switch response pad P/N 1141) placed in their dominant hand. Although the experiment was designed to measure ERPs, the detection rate of the target stimuli was also analysed to ensure that the participants had attended to

the screen. The analyses revealed that the participants detected an average of 100% of the targets, indicating that they were highly attentive to the stimuli. The participants were instructed to try to time their eye blinks to the intervals between trials.

2.3 EEG recording and ERP procedures

The EEG was recorded with 21 electrodes in an elastic cap (Electro-Cap International Inc.). One electrode was attached to the left mastoid and used as an online reference. The electrodes were placed according to the international 10-20 system. All impedances were kept below 5 k Ω . Horizontal (HEOG) and vertical eye movements (VEOG) were monitored with two pairs of bipolar electrodes placed in the outer canthi of the eyes and in the inferior and superior areas of the left orbit. The EEG signal was amplified with a gain of 5000 and bandpass filtered between 0.1-100 Hz (Syn-Amps/Neuroscan 4.3, Neuroscan Inc.). The EEG was filtered offline between 0.1- 30 Hz. The raw signal was digitized with a sampling rate of 500 Hz, and trials with HEOG or VEOG exceeding $\pm 50 \mu\text{V}$ were eliminated. The data from two participants had to be discarded due to insufficient number of accepted trials (less than 25 / 64). The data from the remaining 20 participants was averaged for each condition and each participant respectively in epochs beginning 100 ms before stimulus onset and ending 500 ms after stimulus onset. The epochs were baseline corrected against the 100-ms pre-stimulus period.

2.4 Data analysis

The peak amplitudes and latencies of the visual components P100 and N170 were extracted automatically from the average waveforms for the posterior electrodes T5, T6, O1 and O2. The P100 component was analysed from the data from electrodes O1 and O2, and the N170 was analysed from electrodes T5 and T6. Based on visual inspection of the grand average waveforms, the P100 peak amplitude was extracted from a latency window of 80-120 ms and the N170 from 120-200 ms. The latency windows were in accordance with prior literature (Williams et al., 2006). Repeated measures analyses of variance (ANOVAs) were conducted for P100 latency and amplitude, and N170 latency and amplitude respectively. The factors used in these analyses were facial expression (fearful or neutral), condition (isolated eyes, full face or full face with sunglasses) and hemisphere. Electrode Fz was used as an offline reference in these analyses because the mastoid's close proximity to the posterior channels might attenuate posterior components.

3. RESULTS

The following figures show the grand average ERP waveforms for all 20 subjects for the fearful and neutral facial expressions for electrodes T5 and T6 in the three different conditions.

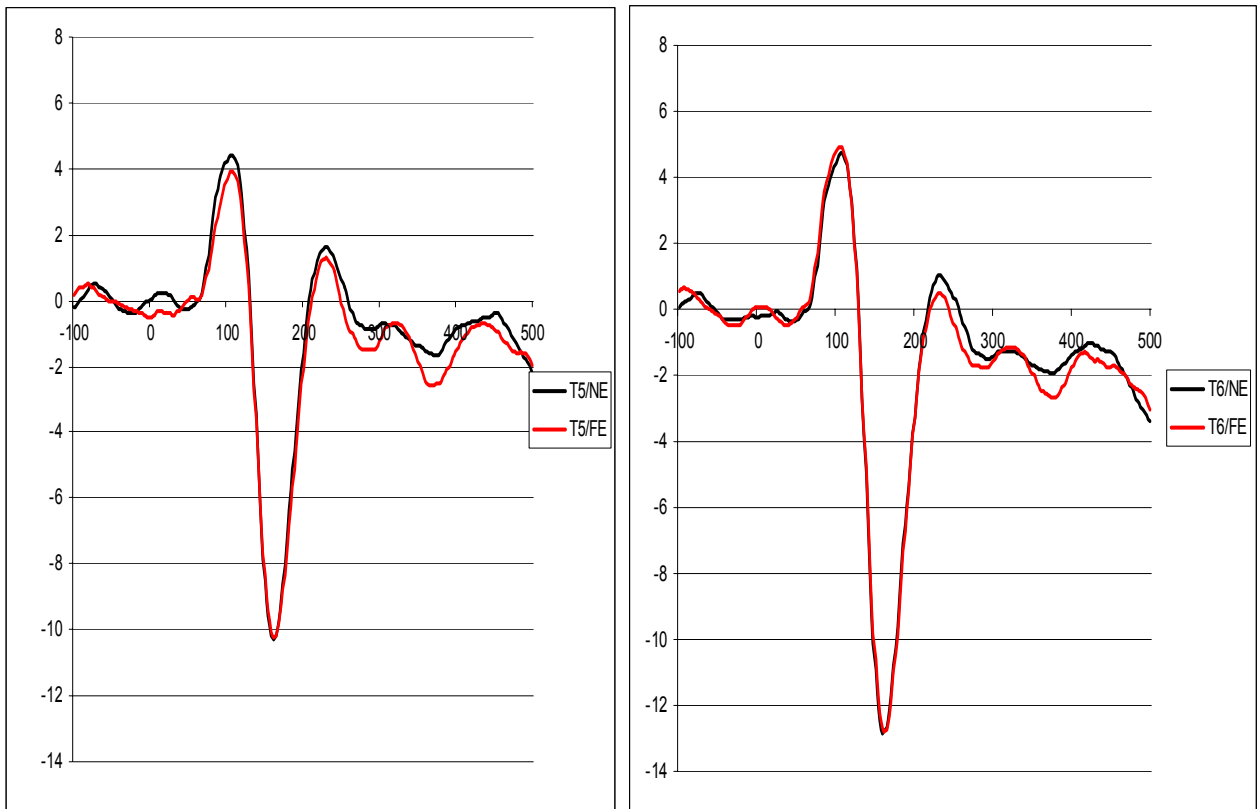


Fig. 2 and 3 Isolated eyes condition for T5 and T6 respectively

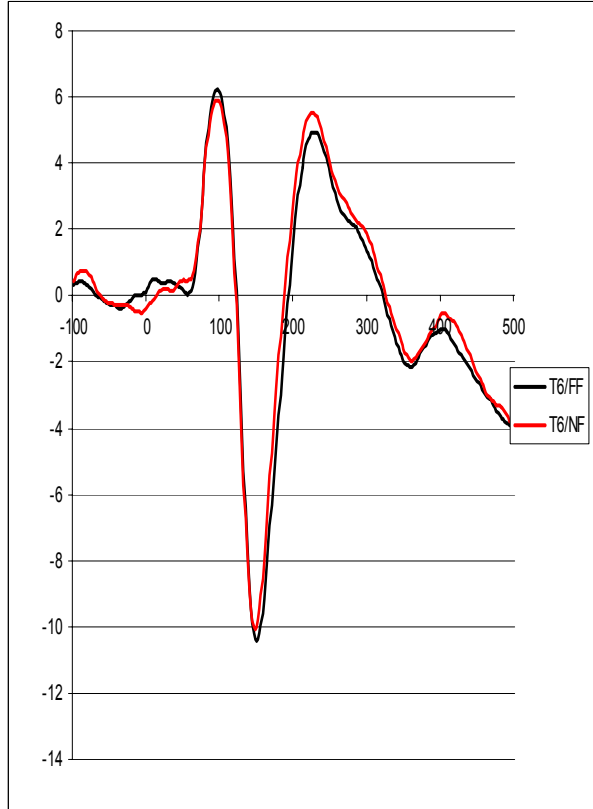
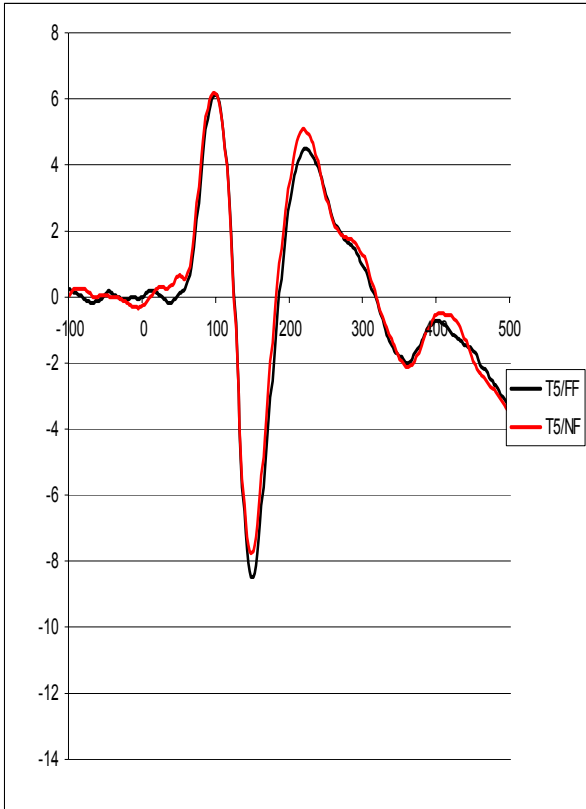


Fig. 4 and 5 Full face condition (T5 and T6)

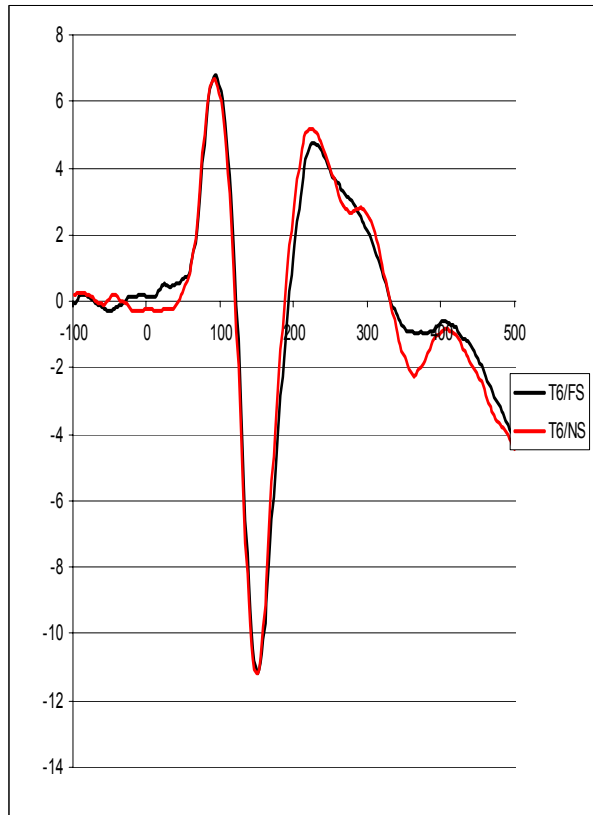
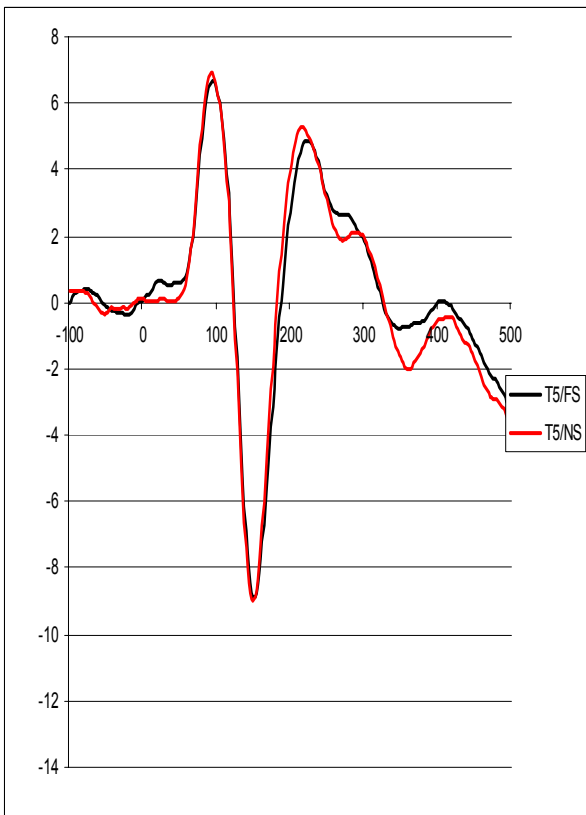


Fig. 6 and 7 Full face with sunglasses condition (T5 and T6)

3.1 P100

Amplitude and latency scores from electrodes O1 and O2, overlaying occipital scalp regions, were used in these analyses. A three-way (Expression x Condition x Hemisphere) repeated measures ANOVA was conducted for the P100 amplitude and P100 latency scores respectively.

3.1.1 P100 amplitude

The P100 amplitude showed a significant main effect of condition [$F(2, 38) = 7.39, p = .002$]. Pairwise Bonferroni corrected comparisons showed that the isolated eyes condition yielded a smaller average peak amplitude ($M = 6.48 \mu V$) than the full face condition ($M = 8.84 \mu V$), $p = .009$. There was a similar trend that approached significance between the isolated eyes condition and the full face with sunglasses ($M = 8.74 \mu V$), $p = .06$. The ERPs evoked by the full face conditions with and without sunglasses did not differ significantly from each other. Factors Expression and Hemisphere yielded no significant differences in the amplitude of the P100 component.

3.1.2 P100 latency

The P100 latency also showed a significant main effect of condition [$F(2,38) = 23.67, p = .0001$]. Pairwise Bonferroni corrected comparisons revealed that the P100 component peaked significantly later in the isolated eyes condition ($M = 108.20$ ms) than it did in either of the full face conditions (full face $M = 98.45$ ms and full face with sunglasses $M = 95.18$ ms, $p = .0001$ for both comparisons). The difference between the two full face conditions was marginal, $p = .057$. Factors Expression and Hemisphere yielded no significant effects on the latency of the P100 component.

3.2 N170

Amplitude and latency scores from electrodes T5 and T6, overlaying lateral occipital-temporal scalp regions, were used in these analyses. A three-way (Expression x Condition x Hemisphere) repeated measures ANOVA was conducted on N170 amplitude and N170 latency scores respectively.

3.2.1 N170 amplitude

There were significant main effects of hemisphere [$F(1,19) = 7.89, p = .011$] and condition [$F(2,38) = 15.33, p = .0001$] on the N170 amplitude. The hemisphere difference reflected larger average

peak amplitude in the right hemisphere (electrode T6) across all conditions. The means for the three conditions were: isolated eyes $M = -13.92 \mu\text{V}$ (right hemisphere) and $M = -11.36 \mu\text{V}$ (left hemisphere), full face condition $M = -11.18 \mu\text{V}$ (right hemisphere) and $M = -8.75 \mu\text{V}$ (left hemisphere), and full face with sunglasses condition $M = -12.24 \mu\text{V}$ (right hemisphere) and $M = -9.66 \mu\text{V}$ (left hemisphere). The main effect of condition was further analyzed by pairwise Bonferroni corrected comparisons. These analyses revealed that the isolated eyes condition evoked larger average peak amplitude ($M = -12.64 \mu\text{V}$) than either one of the full face conditions (full face $M = -9.96 \mu\text{V}$ and full face with sunglasses $M = -10.95 \mu\text{V}$, $p = .0001$ and $p = .021$ respectively). The two full face conditions did not significantly differ from each other, $p = .082$. The factor Expression yielded no significant effects on N170 amplitude.

3.2.2 N170 latency

The N170 latency showed the main effects of condition [$F(2,38) = 40.61$, $p = .0001$] and facial expression [$F(1,19) = 10.88$, $p = .004$]. Pairwise Bonferroni corrected comparisons on the main effect of condition revealed that the N170 component peaked significantly later in the isolated eyes condition ($M = 162.23$ ms) than it did in either of the full face conditions (full face $M = 148.90$ ms and full face with sunglasses $M = 150.53$ ms), $p = .0001$ for both comparisons. The two full face conditions did not differ from each other. The main effect of facial expression reflected the fact that the N170 component peaked significantly later when the expression was fearful ($M = 154.48$ ms) than when it was neutral ($M = 153.28$ ms), $p = .004$. This effect was significant across all conditions. No significant interactions between any of the factors surfaced in any analyses conducted in this study.

4. DISCUSSION

The purpose of the present study was to examine differences in early ERPs to fearful as opposed to neutral faces, and the importance of the eye region for face processing and the ERP differentiation of fearful and neutral faces. The experiment was conducted on healthy volunteer adults. The participants viewed photographs of male and female faces on a computer screen. The photographs displayed one of three conditions regarding the eye region: an intact full face with a fearful or neutral expression, a fearful or neutral full face with the eyes covered with sunglasses, or isolated

eyes that were either fearful or neutral. The participants passively viewed the faces but were instructed to press the reaction button when they saw a computer-drawn picture of a car. This was done to ensure attention to the stimuli. The data from the car trials was not analysed. The results are discussed in the following with respect to the hypotheses regarding the importance of the eyes for rapid discrimination of fearful and neutral facial expressions, and the importance of eyes for early face processing more generally.

The results of the present study showed the main effect of the eye region on the P100 amplitude and latency. The P100 component was delayed when the participants viewed isolated eyes as opposed to either of the full face conditions. The P100 component was also significantly attenuated for the isolated eyes as opposed to the intact full face stimuli. There was a similar trend between the isolated eyes and the full face with sunglasses that approached significance. The full face conditions did not differ from each other. These results may be partly due to the fact that the isolated eyes stimulus was smaller in size than either of the full face stimuli. The factors of facial expression or hemisphere yielded no significant effects in regard to the P100 component. This is in disagreement with a prior study (Williams et al., 2006) where a fearful expression enhanced the P120 component relative to neutral expressions. The present study did not lend support to this indicator of the early processing of threat cues hypothesis that this prior study proposed.

The N170 component was larger over the right hemisphere regardless of the visibility of the eye region or the facial expression. This is in agreement with the right hemisphere dominance hypothesis for faces for which support has been found in previous studies (e.g., Bentin et al., 1996; Eger et al., 2003; Williams et al., 2006). It seems that according to the results of the present study it is the face or eye stimuli per se that evoke stronger activity in the right hemisphere than in the left. Noesselt and colleagues (2005) found the right hemisphere advantage only for fearful faces and not for neutral ones. It is possible that the difference between their results and the results of the present study has to do with the presentation of the stimuli. They used a bilateral display whereas a central display with a single image was used in the present experiment. The results of the present study also showed larger N170 amplitude to isolated eyes than either of the full face stimuli in accordance with prior research (e.g., Bentin et al., 1996; Taylor et al., 2001a). The full face conditions did not differ from each other. Contrary to Batty and Taylor (2003) who found significantly enhanced N170 amplitude to fearful expressions as opposed to all other five basic expressions they investigated, no significant differences were found between the fearful and neutral expressions on the N170 amplitude in the present study. This was a surprising result, since a difference was expected to surface. It could be that the eye region was a more salient cue than the expression per se, and that the eyes took precedence over the analysis of the expression but this is mere speculation.

The results of the present study showed longer latency for the N170 component to isolated eyes than either of the full face stimuli. This is in agreement with prior studies (e.g., Taylor et al., 2001b). No difference was found in the present study between the two full face conditions. Contrary to this result, Taylor and colleagues (2001b) found longer N170 latency to the eyes closed condition as opposed to intact full faces. This eyes closed condition is roughly equivalent to the full face with sunglasses condition used in the present experiment. It is possible that when a face with sunglasses is viewed, the effect is different from the eyes closed condition because the participants can imagine the eyes being open behind the sunglasses and thus relevant for the facial expression, whereas a face with the eyes closed might be viewed as not attentive to the world around us and thus not holding relevant information for the observer. The delayed latency measured to isolated eyes could also be related to Goffaux and Rossion's (2006) proposal that holistic processing of faces precedes local feature analysis. This is to say that the full face stimuli are probably processed holistically whereas the isolated eyes could be processed in a part-based manner as a local feature. This would explain the longer latency to the isolated eyes as they would be processed slightly later than the full faces.

Furthermore, and most interestingly with respect to my hypotheses, the present study showed a significant main effect of facial expression on the N170 latency. A delayed N170 component was found for fearful expressions as opposed to neutral ones. This effect persisted through all conditions. This is contrary to Holmes and colleagues (2003) who found no effects of emotional expression on the N170 but in agreement with Batty and Taylor (2003). Batty and Taylor studied the six basic emotional facial expressions and found delayed latencies for all negative emotions in comparison with positive emotions and neutral expressions. They explained the delay with information arriving from the subcortical route for the processing of negative emotional expressions. This sounds like a plausible explanation since activation of the subcortical route has been found in connection with emotion processing (Johnson, 2005). This might also be related to the importance of the eyes for recognizing facial expressions (especially when the expression is fearful) because the amygdala aids the processing of information from the eyes (Vuilleumier, 2005). Another possible explanation for the delayed N170 latency to fearful faces is the disengagement of attention from the stimulus (Pourtois et al., 2004). It could be that the fearful stimulus held the attention of the participants more effectively and thus made its processing a little slower than that of the neutral stimulus.

The N170 component is said to reflect the activity of the face responsive regions in the human brain. There has been considerable debate on whether the N170 reflects the structural encoding of whole faces (Eimer, 1998a) or the functions of a specialized eye processor (Bentin et

al., 1996; Taylor et al., 2001a). In agreement with prior studies (Eimer, 1998a), no amplitude differences between the two full face conditions were found on the N170 component in the present study. Eimer took a similar result as evidence against the eye processor hypothesis but it is noteworthy that his study did not employ isolated eyes as stimuli, only intact full faces and faces with the eye region removed (blurred). Eimer (1998a) argued that the reason why isolated eyes evoke an N170 response is because a single salient feature alone can evoke structural encoding processes. He did not explain though why the amplitude of the N170 component is usually larger for isolated eyes. Bentin and colleagues (1996) explained this enhanced amplitude effect with the eye detector hypothesis, and stated that the effect is the result of a large body of eye-specific neurons responding to the stimulus and this is reflected in the N170 component. They also stated that the context in which the eyes are viewed alters the N170 response and that is the reason for the smaller N170 amplitude to full faces.

Eimer (1998a) did find delayed N170 latency for the no eyes condition which he stated was similar to the latency delay with isolated eyes and inverted faces. He proposed this was due to the N170 timing being affected by altered facial configuration. The fact that larger N170 amplitude and delayed N170 latency was found in the present study for isolated eyes and no difference surfaced between the two full face conditions argues against Eimer's (2000d) hypothesis that faces that are not entirely intact produce attenuated responses because the stimuli differ from "optimal" faces. He did say though that this attenuation is a function of the degree to which the faces are different from the optimal, and it could be that in the case of the eyes covered with sunglasses, the difference in comparison to an optimal face was not large enough to produce effects. It is also noteworthy that there was one difference between Eimer's (1998a) stimuli and the stimuli used in the present study: in his no eyes condition the eyebrows were removed from the photograph and in the sunglasses condition in this study they were visible. This could be the reason why there was no significant difference between the full face stimuli in the present study. The participants may have been able to deduce the facial expression from the eye region in spite of the sunglasses just by looking at the eyebrows that were more elevated in the fearful expression. However, since the results of the present study were more in agreement with Bentin and colleagues (1996) who did not find this effect of optimal facial configuration, another possible explanation for this difference in results is worth considering. It is possible that the image with the sunglasses simply differs from the image with the eyes blurred in that people are used to seeing other people wearing sunglasses but are not used to viewing images of faces with blurred eyes. The sunglasses probably appear more natural than a face with the eyes erased and therefore are more similar a stimulus as the intact full face.

The results of the present study showed the effects of emotional expressions on a different component than some prior studies. The present study showed an effect of the fearful expression on the N170 component whereas Holmes and colleagues (2003) found a frontal positivity corresponding to the P100 latency range that was larger to fearful as opposed to neutral faces. They found no effects of emotion on the N170. This led them to suggest that emotional facial expressions are processed before and independently of the structural encoding stage that the N170 reflects. Williams and colleagues (2006) also found an enhanced P120 to fearful cues over frontal and temporal regions. They link the early positive components to the threat-related valence of the stimuli and stated that they may serve an early alerting function. Differing from the above mentioned results, Batty and Taylor (2003) found that emotional facial expressions modulated both the P100 and the N170 components. Their results showed that emotion processing occurs coincidentally with other encoding stages of face processing and the results of the present study lend further support for this proposal, although no effects of emotional expression were found on the P100 component. The result of the present study may be due to the fact that the P100 component was only analyzed from two electrodes, because the preliminary analyses revealed no significant effects on other electrodes. Further investigation is thus needed. Holmes and colleagues (2003) only found an attentional effect on the N170. They explain this result by stating that it is possible that the N170 reflects face processing at an earlier anatomical stage besides the FG or that it is an indicator of an early expression-independent stage of face processing in the FG. The results of the present study on fearful expression modulating N170 latency across all conditions disagree with this explanation and show that the N170 component is related to emotional expression processing.

There are methodological issues connected with the present study that must be taken under consideration when interpreting the results. One of these has to do with the presentation of the stimuli. Although results have been obtained with centrally presented stimuli in prior studies, studies using peripheral cues and bilateral displays have been conducted in the past few years with promising results (de Gelder & Stekelenburg, 2004; Noesselt et al., 2005; Pourtois et al., 2004; Pourtois et al., 2005). Noesselt and colleagues (2005) argue that using central, single image displays is not sufficient to produce laterality effects for emotional stimuli. Their study showed these effects when they employed bilateral stimuli. Another point worth considering is that the present study only measured EEG activity from 21 electrodes. This array is not very dense, and according to the criticism presented by Eger and colleagues (2003), using denser arrays might show clearer effects of emotional facial expressions. Therefore a denser electrode array could be useful in future studies. The third concern has to do with attentional factors. Holmes and colleagues (2003), who did not

find an N170 response to emotional facial expressions, did find an enhanced N170 to attended faces. They added an attentional element and even more complexity to the bilateral display by presenting four images simultaneously (on the left and right side, and above and below the central fixation) and out of these images two (either the horizontal or the vertical pair) were attended. They explained their result on attention by saying that the N170 amplitudes can be modulated by attention if the demands on attentional selectivity are sufficiently high. The present study had no distractor stimuli and the stimuli were all attended (although not actively processed), so no comment can be made on attentional effects based on this experiment. It is noteworthy however, that evidence has been found for unattended faces being processed as well, and N170 modulations have been obtained for unattended and even peripherally presented stimuli (e.g., de Gelder & Stekelenburg, 2004). Attentional factors are an important concern in studying face and emotional expression processing, so these issues need to be addressed in future studies. The fourth and possibly most important concern has to do with the context in which the eyes are viewed. Eimer (1998a) found a latency difference in the N170 component between his no eyes condition and the intact full face condition. No such difference was found between the full face stimuli in the present study. It would be interesting to see if the two full face stimuli used in the present study would display a similar difference as in Eimer's study if the eyebrows could not be seen from behind the sunglasses. Then the participants would not be able to deduce the openness of the eyes judging from the eyebrows.

There are several interesting questions connected to the present study that would be worth studying in the future. For example, Kanwisher and colleagues (1997) pointed out the possible effect of handedness on the right hemisphere advantage in face processing because all of their participants who showed the right hemisphere advantage were right-handed. The participants in the present study were all right-handed, so this dependency on handedness cannot be disputed or supported by the present results. The question of the effect of handedness on laterality is intriguing though. The effect of sclera size and its relation to recognizing a fearful expression is definitely another question that calls for further investigation. Bentin and colleagues (1996) explained the lack of N170 response to monkey faces with the absence of white sclera in monkey eyes in accordance with their eye processor hypothesis. Whalen and colleagues (2004) had an interesting stimulus design for investigating the effects of sclera size. The only thing visible in their face/eye cues was the eye whites that were of different size depending on whether the expression in the original image was happy or fearful, and they got very promising results on amygdala activation with these stimuli. It seems that the size of the sclera alone is enough to produce amygdala activation that differentiates

between emotional facial expressions. It would be interesting to see what effects these kinds of stimuli would produce on ERP measurements.

In conclusion, the results of the present study lent support to the notion that the eyes are a special facial feature but did not yield conclusive clarification as to how important they are for facial expressions and in what way. In accordance with the hypotheses, the isolated eyes evoked enhanced and delayed N170 responses, and the N170 responses were enhanced in the right hemisphere for all face and eye stimuli. The fearful expression evoked a clear N170 latency difference compared to the neutral expression, but not the expected amplitude difference. Also contrary to the hypotheses, no differences were found between the two full face conditions, and the covered eyes did not diminish the difference between the fearful and neutral stimuli. No emotion-dependent effects were seen on the P100 component but the isolated eyes did evoke significantly different P100 latency and amplitude than the full face stimuli. Evidence were found to support the eye detector hypothesis in the context of isolated eyes being processed differently from full faces but further investigation is needed to elucidate the issue of the connection of the eyes to emotion processing. Different types of stimuli and experimental designs need to be tried to further illuminate the part that the eyes play in the perception and recognition of emotional expressions.

REFERENCES

- Allison, T., Puce, A. & McCarthy, G. (2002). Category-sensitive excitatory and inhibitory processes in human extrastriate cortex. *Journal of Neurophysiology*, 88, 2864-2868.
- Armony, J. L. & Dolan, R. J. (2002). Modulation of spatial attention by fear-conditioned stimuli: an event-related fMRI study. *Neuropsychologia*, 40, 817-826.
- Batty, M. & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research*, 17, 613-620.
- Baylis, G. C., Rolls, E. T. & Leonard, C. M. (1987). Functional subdivisions of the temporal lobe neocortex. *The Journal of Neuroscience*, 7, 330-342.
- Bentin, S., Allison, T., Puce, A., Perez, E. & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8, 551-565.
- Bentley, P., Vuilleumier, P., Thiel, C. M., Driver, J. & Dolan, R. J. (2003). Cholinergic enhancement modulates neural correlates of selective attention and emotional processing. *NeuroImage*, 20, 58-70.
- Borod, J. C., Bloom, R. L., Brickman, A. M., Nakhutina, L. & Curko, E. A. (2002). Emotional processing deficits in individuals with unilateral brain damage. *Applied Neuropsychology*, 9, 23-36.
- Bradley, B. P., Mogg, K., Millar, N., Bonham-Carter, C., Fergusson, E., Jenkins, J. & Parr, M. (1997). Attentional biases for emotional faces. *Cognition and Emotion*, 11, 25-42.
- Bushnell, I. W. R. (2001). Mother's face recognition in newborn infants: Learning and memory. *Infant and Child Development*, 10, 67-74.
- Carmel, D. & Bentin, S. (2002). Domain specificity versus expertise: Factors influencing distinct processing of faces. *Cognition*, 83, 1-29.

- de Gelder, B. & Stekelenburg, J. J. (2004). Naso-temporal asymmetry of the N170 for processing faces in normal viewers but not in developmental prosopagnosia. *Neuroscience Letters*, 376, 40-45.
- Eger, E., Jedynak, A., Iwaki, T. & Skrandies, W. (2003). Rapid extraction of emotional expression: Evidence from evoked potential fields during brief presentation of face stimuli. *Neuropsychologia*, 41, 808-817.
- Eimer, M. (1998a). Does the face-specific N170 component reflect the activity of a specialized eye processor? *NeuroReport*, 9, 2945-2948.
- Eimer, M. (1998b). Mechanisms of visuospatial attention: Evidence from event-related brain potentials. *Visual Cognition*, 5, 257-286.
- Eimer, M. (2000a). Attention modulations of event-related brain potentials sensitive to faces. *Cognitive Neuropsychology*, 17, 103-116.
- Eimer, M. (2000b). Effects of face inversion on the structural encoding and recognition of faces: Evidence from event-related brain potentials. *Cognitive Brain Research*, 10, 145-158.
- Eimer, M. (2000c). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology*, 111, 694-705.
- Eimer, M. (2000d). The face-specific N170 component reflects late stages in the structural encoding of faces. *NeuroReport*, 11, 2319-2324.
- Emery, N. J. (2000). The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, 24, 581-604.
- Farah, M. J., Wilson, K. D., Drain, M. & Tanaka, J. (1998). What is “special” about face perception? *Psychological Review*, 105, 482-498.
- Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C. & Anderson, A. W. (2000). The fusiform “face area” is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, 12, 495-504.

- Gazzaniga, M. S., Ivry, R. B. & Mangun, G. R. (2002). *Cognitive neuroscience: the biology of the mind*. New York, London: W. W. Norton & Company.
- George, N., Dolan, R. J., Fink, G. R., Baylis, G. C., Russell, C. & Driver, J. (1999). Contrast polarity and face recognition in the human fusiform gyrus. *Nature Neuroscience*, 2, 574-580.
- Grill-Spector, K., Knouf, N. & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience*, 7, 555-562.
- Goffaux, V. & Rossion, B. (2006). Faces are “spatial” – Holistic face perception is supported by low spatial frequencies. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 1023-1039.
- Halgren, E., Raij, T., Marinkovic, K., Jousimäki, V. & Hari, R. (2000). Cognitive response profile of the human fusiform face area as determined by MEG. *Cerebral Cortex*, 10, 69-81.
- Haxby, J. V., Hoffman, E. A. & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4, 223-233.
- Herrmann, M. J., Ehlis, A.-C., Muehlberger, A. & Fallgatter, A. J. (2005). Source localization of early stages of face processing. *Brain Topography*, 18, 77-85.
- Hietanen, J. K., (1999). Does your gaze direction and head orientation shift my visual attention? *NeuroReport*, 10, 3443-3447.
- Hietanen, J. K. (2002). Social attention orienting integrates visual information from head and body orientation. *Psychological Research*, 66, 174-179.
- Hietanen, J. K. & Leppänen, J. M. (2003). Does facial expression affect attention orienting by gaze direction cues? *Journal of Experimental Psychology: Human Perception and Performance*, 29, 1228-1243.

- Holmes, A., Vuilleumier, P. & Eimer, M. (2003). The processing of emotional facial expression is gated by spatial attention: Evidence from event-related brain potentials. *Cognitive Brain Research*, 16, 174-184.
- Itier, R. J., Latinus, M. & Taylor, M. J. (2005). Face, eye and object early processing: What is the face specificity? *NeuroImage*, 29, 667-676.
- Itier, R. J. & Taylor, M. J. (2004). Source analysis of the N170 to faces and objects. *NeuroReport*, 15, 1261-1265.
- Johnson, M. H. (2005). Subcortical face processing. *Nature reviews. Neuroscience*, 6, 766-774.
- Kalat, J. W. (2007). *Biological psychology* (9th ed.). Belmont, CA: Thomson Wadsworth.
- Kanwisher, N., McDermott, J. & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, 17, 4302-4311.
- Latinus, M. & Taylor, M. J. (2005). Holistic processing of faces: Learning effects with Mooney faces. *Journal of Cognitive Neuroscience*, 17, 1316-1327.
- Leppänen, J. M. & Hietanen, J. K. (2004). Kasvonilmeiden havaitseminen, emootio ja kognitio. *Psykologia*, 01/04, 8-18.
- Marinkovic, K., Trebon, P., Chauvel, P. & Halgren, E. (2000). Localized face processing by the human prefrontal cortex: Face-selective intracerebral potentials and post-lesion deficits. *Cognitive Neuropsychology*, 17, 187-199.
- Mathews, A., Fox, E., Yiend, J. & Calder, A. (2003). The face of fear: Effects of eye gaze and emotion on visual attention. *Visual Cognition*, 10, 823-835.
- McCarthy, G., Puce, A., Gore, J.C. & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, 9, 605-610.

- Noesselt, T., Driver, J., Heinze, H.-J. & Dolan, R. (2005). Asymmetrical activation in the human brain during processing of fearful faces. *Current Biology*, 15, 424-429.
- Perrett, D. I., Hietanen, J. K., Oram, M. W. & Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society of London, B*, 355, 23-30.
- Pourtois, G., Grandjean, D., Sander, D & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, 14, 619-633.
- Pourtois, G., Thut, G., de Peralta, R. G., Michel, C. & Vuilleumier, P. (2005). Two electrophysiological stages of spatial orienting towards fearful faces: Early temporo-parietal activation preceding gain control in extrastriate visual cortex. *NeuroImage*, 26, 149-163.
- Puce, A., Smith, A. & Allison, T. (2000). ERPs evoked by viewing facial movements. *Cognitive Neuropsychology*, 17, 221-239.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A.- M., Lazeyras, F. & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain*, 126, 2381-2395.
- Rossion, B., Dricot, L., Devolder, A., Bodart, J.-M., Crommelinck, M., de Gelder, B. & Zoontjes, R. (2000a). Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, 12, 793-802.
- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S. & Crommelinck, M. (2000b). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. *NeuroReport*, 11, 69-74.
- Rousselet, G. A., Macé, M. J.-M. & Fabre-Thorpe, M. (2004). Animal and human faces in natural scenes: How specific to human faces is the N170 ERP component? *Journal of Vision*, 4, 13-21.

- Sagiv, N. & Bentin, S. (2001). Structural encoding of human and schematic faces: Holistic and part-based processes. *Journal of Cognitive Neuroscience*, 13, 937-951.
- Schiltz, C. & Rossion, B. (2006). Faces are represented holistically in the human occipito-temporal cortex. *NeuroImage*, 32, 1385-1394.
- Steeves, J. K. E., Culham, J. C., Duchaine, B. C., Pratesi, C. C., Valyear, K. F., Schindler, I., Humphrey, G. K., Milner, A. D. & Goodale, M. A. (2005). The fusiform face area is not sufficient for face recognition: Evidence from a patient with dense prosopagnosia and no occipital face area. *Neuropsychologia*, 44, 594-609.
- Taylor, M. J., Edmonds, G.E., McCarthy, G. & Allison, T. (2001a). Eyes first! Eye processing develops before face processing in children. *NeuroReport*, 12, 1671-1676.
- Taylor, M. J., Itier, R. J., Allison, T. & Edmonds, G. E. (2001b). Direction of gaze effects on early face processing: Eyes-only versus full faces. *Cognitive Brain Research*, 10, 333-340.
- Vuilleumier, P. (2005). Staring fear in the face. *Nature*, 433, 22.
- Vuilleumier, P., Armony, J. L., Driver, J. & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience*, 6, 624-631.
- Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J. & Dolan R. J. (2004). Distant influences of amygdala lesions on visual cortical activation during emotional face processing. *Nature Neuroscience*, 7, 1271-1278.
- Wenger, M. J. & Ingvalson, E. M. (2003). Preserving informational separability and violating decisional separability in facial perception and recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 29, 1106-1118.
- Whalen, P. J., Kagan, J., Cook, R. G., Davis, C., Kim, H., Polis, S., McLaren, D. G., Somerville, L. H., McLean, A. A., Maxwell, J. S. & Johnstone, T. (2004). Human amygdale responsivity to masked fearful eye whites. *Science*, 306, 2061.

Williams, L. M., Palmer, D., Liddell, B. J., Song, L. & Gordon E. (2006). The 'when' and 'where' of perceiving signals of threat versus non-threat. *NeuroImage*, 31, 458-467.

Winston, J. S., Vuilleumier, P. & Dolan, R. J. (2003). Effects of low-spatial frequency components of fearful faces on fusiform cortex activity. *Current Biology*, 13, 1824-1829.

Yovel, G. & Kanwisher, N. (2004). Face perception: Domain specific, not process specific. *Neuron*, 44, 889-898.